Mixoplankton in the context of Natural Capital and Policy

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Mixoplankton in the context of natural capital and policy. Report for NC 34 Pelagic Program ("PelCap").
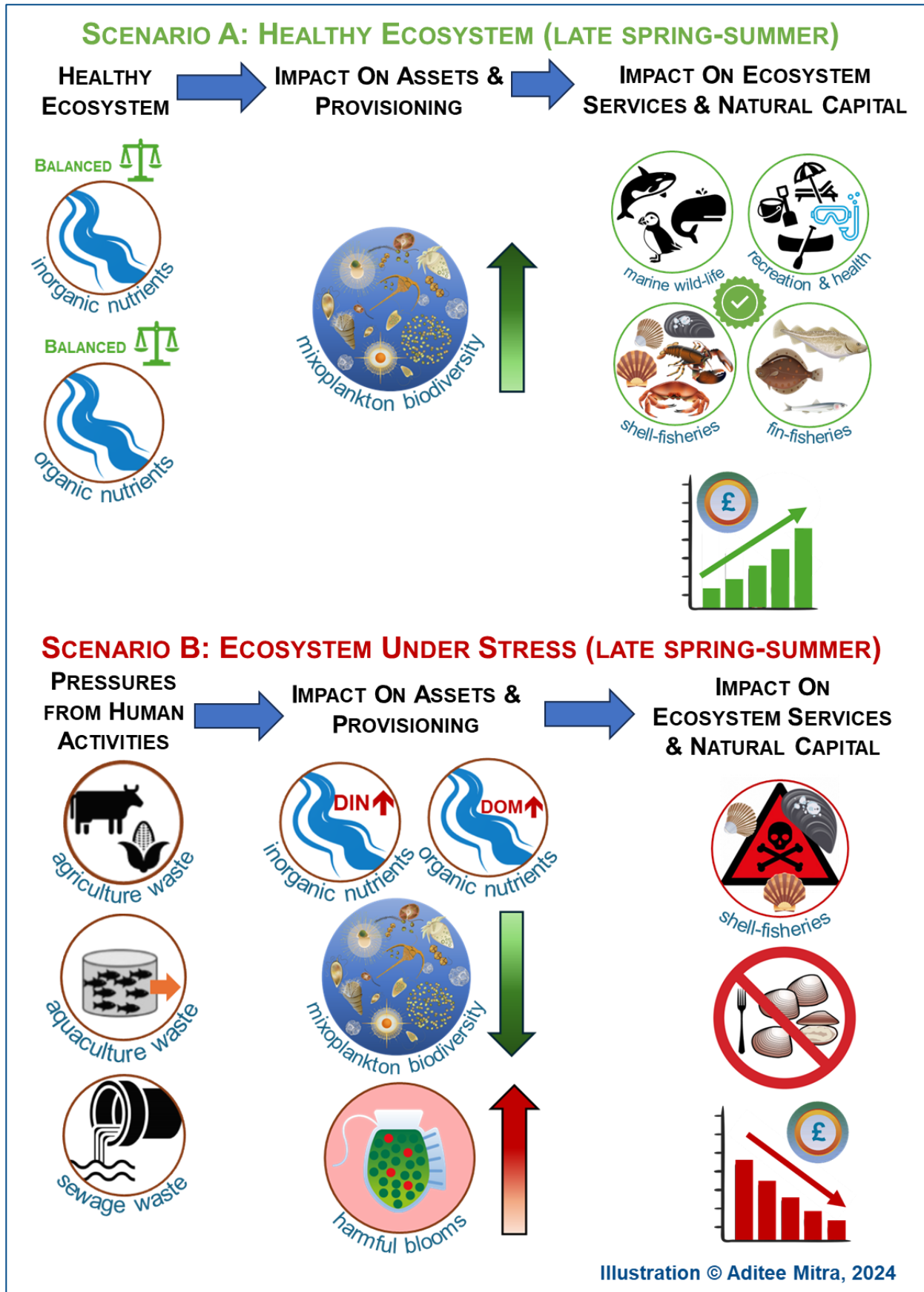
1. Executive Summary

The purpose of this report is to explore the natural capital attributes of a group of organisms called the mixoplankton. These organisms are fundamental to the functioning of many marine food webs in UK coastal and marine waters.

- The conceptual basis upon which monitoring and management tools for our ocean, seas and coasts have operated are out-of-date. These tools, and allied policies relating to fisheries production and global change in marine waters, operate within a paradigm that builds on a simple division between 'plant-like' phytoplankton and their consumers, the 'animal-like' zooplankton at the base of the marine food web. It has been shown that this plant-animal paradigm represents, at the least, a gross simplification, if not a falsehood.

- It is now recognised that most phytoplankton and as much as half the protist-zooplankton combine both plant-like photosynthesis and animal-like consumer activity synergistically within the same single-cell. These are the mixoplankton.

- Mixoplankton are not hybrids of phytoplankton or zooplankton, neither did they originate from phytoplankton. Rather phytoplankton originated from mixoplankton. The recently published Mixoplankton Database reveals that various marine mixoplankton were previously mislabelled as phytoplankton or zooplankton.

- Over decades, the importance of the role of mixoplankton in marine ecology, monitoring, management and policies has been ignored due to a fixation with the established plant-animal dichotomy. However, over the last two decades, various studies have shown that mixoplankton play an important role in structuring, functioning and provisioning of food webs in coastal and marine waters. This has led to the emergence of a new paradigm in marine ecology – the *mixoplankton paradigm*.

- In UK coastal and marine waters, records from the Ocean Biogeographic Information System (OBIS) database reveal the occurrence of 126 species of mixoplankton. These exhibit a size range over many orders of magnitude (akin to that of mouse to elephant) and express diverse prey preferences (e.g., virus, bacteria, cyanobacteria, diatoms, multicellular animals such as copepods, shrimps, snail larvae etc.). Mixoplankton thus defy attempts to pigeonhole them into a one-size fits all scenario configuration.

- The positive asset value of mixoplankton correlates directly with their critical role in UK coastal and marine waters especially from late-spring to summer period. This is the time for growth of shellfish and finfish juveniles and they require a good and varied diet. This is also the time when coastal and marine habitats support recreation and tourism. According to the 2023 UK natural capital report from the Office for National Statistics, ca. 22.38% of the asset value for 'health benefits from recreation' and ca. 34.05% of the asset value for 'recreation and tourism (expenditure)' are attributed to 'coastal and marine' habitats. A healthy marine ecosystem, and especially a healthy shelf-coastal system, depends greatly on the proliferation of diverse populations of mixoplankton. See graphic abstract.

- The flip side to the positive asset value is seen when environmental conditions conspire to promote proliferation and accumulation of noxious mixoplankton. These impose a negative asset value. There are records of 350 harmful algal bloom (HAB) events in UK waters within the Harmful Algal Event Database (HAEDAT). > 60% of these events were associated with mixoplankton species and only 9% with phytoplankton species. Most of these events were recorded in Scottish waters (70%) and the ecosystem service most impacted were the mussels (43%).

- Application of the precautionary principle now places an onus on regulators to take account of the known existence of mixoplankton and of their diverse nutritional mechanisms and ecological interactions. The following recommendations provide a roadmap for this.

  i) Recognising the importance of 'mixoplankton' in environmental monitoring and management. Mixoplankton are primary producers and consumers. They are not 'mixotrophic phytoplankton' or 'mixotrophic zooplankton'. Accordingly, the term 'mixoplankton' must not be used synonymously with the term 'mixotroph'. It is thus recommended that functional group and lifeform descriptions used in marine monitoring and management are revised.

  ii) Policies on monitoring and management of UK coastal and marine waters. Monitoring and management tools based on the old paradigm where plankton are identified as either primary producers or consumers, need revision. Mixoplankton as primary producers and consumers are important to marine ecosystem structure and function and thus ecosystem services. The synergistic role of primary production and prey consumption in the one-celled mixoplankton have different implications for food webs under different pressures on the marine environment. It is recommended that monitoring and management methodologies and policies are revised such that the multi-trophic impact of mixoplankton are integrated.

  iii) Policies on management of organic eutrophication. Wastes from sewage, agriculture and aquaculture include dissolved organics as well as inorganic nutrients. Currently, marine and coastal monitoring, management and policies focus on dissolved inorganic nutrients. It is recommended that concentration, types and sources of organic nutrients (sewage, agriculture, aquaculture) should be considered in policies relating to the management of eutrophication of marine and coastal waters. Such organic eutrophication can support the growth of mixoplankton, including HAB species.

  iv) Policies on management of removal of phosphorus and nitrogen from sewage. The ratios of elements in inorganic nutrients – nitrogen, phosphorus and silica (N:P:Si) – have important implications. Heavily skewed ratios of N:P:Si select for deleterious mixoplankton growth and toxicity. It is recommended that removal of phosphorus (P) from sewage and effluent treatment needs to be balanced by the removal of nitrogen (N).

  v) Policies on building marine infrastructures. The building of infrastructures affects turbulence (altering water column stability), flushing rates and salinity of marine coastal environment. These processes are potential promoters of deleterious mixoplankton blooms. It is recommended that planning policies should conduct assessments on how such constructions could risk marine ecosystem health through potentially supporting mixoplankton blooms.

1.1 Graphical Abstract

SCENARIO A: HEALTHY ECOSYSTEM (LATE SPRING-SUMMER)

HEALTHY ECOSYSTEM → IMPACT ON ASSETS & PROVISIONING → IMPACT ON ECOSYSTEM SERVICES & NATURAL CAPITAL

SCENARIO B: ECOSYSTEM UNDER STRESS (LATE SPRING-SUMMER)

PRESSURES FROM HUMAN ACTIVITIES → IMPACT ON ASSETS & PROVISIONING → IMPACT ON ECOSYSTEM SERVICES & NATURAL CAPITAL

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2. The Purpose of this report

2.1 Interpretation of 'natural capital'

The term 'natural capital' originated in ecological economics (Akerman, 2003; Missemer 2018) with the main objective to ensure "*the sustainability of humans in the biosphere*" (Costanza et al., 1997). Applications of this objective have involved efforts to generate inventories of products from earth's natural ecosystems that benefit humanity; these are termed 'ecosystem services' (Daily, 1997; Constanza et al., 1997). However, categorising natural products as assets is far from straight-forward. As the Dasgupta review (2021) states:

"*Much of Nature and the process governing it are also silent and invisible. The three pervasive features – mobility, silence and invisibility – make it impossible for markets to record adequately the use we make of Nature's good and services.*"

A literature review conducted for this current report (on mixoplankton) on the topics of ecosystem services, functions and assets associated with natural capital show that most of these studies are primarily focussed on the plant and animal kingdoms (e.g., Mace et al., 2015; Costanza et al., 2017). This could be attributed to the relative ease of being able to allocate 'stock value' to these assets.

The purpose of this report is to explore the natural capital attributes of a group of organisms called the mixoplankton. These organisms are fundamental to the functioning of many marine food webs, and importantly of those affecting fisheries (finfish and shellfish) and other valued assets of the marine environment, such as water bathing quality and aesthetics.

These microbial organisms, mirroring the "*three pervasive features*" of Nature – "*mobility, silence and invisibility*", have been left in the shadows. The following sections will focus on why mixoplankton need to be considered as assets in discussions of UK natural capital and thence policy.

2.2 Marine coastal and open-water science has changed

Over the last decade, there has been a fundamental change in our understanding of the structure and functioning of coastal and open-water marine ecosystems. The traditional interpretation of the base of the marine food web assumes a plant-animal like dichotomy, based on phytoplankton-zooplankton, analogous to that of terrestrial systems where plants produce food and animals are the consumers. However, this traditional view is at best incomplete, if not arguably flawed (Flynn et al., 2013; Mitra et al., 2016; Mitra & Leles, 2023). The reason for this is that we now know that many of the single-celled planktonic organisms, hitherto labelled either as 'phytoplankton' or as single-celled 'zooplankton', are actually capable of both photosynthesising (like plants) and also hunting and consuming prey (like animals). They engage in both these producer and consumer processes synergistically (Flynn & Mitra, 2009; 2023). They thus simultaneously, with their

dual nutritional modes, defy the traditional interpretations of what limits plankton growth (Mitra et al., 2024). These organisms are the 'mixoplankton' (Flynn et al., 2019).

Over decades, the importance of the role of mixoplankton in marine ecology has been ignored due to a fixation with the established plant-animal dichotomy. Our research methods, our conceptual and mathematical models, and our ecosystem management approaches, have all been dominated by this assumed dichotomy. However, over the last two decades, various studies have shown how mixoplankton play an important role in functioning and provisioning in coastal and marine waters. This has led to the emergence of a new paradigm in marine ecology – the *mixoplankton paradigm* (Glibert & Mitra, 2022), which sees a restructuring of the plankton food web (**Figure 1**).
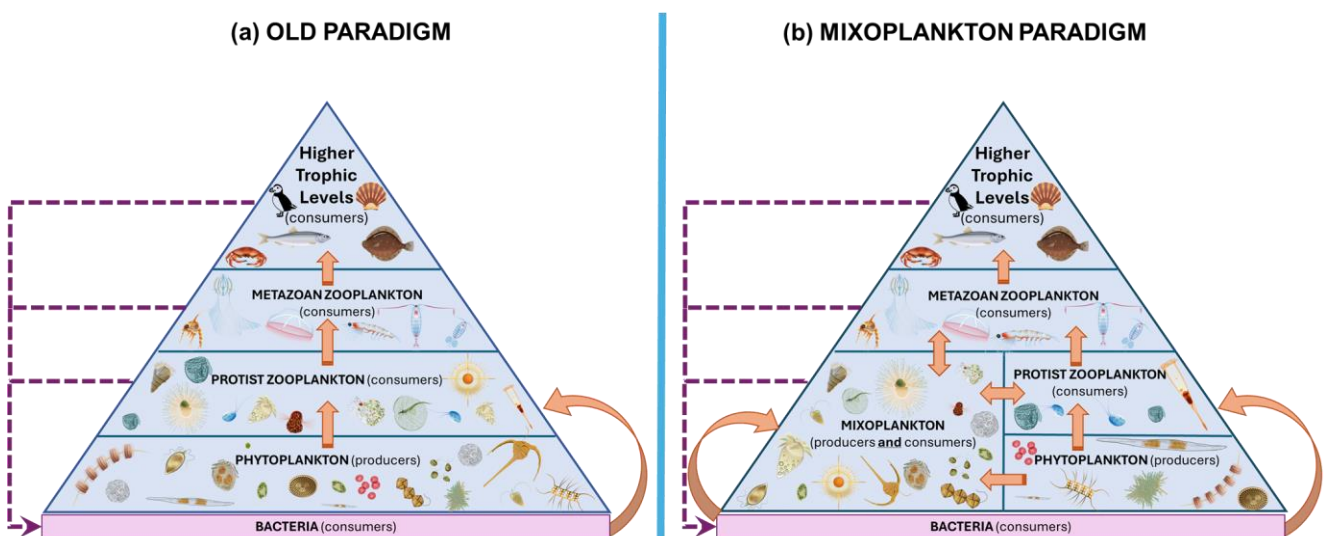
Figure 1. Restructuring of the marine food web under the new mixoplankton paradigm. Panel (a): Old paradigm where phytoplankton are the only producers of food with rest of the trophic levels including only consumers. **Panel (b)** Mixoplankton paradigm where the base of the food web comprises phytoplankton and mixoplankton. In this revised food web, mixoplankton occupying the base of the marine food webs are producers as well as consumers. Mixoplankton are single-celled plankton that photosynthesize and consume prey for their nourishment. Mixoplankton can consume microbial plankton as well as metazoan grazers. Plankton images not to scale. Figure adapted from Mitra & Leles (2023).

The *mixoplankton paradigm* represents the third major change in the conceptual understanding of marine ecology, coming after the *microbial loop* (which acknowledged the role of bacteria and other pico- and nano- sized plankton in marine ecology; Pomeroy, 1974; Azam et al., 1983), and the *viral shunt* (acknowledging the role of viruses in the dynamics of marine plankton; Wilhelm & Suttle, 1999; Jiao et al., 2010). The *mixoplankton paradigm* not only overlaps and reinforces the importance of the *microbial loop* and the *viral shunt*, but it fundamentally denies the acceptability of the phytoplankton-zooplankton concept which has been the bedrock of marine biology and ecology.

Of critical importance, the *mixoplankton paradigm* sees the explicit labelling and thus the identification of the dual and synergistic nutritional mechanisms of phototrophy (photosynthesis) and phagotrophy (consumption of prey) in many single-celled marine plankton (Mitra et al., 2023). In the past these single-celled marine plankton have typically been considered to be either plant-like phytoplankton or animal-like zooplankton. The

mixoplankton paradigm thus overturns our understanding of the physiology, ecological functioning and role of various planktonic organisms that we thought we understood (**Figure 1**). We now know that various marine plankton which had been previously mislabelled as phytoplankton or zooplankton are in fact mixoplankton.

A good model organism of such a mislabelling is the coccolithophorid, *Emiliania huxleyi* – an example of organisms which, over millennia, contributed towards the making of the limestone white cliffs of Dover. This cosmopolitan planktonic organism has traditionally been viewed as a phytoplankton, with its growth limited by light and inorganic nutrients, similar to the needs of higher crop plants. However, we now know that *E. huxleyi*, like many other similarly mislabelled 'phytoplankton', are capable of eating bacteria (Avrahami & Frada, 2020). Consumption of bacterial prey enables the *E. huxleyi* to obtain nutrients that supplement or replace its need for inorganic nutrients. *E. huxleyi* is thus not a phytoplankton but is a mixoplankton that can photosynthesize and consume prey.

The significance of the *mixoplankton paradigm* is underpinned by a series of publications, through integration of the paradigm into various global databases, and also establishment of international working groups. Some examples are listed here:

- Mixotrophic protists and a new paradigm for marine ecology: where does plankton Research go now? (Flynn et al., 2019)
- Eco-evolutionary perspectives on mixoplankton (Mansour & Anestis, 2021)
- From webs, loops, shunts, and pumps to microbial multitasking: Evolving concepts of marine microbial ecology, the mixoplankton paradigm, and implications for a future ocean (Glibert & Mitra, 2022)
- Differences in physiology explain succession of mixoplankton functional types and affect carbon fluxes in temperate seas (Leles et al., 2021)
- The Mixoplankton Database (MDB): Diversity of photo-phago-trophic plankton in form, function, and distribution across the global ocean. (Mitra et al., 2023).
- Establishment of International Working Group (2022), MixONET, funded by the Scientific Committee on Oceanic Research (SCOR)
- Integration of revised plankton groups in the World Register of Marine Species (WoRMS). Following the publication of the Mixoplankton Database, the traits of protist plankton species is being revised in WoRMs database to portray their corrected functional classification. For example, the attributes of *Karenia mikimotoi* and *Laboea strobila*, previously considered to be phytoplankton and zooplankton, respectively, have now been corrected to identify these organisms as mixoplankton.
- The WoRMS database is used by various international meta-databases such as UNESCO's Ocean Biodiversity Information System (OBIS) within which the revised classification of marine plankton following the *mixoplankton paradigm* have been incorporated.
- The Mixoplankton Database has also been integrated into the PR^2 database. "*The PR2 (Protist Ribosomal Reference) database ecosystem is a set of three interconnected 18S rRNA databases that are useful in particular for metabarcoding applications.*"

- 'Mixoplankton' have also been highlighted as one of '*13 discoveries that could change everything*' in the Special Issue of Scientific American on 'Revolutions in Science':

In short, life at the base of the marine food web, a web that supports the vast bulk of marine fisheries, does not function as we once thought it did (Figure 1).

2.3 Why 'mixoplankton' and not 'mixotroph'?

The organisms that we now term mixoplankton are not new to science; scientists have known about them for many decades (Pringsheim, 1958; Sanders, 1991; Stoecker, 1998; Stoecker et al., 2009).. However, due to the bias towards the plant-animal dichotomy, these organisms have been considered as oddities or freaks of nature and have been categorised as subsets of either the plant-like phytoplankton or the animal-like zooplankton. As a result, they have typically been described as either 'phytoplankton that eat' (i.e., mixotrophic phytoplankton) or 'zooplankton that photosynthesize' (i.e., mixotrophic zooplankton).

The term 'mixotroph' in reference to marine plankton describes a planktonic organism that combines chlorophyll-based photosynthesis together with the use of organic nutrition for growth and nourishment. Photosynthesis (also 'phototrophy') requires light (energy), carbon dioxide (CO_2) and dissolved inorganic nutrients (DIN, such as ammonium, nitrate). Acquisition of organic nutrients refers to the use of dissolved organics (DOM, such as sugars, amino acids etc.) via 'osmotrophy' and/or to the consumption of prey (in these organisms achieved via the process of 'phagotrophy').

All phytoplankton are able to photosynthesize <u>and</u> use dissolved organics (i.e., employ phototrophy <u>plus</u> osmotrophy; **Figure 2a**) and thus **are mixotrophs**. For example, diatoms and cyanobacteria, neither of which can consume prey, are well known to be mixotrophic by virtue of phototrophy and osmotrophy (Hellebust, 1978; Flynn & Butler, 1986; Antia et al., 1991).

Mixoplankton are mixotrophic organisms that **can perform phagotrophy in addition to phototrophy <u>and</u> osmotrophy**. They thus have a third nutritional route through consumption of prey (**Figure 2b**). Furthermore, digestion of prey leads to production of dissolved inorganic nutrients (DIN; e.g., ammonium) as excretory products of digestion. DIN are crucial for photosynthesis and thus phototrophic growth. Thus, DIN excreted from digestion of prey within a mixoplankton cell are recycled internally to drive photosynthesis (**Figure 2b**; Flynn & Mitra, 2009; Mitra & Flynn, 2023).

The function of photo-osmo-phago-mixotrophic mixoplankton (**Figure 2b**) in the ecosystem are significantly different from photo-osmo-mixotrophic phytoplankton (**Figure 2a**).
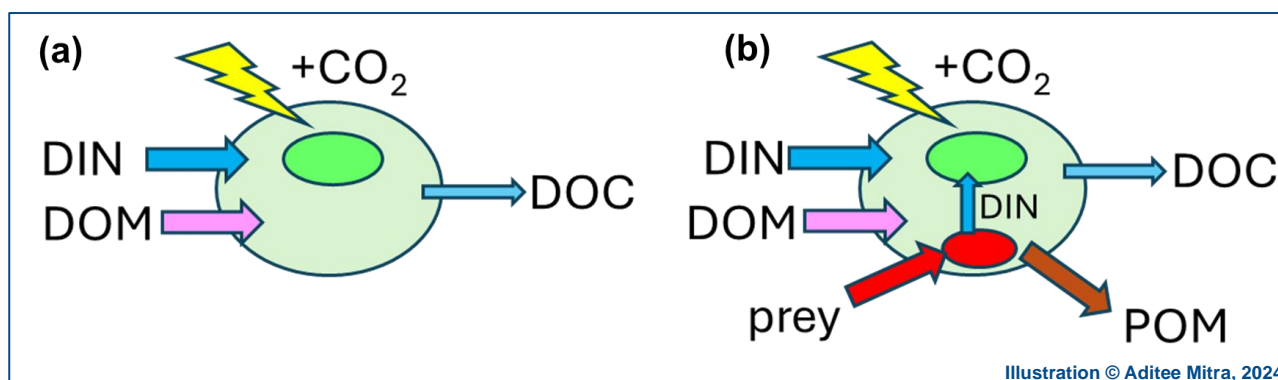
Figure 2. Different forms of mixotrophy in phytoplankton versus mixoplankton. Panel (a): Mixotrophy in phytoplankton combines photosynthesis (via phototrophy) and acquisition of dissolved organic nutrients (DOM, via osmotrophy). Phototrophy uses light energy, dissolved inorganic nutrients (DIN such as ammonium, phosphate and iron) and carbon dioxide (CO_2) while osmotrophy involves uptake of dissolved organic material (DOM such as sugars, amino acids). These mixotrophs leak dissolved organic carbon (e.g., mucus) as a byproduct. **Panel (b)**: Mixotrophy in mixoplankton combines phototrophy, osmotrophy and consumption of prey (via phagotrophy). Digestion of prey within the mixoplankton releases DIN (e.g., ammonium) which is internally recycled to help drive photosynthesis. Thus, under nutrient limiting conditions, the mixoplankton have an advantage over the non-phagotrophic phytoplankton as they can obtain nutrients from another source. That food source may additionally constitute competitors (**Figure 1**), so mixoplankton also grow directly at the expense of their competitors. See also **Boxes 1 and 2**.

The term 'mixoplankton' was proposed by Flynn et al. (2019) as providing a single-word descriptor for the photo-osmo-phago-trophic protist plankton that meet their needs for nutrition and growth through acquisition of dissolved organic nutrients (osmotrophy) and also through synergistic employment of photosynthesis (phototrophy) and predation (phagotrophy) (**Figure 2b**).

To provide clarity, Flynn et al. (2019) not only proposed 'mixoplankton' to encompass all plankton capable of photo-osmo-phago-trophy (**Figure 2b**), but they also proposed that the term 'phytoplankton' should be restricted solely to those photosynthetic plankton that are incapable of phagotrophy (**Figure 2a**). Diatoms and cyanobacteria are thus phytoplankton,

and like all phytoplankton, they are also mixotrophs. The term mixoplankton should not thus be confused as a synonym for 'mixotrophic phytoplankton'.

The recommendation to differentiate between phytoplankton and mixoplankton was made to provide a clear and easy distinction between the functional traits of marine planktonic mixotrophs that consume prey and those that cannot eat. Mixoplankton activity (**Figures 1 and 2b**) has very different consequences for food web structure and ecological function. **Mixoplankton directly affect trophic dynamics by being able to consume other organisms including their competitors and even their own predators.** In contrast, growth of mixotrophic phytoplankton (e.g., cyanobacteria, diatoms) do not directly lead to removal of competitors or indeed predators from higher trophic levels through predation. Additionally, consumption of dissolved organics by mixotrophic phytoplankton brings them into competition with bacteria and other osmotrophs (Mitra et al., 2014a).

BOX 1 ORGANISMS

Mixoplankton are chlorophyll-containing protist microbes that <u>are</u> capable of predation. They are mixotrophs by combining photosynthesis, an ability to use dissolved organic nutrients (e.g., amino acids, sugars), and also by grazing. They are <u>not</u> 'plants-that-eat'; they are <u>not</u> 'animals-that-photosynthesize'; they are <u>not</u> a subset of 'phytoplankton'; they are <u>not</u> a subset of protist-zooplankton; they are not hybrids of phytoplankton and zooplankton. Examples include many photoflagellates (including Chl-containing dinoflagellates) and many ciliates.

Phytoplankton are chlorophyll-containing microbes (prokaryote or protist) that are <u>not</u> capable of consumption of other organisms. They are <u>mixotrophs</u> by combining photosynthesis and an ability to use dissolved organic nutrients (e.g., amino acids, sugars). They are <u>not</u> 'plants'. Examples include cyanobacteria and diatoms.

Protists are single celled eukaryote microbes. They have a higher level of cellular complexity than do the prokaryote bacteria, archaea and cyanobacteria.

Zooplankton are planktonic predators. Most are protists (i.e., protist-zooplankton, sometimes termed, microzooplankton), while the other are recognisably animals (metazoa-zooplankton). The former are single-celled microbes while the latter include multi-cellular animals of many mm (e.g., copepods), cm (e.g., krill), or even m dimension (jellies).

> **BOX 2 FEEDING MODES USED BY MICROBIAL PLANKTON**
>
> **Osmotrophy** is a mode of nutrition involving the use of dissolved organic molecules, such as sugars and amino acids. It is the most primitive of nutritional modes and is ubiquitous in microbes.
>
> **Phagotrophy** is a mode of nutrition in which particles, typically other organisms, are consumed by protists. It is a primitive nutritional mode.
>
> **Phototrophy** is a mode of nutrition the uses light energy capture by chlorophyll-based processes (i.e., photosynthesis), together with the incorporation of inorganic nutrients such as ammonium, nitrate and phosphate. Originating in organisms we now identify as cyanobacteria, phototrophy was the most recent nutritional mode to be developed in protists.

The *mixoplankton paradigm,* and related research, highlights the importance of <u>not</u> using the terms mixotroph and mixoplankton synonymously in order to avoid confusion and ambiguity (see also **Section 3**).

Care needs to be taken when interpreting the literature from article titles and abstracts as, especially historically (pre-2019), it may not be immediately clear whether the work is indeed on the subject of mixoplankton (i.e., photo-osmo-phago-mixotrophic plankton) or some other facet of mixotrophy (e.g., photo-osmo-mixotrophic phytoplankton).

2.4 Structure of this report

The purpose of this report is to explain why mixoplankton are relevant for the UK marine natural capital and ecosystem assessment (mNCEA) programme and thence marine policy. It will achieve this end through consideration of the following.

- Introduction to the mixoplankton paradigm including explanation of what mixoplankton are, how they evolved, their placement within the eukaryotic tree of life and their role in ecosystem structure, function and food web dynamics.
- Explanation of the importance of differentiating between mixotrophy in 'phytoplankton' versus mixotrophy in 'mixoplankton'.
- Interrogation of data from meta-databases to identify the biogeography of different mixoplankton types in UK marine and coastal waters and how these mixoplankton impact UK ecosystem services.
- Investigation of why hitherto mixoplankton have been ignored in marine environmental monitoring, management and policies and whether the mixoplankton paradigm is important for monitoring and management of UK marine and coastal waters.
- Consideration of the value of mixoplankton in the context of natural capital, as positive versus negative assets.

3. Introduction to mixoplankton and the new paradigm

3.1 What are mixoplankton?

Mixoplankton are single-celled plankton that employ photosynthesis and predation synergistically to obtain nourishment. They can also engage in osmotrophy. These organisms are not new discoveries (Pringsheim, 1958; Sanders, 1991; Stoecker, 1998; Stoecker et al., 2009). However, as descriptions of marine food webs have always emphasized the plant-animal, 'phytoplankton-zooplankton', dichotomy, mixoplankton species have previously been labelled as either 'phytoplankton (akin to plants) that eat' or 'microzooplankton (akin to animals) that photosynthesize' (Ostle et al., 2021). Both labels are wrong. **Protists are neither plants nor animals, and mixoplankton are not a subset of phytoplankton or microzooplankton.**

A common definition of 'mixotroph' refers to an organism that employs autotrophy <u>and</u> heterotrophy to obtain nourishment for growth and proliferation (Lawrence, 2016). For chlorophyll containing plankton, autotrophy is supported by photosynthesis (i.e., phototrophy) and heterotrophy is supported by the acquisition of dissolved organic nutrients (i.e., osmotrophy) and by consumption of prey (i.e., phagotrophy); see also **Figure 2** and **Boxes 1, 2**.

Thus, phytoplankton are mixotrophic as they employ osmotrophy <u>plus</u> phototrophy to acquire nourishment (i.e., they cannot eat); mixoplankton are mixotrophic through employing phototrophy <u>plus</u> osmotrophy <u>plus</u> phototrophy plus phagotrophy; protist zooplankton are heterotrophic as they acquire nourishment from dissolved organics and through consumption of prey (i.e., osmotrophy <u>plus</u> phagotrophy; they cannot photosynthesize).

The different combinations of nutritional routes, and the organisms that operate them, are shown in **Figure 3**. The plankton types noted in the old paradigm (**Figure 1a**) – phytoplankton and protist-zooplankton – express two of the three routes, while mixoplankton express all three routes of nutrition (**Figures 1b, 2b**). There are no organisms that express just phototrophy+phagotrophy; likewise, there are no organisms that express just phototrophy (Mitra et al., 2023). Mixoplankton have traditionally been variously ascribed, incorrectly, to phytoplankton or protist-zooplankton, despite having very different physiologies (**Figure 3**).
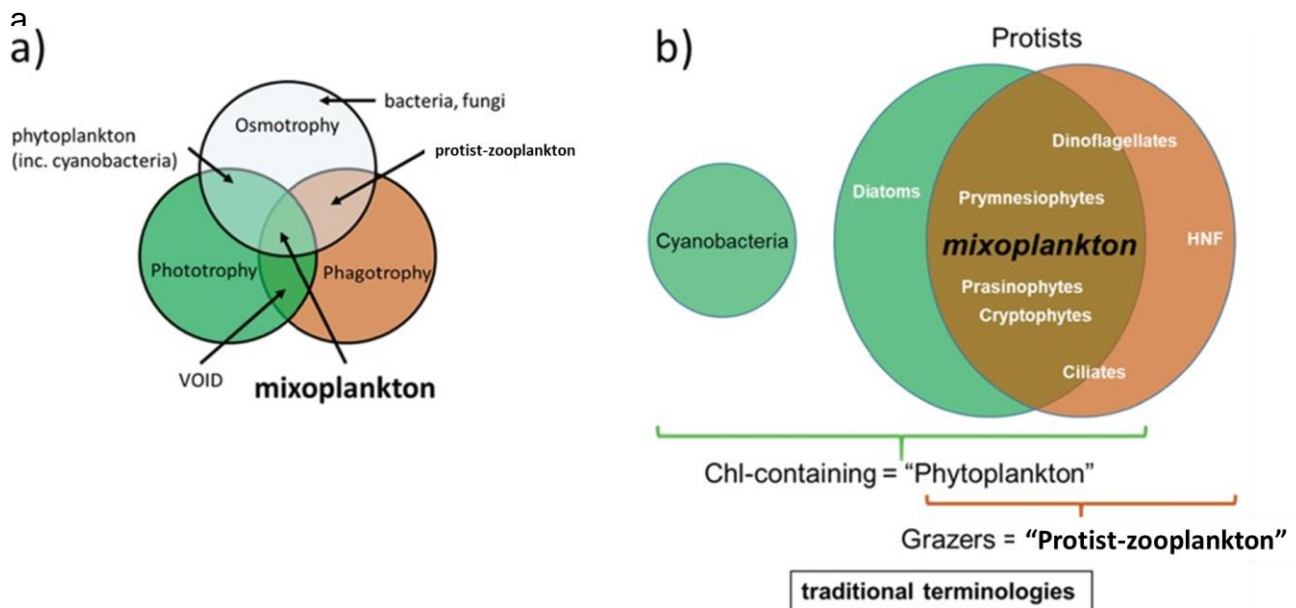
Figure 3. Overlaps in the trophic capacity of the three different groups of marine microbial plankton – phytoplankton, mixoplankton and zooplankton. Panel (a): Venn diagram of overlaps between photo-, osmo- and phago- trophy. "VOID" indicates that no organisms exist in this sector. Mixoplankton are, by definition, capable of all three modes. Phytoplankton are mixotrophic by virtue of employing photo- and osmo-trophy; they cannot consume prey (i.e., phytoplankton are non-phagotrophic). Protist-zooplankton are incapable of phototrophy. **Panel (b):** Overlaps between traditional allocations of chlorophyll (Chl) containing organisms as "phytoplankton" and microbial grazers as "protist-zooplankton". Symbol sizes or area allocations do not apportion significance. Figure adapted from Flynn et al. (2019). See also **Boxes 1 and 2**.

Mixoplankton comprise a diverse sub-group (functional types) of protist plankton. **Figure 4** shows the revised classification key for marine microbial plankton under the mixoplankton paradigm (Mitra et al., 2023). Mixoplankton can be functionally divided broadly into two groups:

(i) Constitutive Mixoplankton (CM): these possess an innate, constitutive ability to perform photosynthesis. Various globally ubiquitous cryptophytes, dinoflagellates and haptophytes such as *Teleaulax amphioxeia*, *Alexandrium tamarense*, *Tripos furca*, *Emiliania huxleyi*, *Phaeocystis globosa* are now recognised to be CMs. These would have traditionally been <u>mislabelled</u> as phytoplankton (i.e., considered as only producers in the food web).

(ii) Non-Constitutive Mixoplankton (NCM): these need to acquire photosynthetic capabilities from consumption of photosynthetic prey. The NCM can be further sub-divided into three types according to how they acquire their phototrophic potential:

- Generalist NCM (GNCM): these acquire photosynthetic capability by using the chloroplasts from a range of different prey items. Various ciliates such as *Laboea strobila*, *Strombidium reticulatum*, *Tontonia ovalis* are now recognised as GNCMs. Traditionally these would have been <u>mislabelled</u> as microzooplankton or protist-zooplankton (i.e., considered as only consumers in the food web).

- plastidic Specialist NCM (pSNCM): these acquire their photosynthetic machinery (including nuclear material) from specific prey taxonomic

groups. Examples include the ubiquitous ciliate *Mesodinium rubrum* and various species from the harmful bloom forming *Dinophysis* genus; these species have previously been <u>incorrectly</u> assigned to microzooplankton (i.e., consumers in the food web).

▪ endosymbiotic specialist NCM (eSNCM): these NCM mixoplankton harbour prey symbionts for photosynthesis within their single cell. The dinoflagellate *Noctiluca scintillans*, various species belonging to the ubiquitous Rhizarians (i.e., foraminiferans, radiolarians) are now recognised to be eSNCMs. These species have previously been <u>incorrectly</u> assigned to microzooplankton or protist-zooplankton (i.e., consumers in the food web).

BOX 3 MIXOPLANKTON TYPES

Constitutive Mixoplankton [**CM**]: innate ability to photosynthesize

Non-Constitutive Mixoplankton [**NCM**]: acquires phototrophic ability from prey

Generalist Non-Constitutive Mixoplankton [**GNCM**]: gained ability to photosynthesize by keeping chloroplasts from diverse (generic) prey

Specialist Non-Constitutive Mixoplankton [**SNCM**]: gained photosynthetic ability from specific prey taxonomic groups

plastidic Specialist Non-Constitutive Mixoplankton [**pSNCM**]: gained ability to photosynthesize by keeping chloroplasts from specific prey

endosymbiotic Specialist Non-Constitutive Mixoplankton [**eSNCM**]: gained ability to photosynthesize by keeping specific prey as symbionts
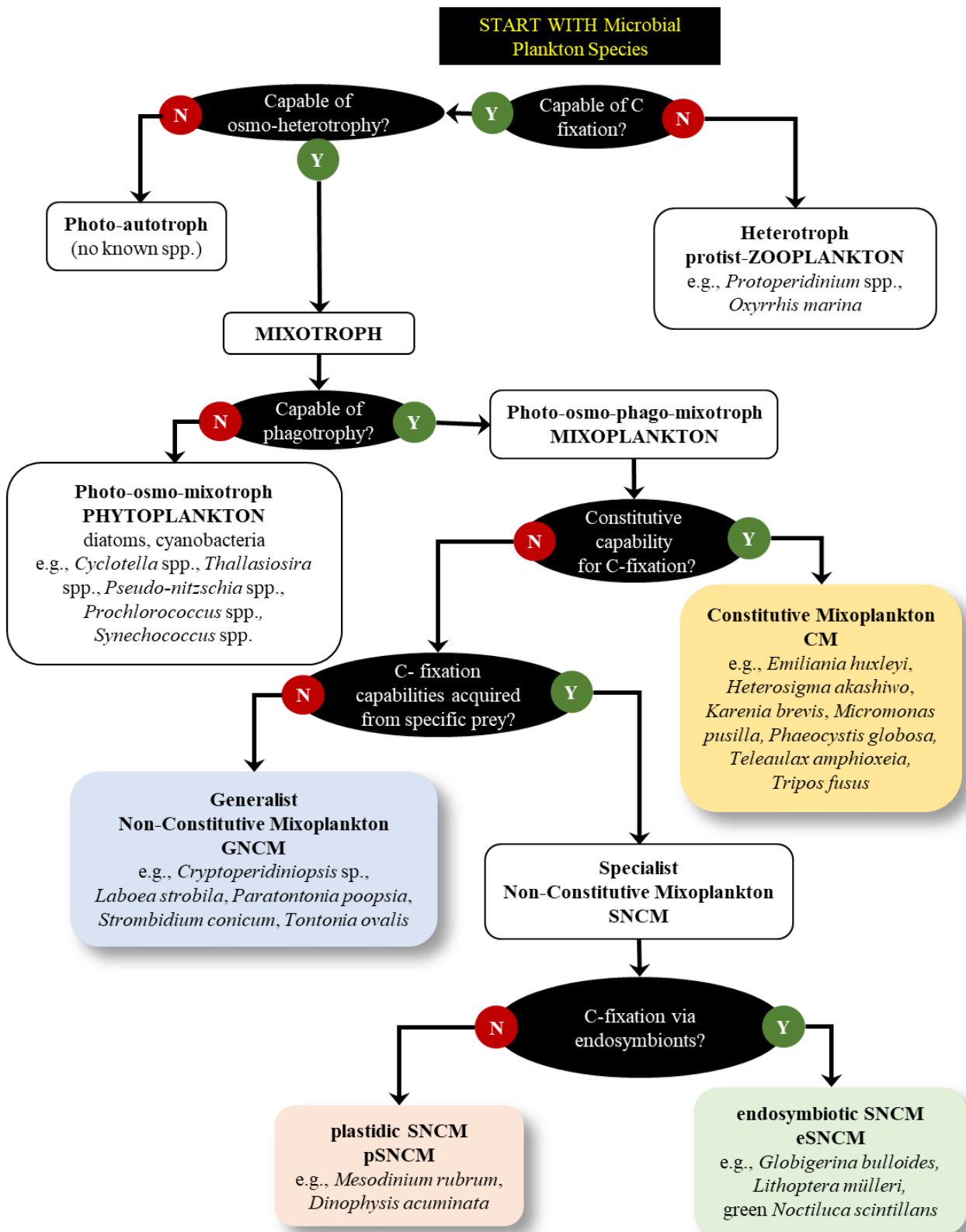
Figure 4. Functional group classification for marine microbial plankton. Figure from Mitra et al. (2023). See also **Figure 3** and **Box 3**.

3.2 Mixoplankton in the Eukaryotic Tree of Life

Mixoplankton are eukaryotes. Broadly, there are four types of eukaryotes – protists, fungi, plants and animals (including humans). Of these, protists are the most biodiverse:

"*Although most of the described species of eukaryotes belong to the multicellular groups of animals (Metazoa), land plants, and fungi, it has long been clear that these three 'kingdoms' represent only a small proportion of high-level eukaryote diversity. The vast bulk of this diversity – including dozens of extant 'kingdom-level' taxa – is found within the 'protists', the eukaryotes that are not animals, plants, or fungi*" – Burki et al. (2020).

An examination of the eukaryotic tree of life indicates mixoplankton to be the most widespread protist plankton with different mixoplankton functional types observed across the different lineage branches (**Figure 5**; see also **Figures 1** and **4** and **Box 3**). While protist-zooplankton are widely distributed across the tree of life (not shown), phytoplankton are restricted to very few groups; this reflects the evolutionary origins of phytoplankton. Phytoplankton originated from mixoplankton species that lost their ability to consume prey (Mitra et al., 2024; further details in **Section 3.3**).

Illustration © Luciana Santoferrara & Aditee Mitra, 2024
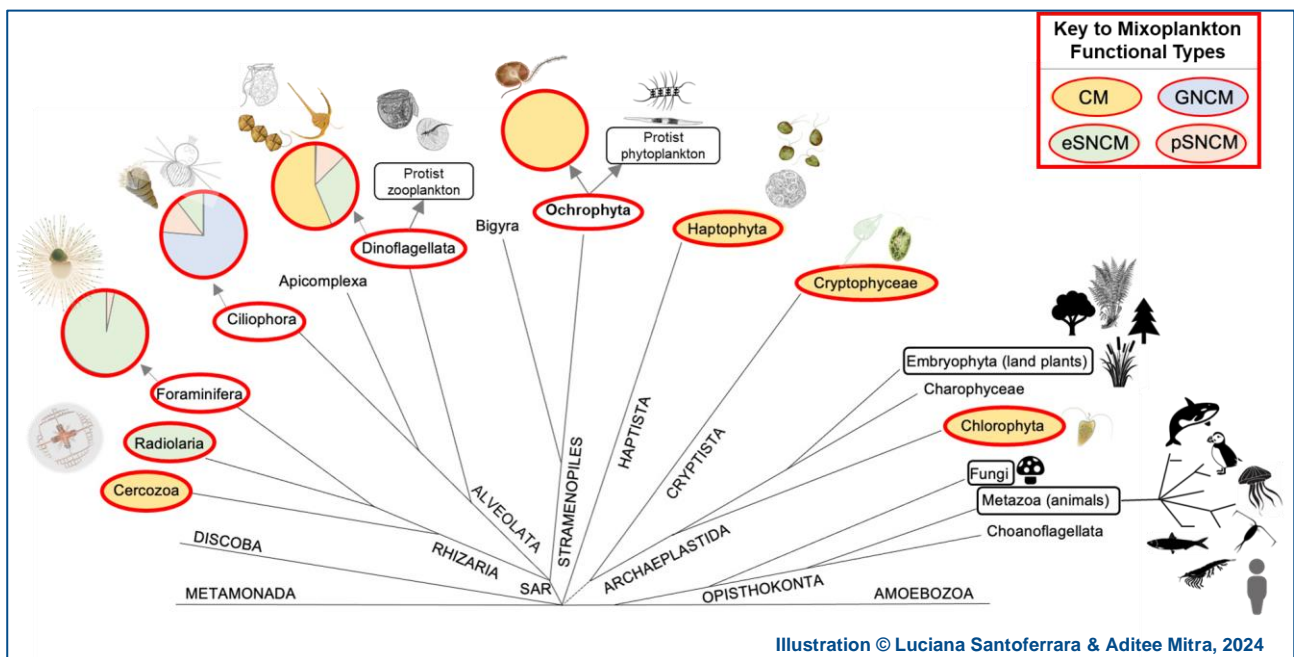
Figure 5. The eukaryotic tree of life showing location of the different mixoplankton functional types in context of other eukaryotic groups. Lineages with representatives of only one functional type are indicated by colored ovals, while lineages with multiple functional types are indicated within the inset pie charts. CM, constitutive mixoplankton; GNCM, generalist non-constitutive mixoplankton; eSNCM, endosymbiotic specialist non-constitutive mixoplankton; pSNCM, plastidic specialist non-constitutive mixoplankton. See also **Section 3.1, Figure 4** and **Boxes 1**-**3** for further information about classification and types of protist plankton. Schematic phylogenic tree adapted from Mitra et al. (2023).

3.3 Mixoplankton Evolution

The organisms that we now refer to as protists represent the earliest form of eukaryote cells. These original forms acquired sub-cellular components, organelles, by capturing and incorporating firstly bacteria and then in some instances cyanobacteria to provide respectively, mitochondria and chloroplast (Ponce-Toledo et al., 2017; Bremer et al., 2022).

In the evolutionary pathway (**Figure 6**), the cell form of protist-zooplankton thus originated first (Raven, 1997; Raven et al., 2009). Over millennia, various protist-zooplankton species acquired the ability to capture and retain their photosynthetic prey within their single-celled body. They exploited these captured prey to photosynthesize. This led to the emergence of organisms that we term as non-constitutive mixoplankton (NCM; **Section 3.1**, **Figure 4**). Present day NCM acquire their phototrophic capability either from retention of the chloroplasts from diverse prey species (i.e., the generalist NCM; GNCM) or from specific prey (i.e., the plastidic specialist NCM; pSNCM).

Over time, various pSNCM species evolved to integrate the genes required to produce and maintain photosystems (i.e., chloroplasts) as a constitutive component of their cell. These organisms became what we term constitutive mixoplankton (CM). CM species have inherent phototrophic capability. This full integration event occurred multiple times, explaining why the CMs have examples spread across the tree of life (**Figure 5**).

At the end of this protist plankton evolutionary pathway are the protist phytoplankton (noting that cyanobacteria are also phytoplankton – **Box 1**). The protist phytoplankton evolved from the CM through the loss of their ability to eat. The protist phytoplankton are thus the most recent forms originating from the mixoplankton. This evolutionary train of events of protist plankton is illustrated in **Figure 6** which provides examples of extant protist plankton species from UK waters.

It is important to note that, mixoplankton did <u>not</u> evolve from phytoplankton by those organisms gaining phagotrophy. Phytoplankton evolved from mixoplankton by <u>losing</u> phagotrophy. Thus, mixoplankton are <u>not</u> 'phytoplankton that eat'. On the contrary, phytoplankton are mixotrophs that lost the ability to eat.

From the line of this evolution, one could also interpret that phytoplankton are specialist, as having lost phagotrophy they specialize in phototrophy. This is consistent with the relative roles of phytoplankton in waters that are nutrient-rich and of low biodiversity (i.e., low prey abundance), and of mixoplankton in mature ecosystems where most nutrient is bound within biomass.
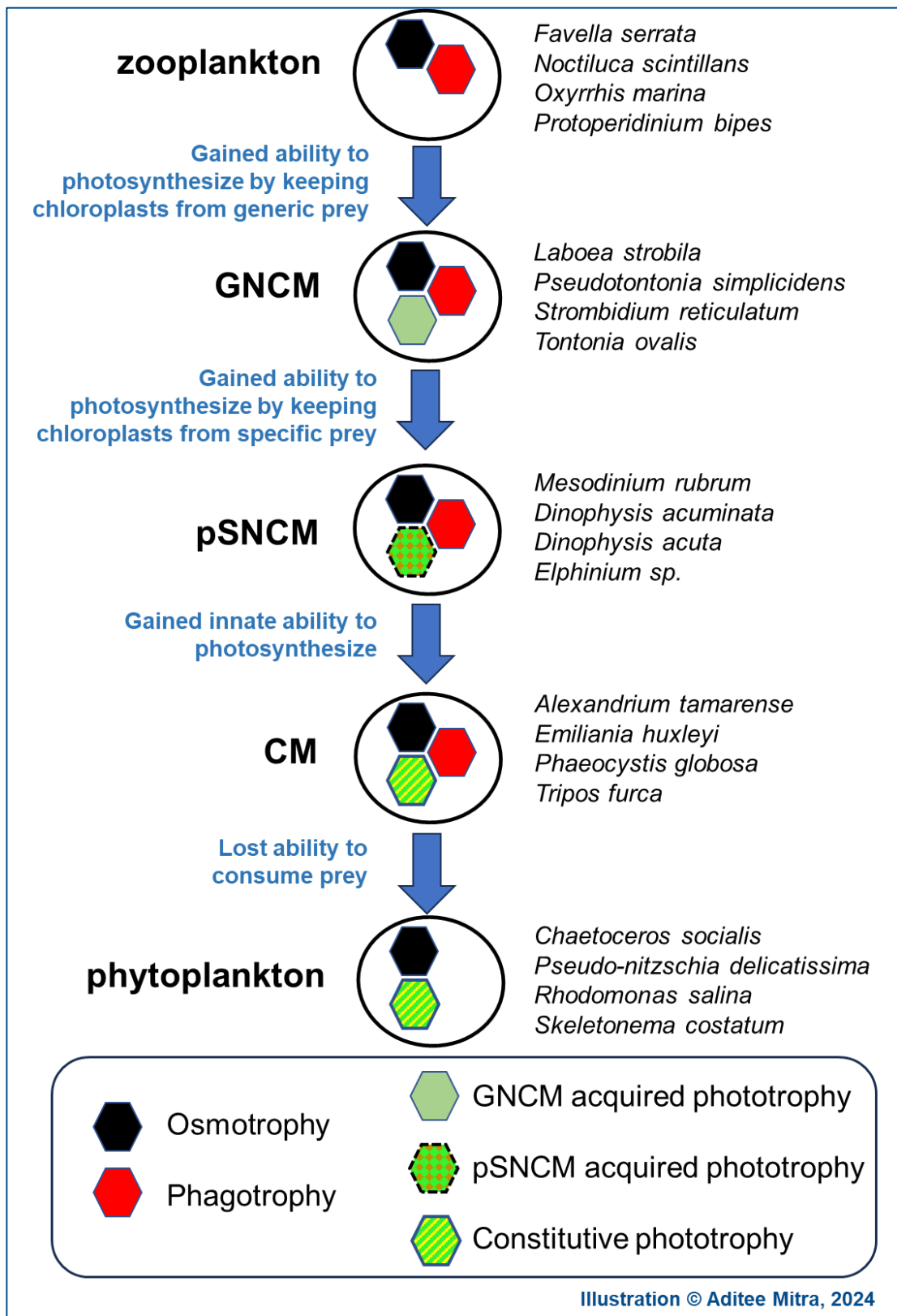
Figure 6. Sequence of protist plankton evolution with examples of extant representative species. GNCM originally acquired phototrophy from cyanobacteria; present day GNCM acquire photosystems from phototrophic protist plankton. Extant GNCMs are all ciliates, extant pSNCMs are dinoflagellates or ciliates, extant CMs occur in various taxonomic groups as seen in the Eukaryotic Tree of Life (**Figure 5**). GNCM, generalist non-constitutive mixoplankton; pSNCM, plastidic specialist non-constitutive mixoplankton; CM, constitutive mixoplankton. Figure developed from Mitra et al. (2024).

Not shown in **Figure 6** are the endosymbiotic specialist NCM (eSNCM) which evolved through a different pathway from the ancestral protist-zooplankton. The eSNCM organisms comprise a protist host cell which acquires its phototrophic capability by harbouring intact photosynthetic microbes (e.g., CM or phytoplankton species) as symbionts (**Figure 7**). This contrasts with the GNCM and pSNCM, which harbour chloroplasts sequestered from their prey and not intact photosynthetic organisms (**Box 3**). Examples of eSNCM are various formaniferans (e.g., *Orbulina universa*), radiolarians (e.g., *Lithoptera mülleri*) and dinoflagellates (e.g., green *Noctiluca scintillans*).
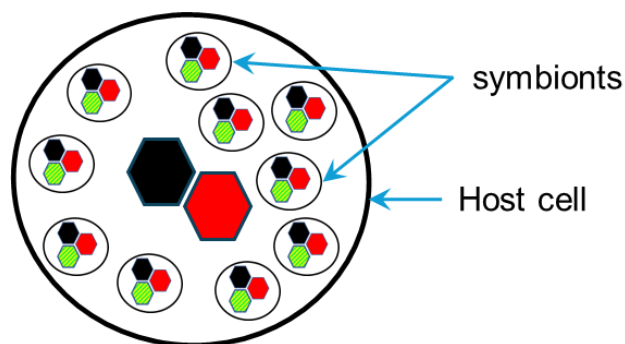
Figure 7. Schematic showing the form of endosymbiotic Specialist Non-Constitutive Mixoplankton (eSNCM). These organisms comprise a protist-zooplankton host, housing a number (10's to 1000's, depending on the species) of a particular phototrophic symbiont. The symbionts exploit light and also nutrients regenerated by the host; the host uses dissolved organics leaked by the symbionts, and may also directly digest symbionts. See also **Figure 6**.

3.4 Mixoplankton size and prey size

Mixoplankton are not confined to a narrow size spectrum. Examples of mixoplankton are found across the whole size spectrum of protist plankton (**Figure 8**), from ca. 2 μm to 2 cm (Flynn et al., 2019; Mitra et al., 2023). The relative size range of mixoplankton is similar to the size range observed from mouse to killer whales as indicated at the top of **Figure 8**. The most abundant species are CM, which are mainly within the size range of 2 μm to 100 μm.

Not only is the size range of mixoplankton expansive, so is the ratio of the size of mixoplankton predator to the size of their prey (**Figure 9**). While metazoan zooplankton (e.g., meroplankton such as copepods) have an optimal predator:prey ratio of <0.1, this ratio for ciliates which include GNCM and pSNCM species, is much greater. The predator:prey ratio is higher again for flagellate CM in general. The optimal ratio for dinoflagellates can exceed their own size, with digestion of prey occurring outside of the main cell using a digestion veil.
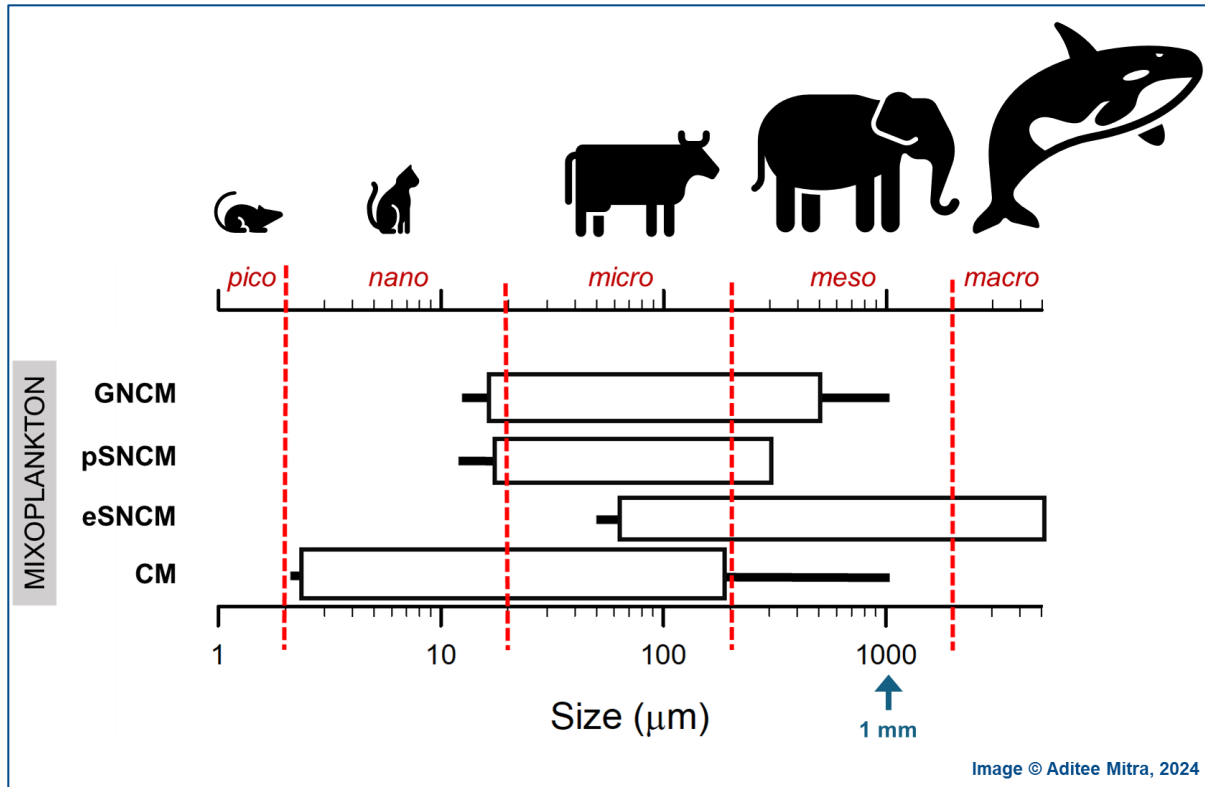
Figure 8. Size ranges for different microbial plankton functional types. As labelled here, phytoplankton (prokaryotic cyanobacteria and allies, and eukaryotic protists) are photo- and osmo- mixotrophic; they are incapable of phagotrophy. Protist-zooplankton are osmo- and phago- trophic; they are incapable of phototrophy. For mixoplankton, which express photo-, osmo- and phago- mixotrophy, the typical size ranges are as indicated by the boxes. Note that in total mixoplankton sizes span all other protist plankton types, though the CM are the dominant examples in the sub 20 μm size categories. The traditional size-based categories used to allometrically group plankton are indicated using vertical red dashed lines; pico, 0.2–2 μm; nano, 2–20 μm; micro, 20–200 μm; meso, 200–20 mm; macro, 20 mm–2 cm. GNCM, generalist non-constitutive mixoplankton; pSNCM, plastidic specialist non-constitutive mixoplankton; eSNCM, endosymbiotic non-constitutive mixoplankton; CM, constitutive mixoplankton. See also **Figures 4** and **5**. The relative size range of mixoplankton is similar to the size range observed from mouse to killer whales as indicated at the top of the figure. Figure adapted from Flynn et al. (2019).
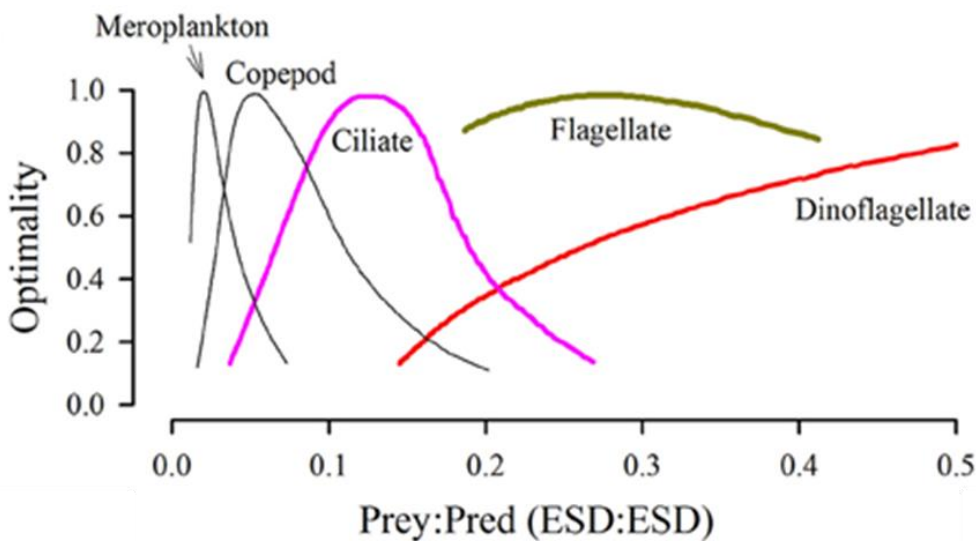
Figure 9. Relationships between relative size of predator and optimal prey size. The dinoflagellate plot peaks at size ratio of 1:1, but there are species of dinoflagellate where the ratio is >10:1. Figure redrawn from Hansen et al. (1994).

The extreme predator:prey size ratios noted in **Figure 9** are enabled by diverse feeding mechanisms. For example, plastidic specialist non-constitutive mixoplankton (pSNCM) species belonging to the *Dinophysis* genus inserts a peduncle (a feeding tube like a straw) to extract the cell contents of their prey (Park et al., 2006; **Figure 10**). Constitutive mixoplankton (CM) species belonging to the *Prorocentrum* genus have been found to form mucus traps to capture and ingest prey (Larsson et al., 2022; Tillmann et al., 2023; **Figure 11**). The constitutive mixoplankton dinoflagellate *Karlodinium armiger* has been found to attack and feed on various metazoan grazers (i.e., multicellular animals, e.g., Berge et al., 2012; **Figure 12**).
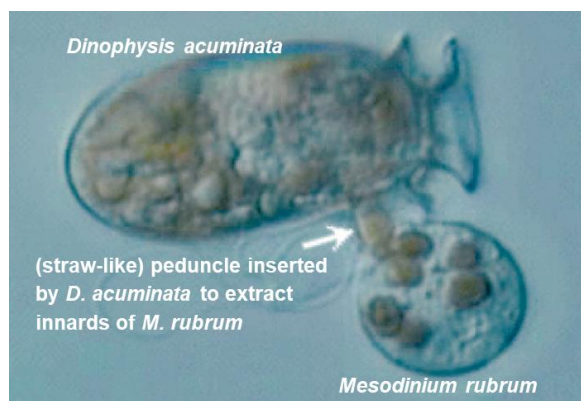
Figure 10. The pSNCM dinoflagellate *Dinophysis acuminata* feeding on the pSNCM ciliate *Mesodinium rubrum*. Here, *D. acuminata* is by extracting the cytoplasm and organelles through a 'straw-like' peduncle from a *M. rubrum* cell. Figure from Park et al. (2006).
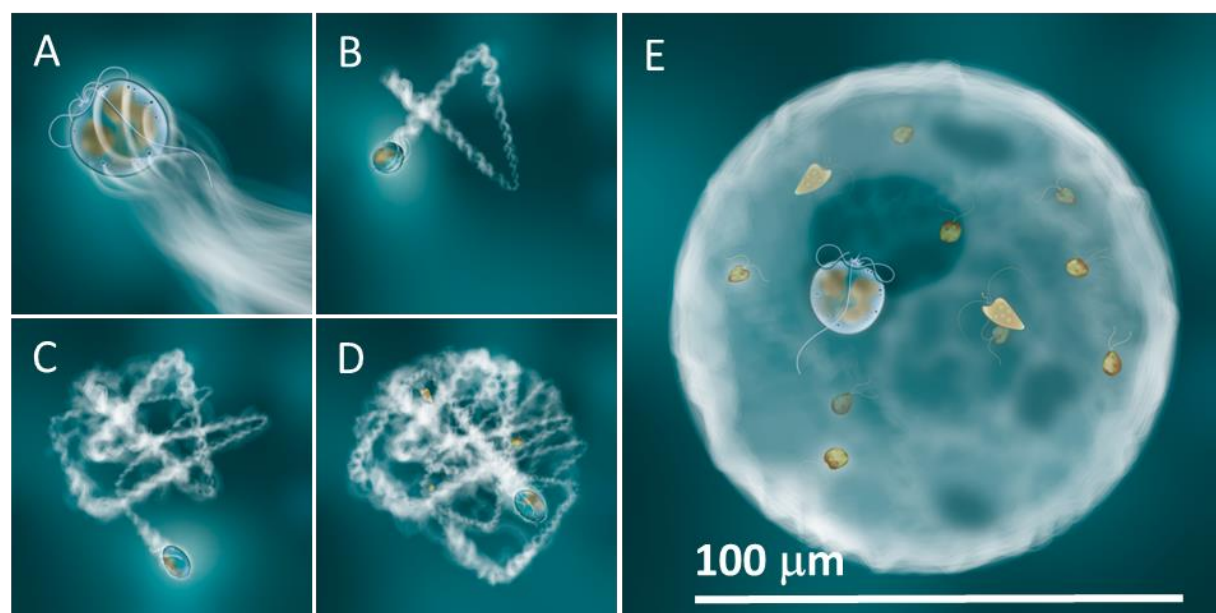
Figure 11. Suggested sequence of events leading to the formation of the mucus trap by *Prorocentrum pervagatum*. (**A**) Solitary cells (cell length ca. 13µm) swim in a spiraling style, releasing mucus from the large pores. (**B**–**D**) Under certain conditions, most likely of very low turbulence, the spiral swimming style coupled with random changes in direction lead to a process of mucus deposition and physical pushing by the *Prorocentrum* cell that leads to the formation of a hollow mucus ball. As the mucus ball takes shape other particles, and notably motile potential prey, become stuck to the outside surface. Towards completion of the trap, with the *Prorocentrum* now located within the hollow ball near one of the few remaining openings, the continuing rotational swimming of the dinoflagellate draws water and particles in through the large opening (a "rotating position"), with water exiting through the porous mucus walls, leaving particles trapped on the inside of mucus ball. Trapped prey are immobilized by a combination of chemical (allelochemical) and physical (mucus threads) means, and may then be consumed (**E**). When the trap is vacated, typically once a day, the decaying remnants then sink, while the *Prorocentrum* builds another trap. Figure from Tillmann et al. (2023).
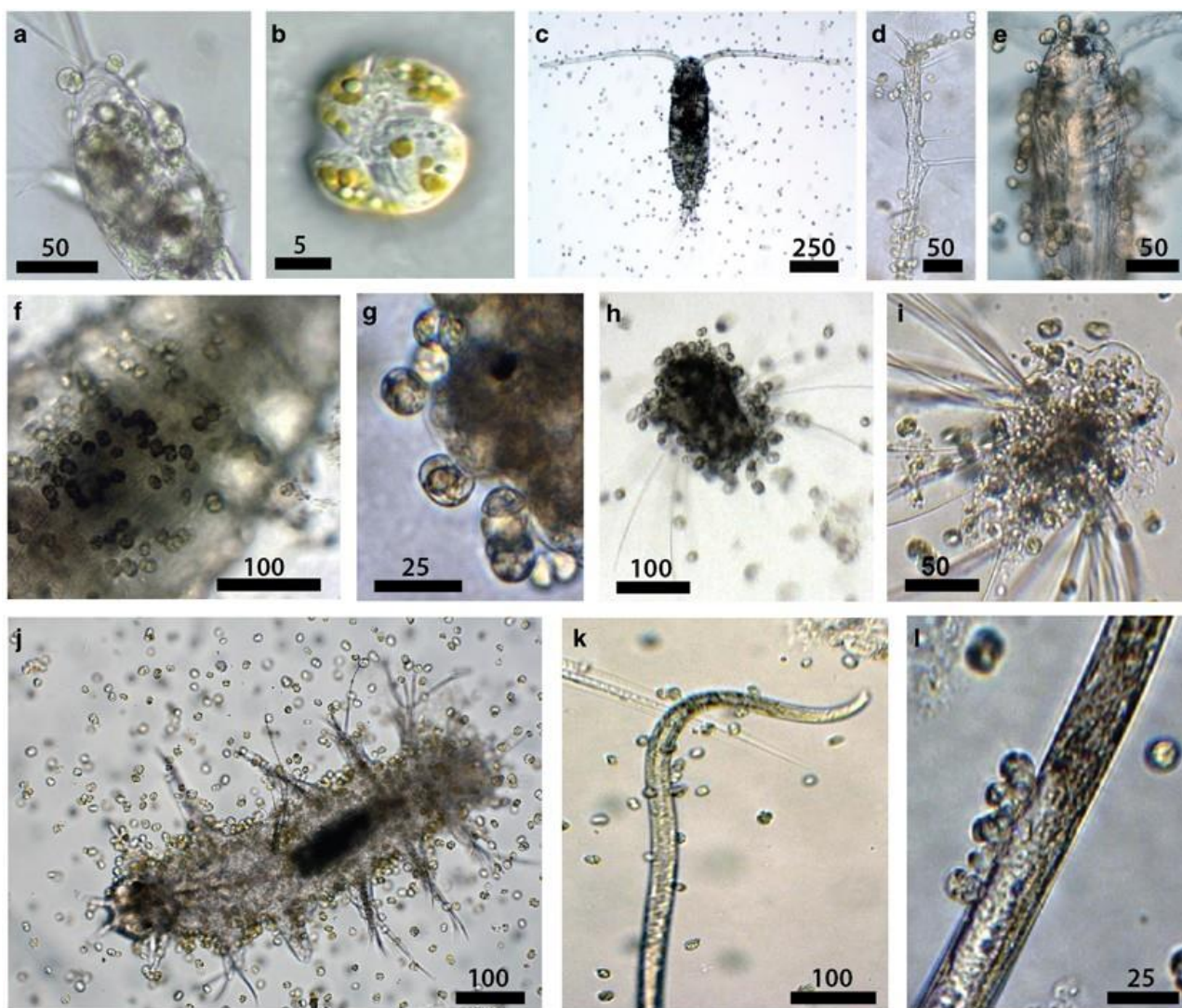
Figure 12. Constitutive mixoplankton (CM) immobilising and eating metazoan zooplankton. (**a**) Frame grabbed micrographs of an unidentified CM dinoflagellate tube feeding on an immobilised copepod nauplius larvae in a natural seawater sample from Denmark; (**b**) Micrograph of *K. armiger* in ventral view (type material). Note many small yellow–green chloroplasts (1–2 µm long); (**c**) Frame grabbed micrograph of the common marine copepod *Acartia tonsa* mixed with a culture of *K. armiger*; (**d**) Frame grabbed micrographs of initial microalgal attacks on the sensory antennae of the copepod (compound image); I *K. armiger* cells swarming around and attaching to an immobilised copepod; (**f**) Accumulations of feeding *K. armiger* cells on the surface of *A. tonsa*; (**g**) Tube feeding on an unidentified planktonic polychaete trochophore larva of *K. armiger*. Note the large food vacuole as dark globules in the central part of *K. armiger*; (**h**) *K. armiger* immobilising and; (**i**) food remnants of the trochophore larva after a day of incubation. A substantial part was removed by tube feeding; (**j**) *K. armiger* swarming around and forming feeding aggregates on an immobilised later stage polychaete-larva; (**k**) *K. armiger* attacking and attaching (**l**) to an unidentified marine nematode. Units on scale bars, µm. Figure from Berge et al. (2012).

To summarise:

Mixoplankton span size ranges of many orders of magnitude and express diverse prey preferences. Mixoplankton thus defy attempts to pigeonhole them into a one-size fits all scenario configuration.

3.5 Mixoplankton distribution in global oceans

As a community, the occurrence of mixoplankton in global oceans is ubiquitous (Faure et al., 2017; Leles et al., 2017, 2019). **Figure 13** shows the most recent results of mixoplankton distribution in global oceans from interrogation of the Ocean Biogeographic Information System (OBIS; http://www.iobis.org/) database. The maps show occurrence of mixoplankton according to the different types (**Box 3**) and allied sizes (Mitra et al., 2023). It is noteworthy that representatives of all the different mixoplankton types (CM, GNCM, pSNCM, eSNCM) occur in waters around the UK.
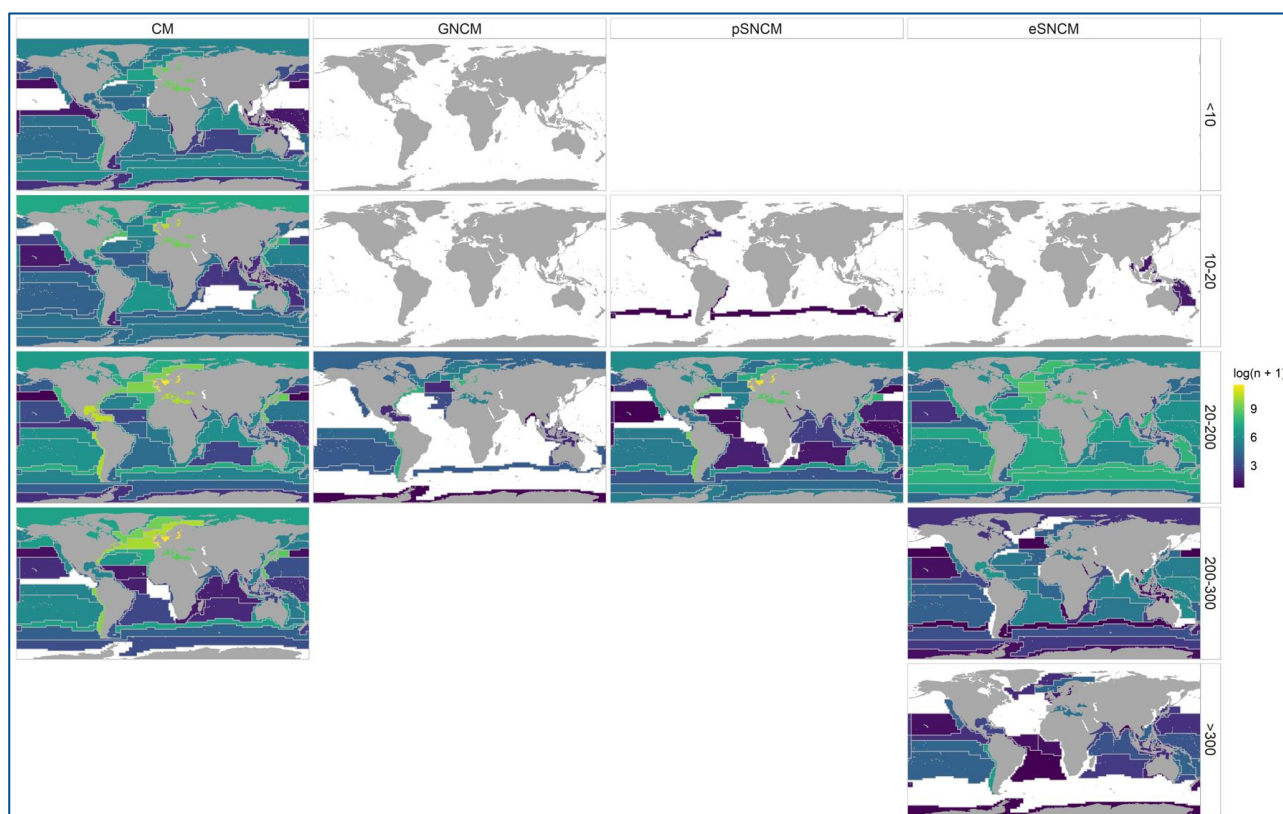
Figure 13. Global distribution of mixoplankton across Longhurst's biogeographical provinces. Distribution maps are shown for different mixoplankton types across different size classes (Y-axes in μm). The colour-casts indicate the number of records (as log (n + 1)) for each combination of mixoplankton type and size class; white provinces indicate no data. The absence of maps indicates that there are no known members of mixoplankton of that size class. See **Box 3** for definitions of mixoplankton types. Figure from Mitra et al. (2023).

4. Methods

4.1 Occurrence of mixoplankton types in UK waters

The Mixoplankton Database (MDB; Mitra et al. 2023) was interrogated, together with OBIS data, to identify those mixoplankton species that occur in UK coastal and open ocean waters. Further cross-referencing with the IOC-UNESCO Harmful Algal Bloom (HAB) database (https://marinespecies.org/hab/) identified those mixoplankton in UK waters that may be toxic or otherwise present a deleterious impact on water quality and ecosystem services. The MDB was also interrogated to ascertain the size classes of the mixoplankton species and, of their respective prey. Within the MDB, these were categorized according to the traditional standard plankton size categories as follows: pico (0.2–2 μm), nano (2–20 μm), micro (20–200 μm), meso (200 μm–20 mm), and, macro (20 mm–2 cm). The taxonomic grouping of the mixoplankton species and their prey have been made in accordance with Adl et al. (2019).

4.2 HAB events in UK waters under the mixoplankton paradigm

Information about Harmful Algal Bloom (HAB) events in UK waters was obtained from the Harmful Algal Event Database (http://haedat.iode.org/):

"*The Harmful Algal Event Database (HAEDAT) is a component of the Harmful Algal Information system (HAIS) within the "International Oceanographic Data and Information Exchange" (IODE) of the "Intergovernmental Oceanographic Commission" (IOC) of UNESCO, and in cooperation with ICES, and PICES. The HAEDAT is a meta database containing records of harmful algal events. HAEDAT contains records from the ICES area (North Atlantic) since 1985, and from the PICES area (North Pacific) since 2000.*"

Data associated with Harmful Algal Bloom (HAB) events in UK waters were acquired through interrogation of the Harmful Algal Event Database (HAEDAT) with the most recent data extracted on 29 February 2024. These data were cross-referenced against the MDB to identify HAB events associated with the different protist plankton types under the mixoplankton paradigm. The data were also analysed to align the difference HAB events recorded in the UK nations to the protist functional types under the mixoplankton paradigm. Furthermore, the relationship between the different protist functional types recorded as causative organisms of the HAB events and the impacted higher trophic levels (i.e., ecosystem assets and thence services) were also investigated.

5. Results & Discussion

5.1 Occurrence of mixoplankton in UK waters

5.1.1 Mixoplankton types in UK waters

Interrogation of the OBIS database in conjunction with the MDB revealed occurrence of 126 mixoplankton species in UK waters (**Tables A1-A4, Appendix**). Of these, 52% belong to the CM functional group, 25% to the eSNCM group and ca. 12% to each of the GNCM and pSNCM groups (left panel, **Figure 14**). The sizes of mixoplankton species found in UK waters range from 2 µm to 20 mm (right panel, **Figure 14**). There are no records of occurrence of macro-sized (> 20 mm) mixoplankton species in UK waters. Cross-referencing with the IOC-UNESCO HAB database reveal that 31 of the 126 species are capable of forming harmful blooms, the majority of which are constitutive mixoplankton (left panel, **Figure 14**, **Table A5**, Appendix).
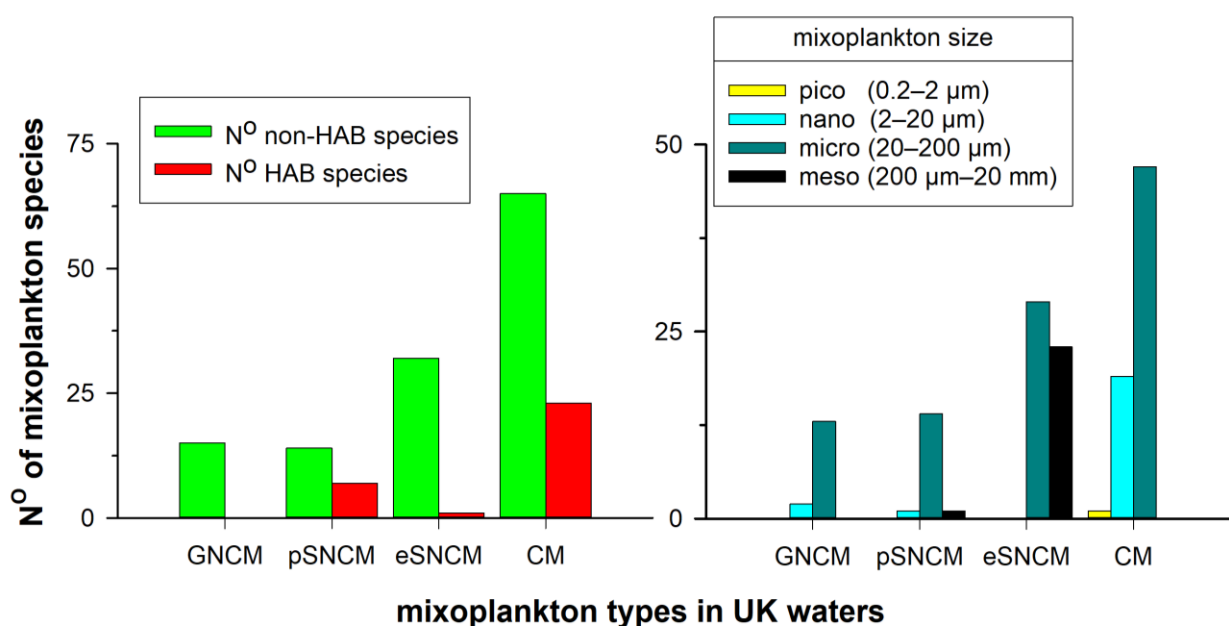
Figure 14. Number of species within each of the four different mixoplankton types recorded around the UK. The left-hand panel shows the numbers of non-HAB and HAB species; the right-hand panel shows the number of species in each type according to their cell size category. GNCM, generalist non-constitutive mixoplankton; pSNCM, plastidic specialist non-constitutive mixoplankton; eSNCM, endosymbiotic specialist non-constitutive mixoplankton; CM, constitutive mixoplankton. HAB, Harmful Algal Bloom. See also **Box 3**.

5.1.2 Mixoplankton predator and their prey: taxonomy and allometry

Tables 1 and 2 provide a list of the 10 most frequently recorded constitutive mixoplankton and non-constitutive mixoplankton species in UK waters, respectively (see also **Tables A1-A4**, **Appendix**). It can be seen that the mixoplankton species occurring in UK waters are capable of ingesting prey from a broad spectrum of sizes and also from different trophic levels.

Table 1. Ten most frequently recorded CM species in OBIS database from UK waters. These species were all categorised as 'phytoplankton' under the old 'phytoplankton-zooplankton' paradigm. MFT, mixoplankton functional type. NR, not recorded. * indicates Harmful bloom species (HABs). See **Tables A1** & **A5**, **Appendix**.

species name	MFT	MFT taxonomy	MFT size class	OBIS records	prey size class	prey taxonomy
Tripos fusus	CM	Dinoflagellata	micro	80719	NR	NR
Tripos furca	CM	Dinoflagellata	micro	56318	nano-micro	NR
Tripos muelleri	CM	Dinoflagellata	micro	53352	NR	NR
Prorocentrum micans	CM	Dinoflagellata	micro	23010	nano	Cryptophyceae Cyanobacteria Diatomea Dinoflagellata Haptophyta Ochrophyta
Heterocapsa rotundata	CM	Dinoflagellata	nano	21246	nano	Bacteria Diatomeae
Tripos longipes	CM	Dinoflagellata	micro	19779	NR	NR
Prorocentrum cordatum*	CM	Dinoflagellata	nano	7340	nano	Cryptophyceae Cyanobacteria Dinoflagellata Haptophyta Ochrophyta
Karenia mikimotoi*	CM	Dinoflagellata	micro	6680	pico-nano	Haptophyta
Dinobryon faculiferum	CM	Ochrophyta	nano	5373	pico	Bacteria
Lingulodinium polyedra*	CM	Dinoflagellata	micro	4606	nano-micro	Cyanobacteria Diatomeae

Table 2. Ten most frequently recorded NCM species in OBIS database from UK waters. These species were all categorised as 'microzooplankton' or 'protist-zooplankton' under the old 'phytoplankton-zooplankton' paradigm. MFT, mixoplankton functional type. NR, not recorded. * indicates Harmful bloom species (HABs). See also **Tables A2-A5, Appendix**.

Species name	MFT	MFT taxonomy	MFT size class	OBIS records	prey size class	prey taxonomy
Mesodinium rubrum	pSNCM	Ciliophora	nano-micro	42031	nano	Cryptophyceae
Dinophysis acuminata*	pSNCM	Dinoflagellata	micro	23474	micro	Ciliophora
Dinophysis norvegica*	pSNCM	Dinoflagellata	micro	11815	micro	Ciliophora
Globigerina bulloides	eSNCM	Foraminifera	micro-meso	11492	micro-meso	Bacteria Copepoda Sarsostraca (Artemia)
Globigerinita glutinata	eSNCM	Foraminifera	micro-meso	8300	micro-meso	NR
Dinophysis acuta*	pSNCM	Dinoflagellata	micro	6941	micro	Ciliophora
Globigerinoides ruber	eSNCM	Foraminifera	micro-meso	5694	micro-meso	Ciliophora Copepoda
Globigerinella siphonifera	eSNCM	Foraminifera	micro-meso	4797	micro-meso	Bacteria, Copepoda Sarsostraca (Artemia)
Orbulina universa	eSNCM	Foraminifera	micro-meso	4500	micro-meso	Ciliophora Copepoda
Globigerina falconensis	eSNCM	Foraminifera	micro-meso	4152	micro-meso	Bacteria, Copepoda Sarsostraca (Artemia)
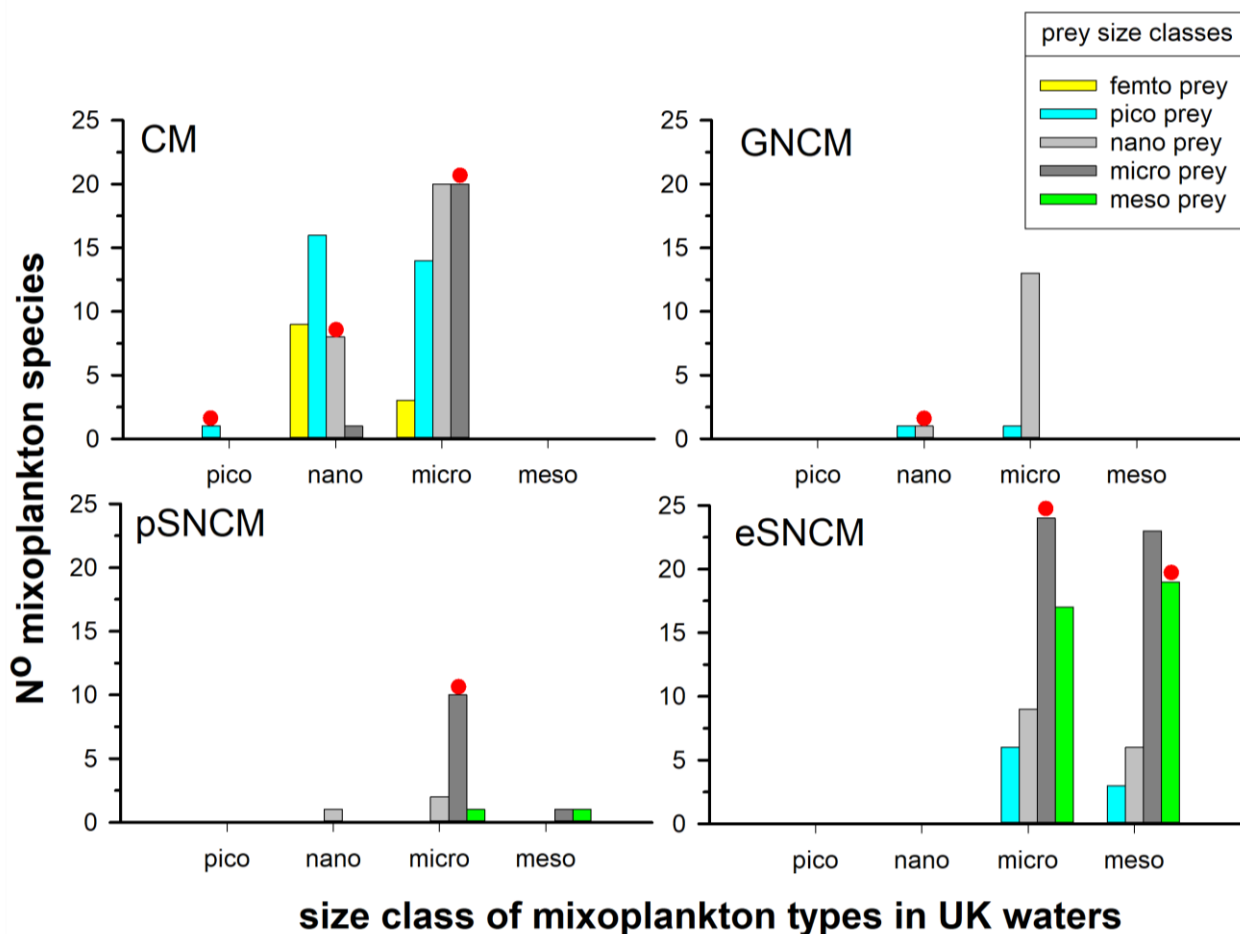
Figure 15. Size classes of the four different mixoplankton types, showing the number of species in each class set against the size of their prey. The red dot indicates prey:predator size ratios of 1:1. GNCM, generalist non-constitutive mixoplankton; pSNCM, plastidic specialist non-constitutive mixoplankton; eSNCM, endosymbiotic specialist non-constitutive mixoplankton; CM, constitutive mixoplankton. See also **Box 3**. femto, <2 µm; pico, 0.2–2 µm; nano, 2–20 µm; micro, 20–200 µm; meso, 200 µm–20 mm. femto sized prey includes virus; pico sized prey includes bacteria and cyanobacterial prey.

Figure 15 presents the allometric relationships for combinations of the mixoplankton predator and their prey recorded within OBIS for UK waters. There are various instances of predation capability within a particular size group (i.e., intraguild predation where prey and predator are of similar sizes; Mitra & Flynn, 2023) and also a significant minority of above-size predation (e.g., Berje et al., 2012). These data demonstrate the diversity of prey (taxonomic as well as allometric) and the breadth of potential food web interactions for mixoplankton in UK waters (cf. **Figures 8, 9**).

Under the traditional 'phytoplankton-zooplankton' paradigm, the constitutive and non-constitutive mixoplankton species listed in **Tables 1** & **Table A1** (**Appendix**) and **Tables 2** and **A2-A4** (**Appendix**) were categorised as 'plant-like' phytoplankton and 'animal-like' zooplankton, respectively. Accordingly, the role of these species in ecosystem structure and functioning were restricted respectively to either primary production only, or as consumers of primary producers.

The phytoplankton-zooplankton plant-animal dichotomy is still assumed as the conceptual core for the majority of marine ecosystem monitoring and management research (e.g., McQuatters-Gollop et al., 2019; McEvoy et al., 2023) and thence used in policy briefings (e.g., Atkinson, 2024; Holland & McQuatters-Gollop, 2024; Tett, 2024).

An example is in the recent 'Plankton Lifeform Extraction Tool' which has been "*designed to make complex plankton datasets accessible and meaningful for policy, public interest, and scientific discovery*" (Ostle et al., 2021). This particular tool assumes the old 'phytoplankton-zooplankton' paradigm typified by inclusion of diatoms as the primary producers, consumed mainly by metazoan copepods. The copepods are consumed by fish and thus are considered to be the main link between the primary producers and ecosystem services such as fisheries. 'Mixotrophy' is included but only as an 'add-on trait' for dinoflagellates and ciliates; such an allocation could be attributed to findings from the 1990s when research on mixoplankton was in its infancy (e.g., Sanders, 1991; Stoecker, 1998; Li et al., 1999). Critically, no clear distinction is made between the different types of mixotrophy employed by phytoplankton versus by mixoplankton (**Figure 3, Box 2**). Furthermore, there is no recognition (explicit or implicit) of the existence of mixoplankton communities in this tool even though the term mixoplankton was coined in 2019 (Flynn et al., 2019) and the importance of these organisms has been documented from the early 2000s (Dolan & Pérez, 2000; Johnson & Stoecker, 2005; Stoecker et al., 2009; Berge et al., 2012; Flynn et al., 2013).

Tools such as that of Ostle et al. (2021) thus fail to account for the activity of mixoplankton to consume other primary producers such as the pico-sized cyanobacteria, the nano-sized flagellates and micro-sized diatoms. Likewise, the potential for mixoplankton species to graze on metazoan consumers such as larvae of crabs, barnacles, oysters as well as fisheries supporting copepods (**Tables A1-A4**, Berge et al., 2012; Mitra et al., 2023), is ignored in such tools. Accordingly, important ecological functionalities of mixoplankton are totally ignored when such tools are used to forecast the diversity and health of marine lifeforms and their impact on ecosystem services (e.g., McEvoy et al., 2023; Corona et al., 2024; Ratnarajah et al., 2024).

Under climate change, picoplankton abundance are expected to increase with increasing temperature (Morán et al., 2015; Giovannoni, 2017; Visintini et al., 2021). According to models of ecosystem management based on the old paradigm, the diatom abundance would be expected to decline under these conditions leading to a decline in copepod populations and thus impacting fisheries. However, it has been shown that various iconic 'phytoplankton' such as *Teleaulax amphioxeia*, *Emiliania huxleyi* and *Phaeocystis globosa* are actually constitutive mixoplankton (Yoo et al., 2017; Avrahami & Frada, 2020; Koppelle et al., 2022) and these CM enhance their photosynthetic capabilities through ingestion of picoplankton (Mitra & Flynn, 2023). Such synergy between photosynthesis and consumption of prey have been found to improve the quality of food for higher trophic levels (Traboni, 2022). Thus, studies of management of ecosystem services such as shellfisheries and finfisheries based on the old paradigm (e.g., Bedford et al., 2020) fail to take into account the potential benefit of such a picoplankton-mixoplankton linkage for higher trophic levels and thus ecosystem services.

A study of the protist plankton distribution in UK's Western Channel Observatory Station L4 has shown varying diversity of distribution of protist plankton across the different seasons and at two different depths (**Figure 16**). It is noteworthy that the plankton biomass in the summer months are dominated by mixoplankton and protist zooplankton. These months are crucial for the growth and development of the juvenile stages of crustaceans, shellfish and finfish (i.e., assets of ecosystem services). Both these protist groups – i.e., mixoplankton and protist zooplankton – are typically ignored or their ecophysiology mislabelled in environmental management and policy studies (e.g., Ostle et al., 2021; McEvoy et al., 2023; Holland & McQuatters-Gollop, 2024; Tett, 2024).
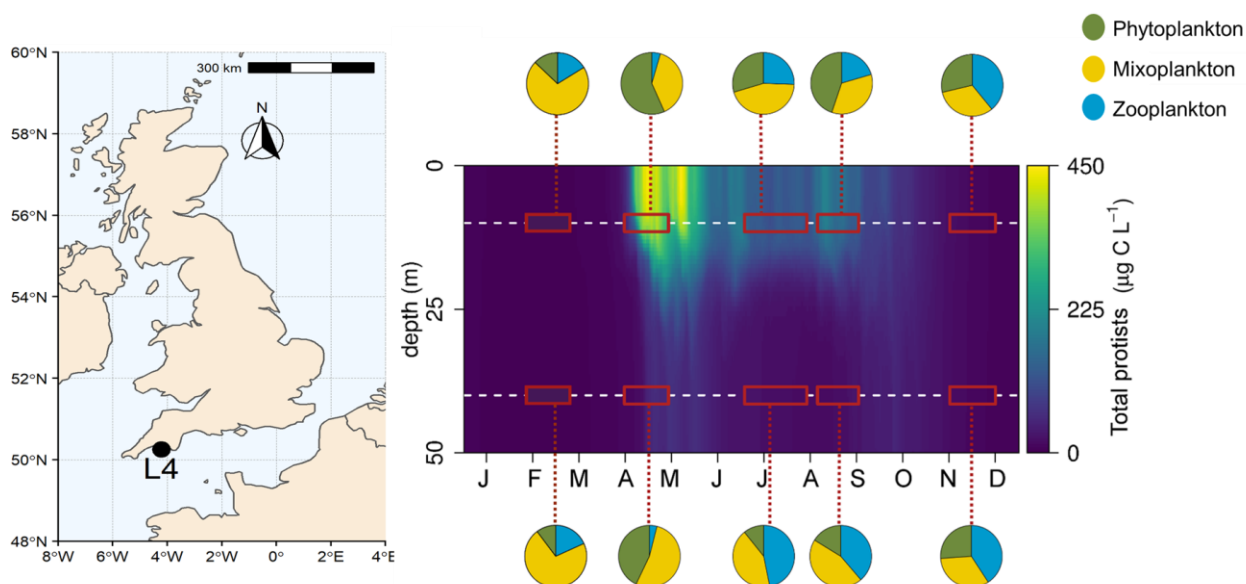
Figure 16. Water column and temporal distribution of different protist plankton types at station L4 in the Western Channel Observatory, UK. Figure modified from Leles et al. (2021).

5.2 HAB events and UK ecosystem services

5.2.1 Impact of mixoplankton paradigm on UK HAB events

Interrogation of the Harmful Algal Event Database (HAEDAT) revealed 360 harmful algal bloom (HAB) events recorded in UK waters since 1960 (**Table A6, Appendix**). Majority (ca. 50%) of these events were associated with blooms of mixoplankton species while only 9% were associated with phytoplankton species (**Figure 17**). Within the mixoplankton functional types, the higher proportion of bloom events were associated with CMs. In these analyses, where only the genus names were recorded in HAEDAT ('***genus recorded***', **Figure 17**), it was assumed that these events were caused by organisms belonging to the same functional type as those where the full taxonomic description were recorded ('***species recorded***', **Figure 17**).

Out of 360 HAB events recorded within HAEDAT in UK waters, 161 records do not have information about the causative organisms (i.e., genus or species names) responsible for

the HAB event. According to the HAEDAT data, nine of these events were associated with production of the toxin domoic acid; a product from the phytoplankton *Pseudo-nitzschia* spp. Accordingly, these events were assigned to the phytoplankton functional type ('***incomplete records***' for P, **Figure 17**). While some of the remaining 152 events do include information about toxin production, these toxins are not unique to any specific plankton species or indeed genus. Accordingly, it was not possible to assign any plankton functional type as causative agents for these events ('***not recorded'***, **Figure 17**). Over decades, changes in methodologies used for detection of HABs has led to better understanding and thus recording of the causative species associated with these HAB events in UK waters (Zingone et al., 2022; **Figure 17 inset**; **Table A6**, **Appendix**).
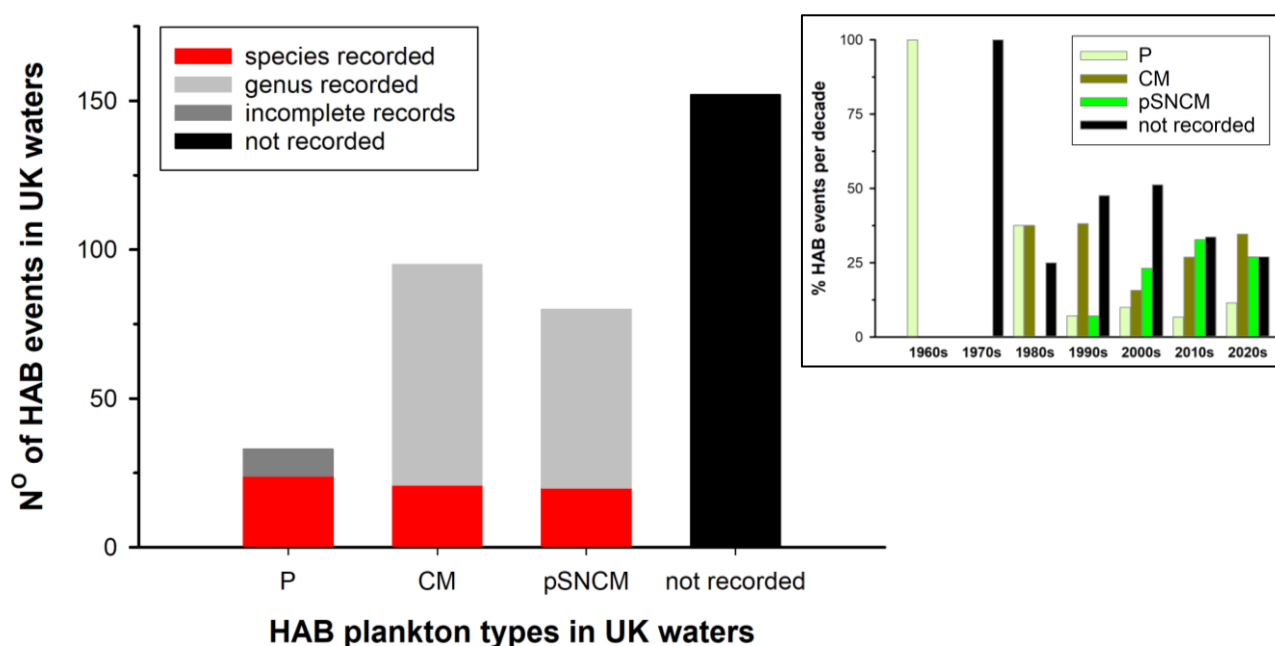
Figure 17. Attribution of HAB events in UK waters since 1960. HAB events attributed to phytoplankton, CM and pSNCM or logged as 'not recorded' according to records from the Harmful Algae Event Database (HAEDAT). Causative organisms where only the genus names are recorded ('genus recorded') are assumed to belong to the same functional type as those with full taxonomic information ('species recorded'). Events without any taxonomic information about the causative organism but associated with domoic acid production were assigned to phytoplankton functional type ('Incomplete records'). Events with no taxonomic information and where the toxin produced is not unique to any taxonomic group have been logged as 'not recorded'. The inset figure shows % of HAB events recorded in UK waters per decade according to the causative organisms (P, CM, pSNCM) where these data are available or as not recorded. P, phytoplankton; CM, constitutive mixoplankton; pSNCM, plastidic specialist non-constitutive mixoplankton. See also **Boxes 1** and **3**, **Table A6**, **Appendix**.

Further interrogation of the data showed that the highest occurrence of HAB events were recorded in Scottish waters (70%) with the pSNCM *Dinophysis* spp. and the CM *Alexandrium* spp. being responsible for 27% and 24%, respectively, of these events (**Figure 18**).
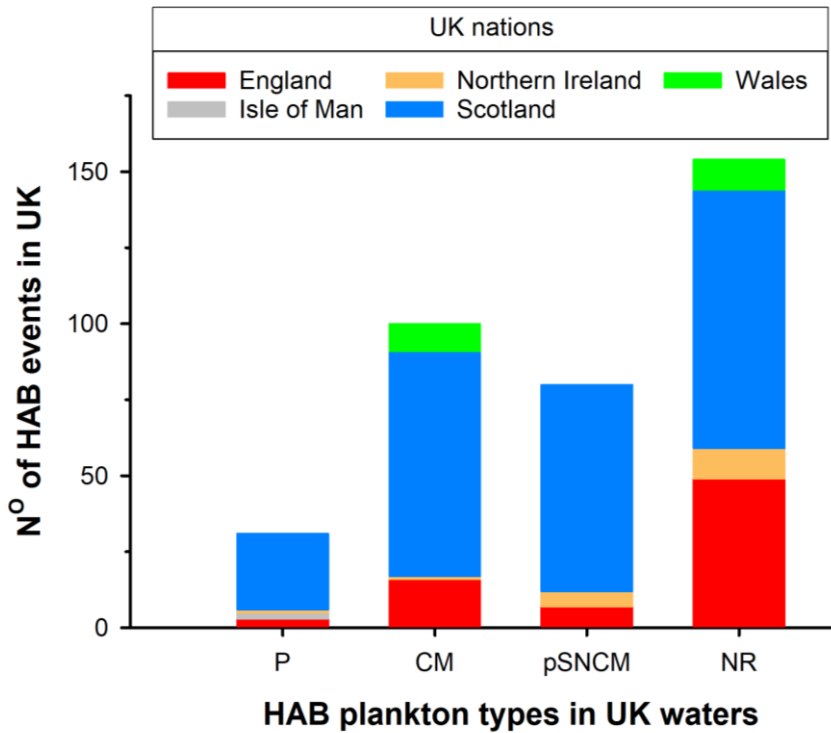
Figure 18. Attribution of HAB events in UK waters by nation since 1960. HAB events attributed to phytoplankton, CM, pSNCM and NR according to records from HAEDAT. NR – causative agent not recorded. P, phytoplankton; CM, constitutive mixoplankton; pSNCM, plastidic specialist non-constitutive mixoplankton. See also **Boxes 1** and **3**; **Table A6, Appendix**.

5.2.2 UK HAB events: mixoplankton and ecosystem services

Interrogation of the Harmful Algae Event Database (HAEDAT) records for impact of the HAB events, on UK ecosystem services showed that the impact of ca. 46% of the events were not recorded against any ecosystem services ('NR', **Figure 19**; **Table A6, Appendix**). Where records of impact on ecosystem services were available, the data indicated that most of the events were associated with shellfish species (**Figure 19**). The most impacted ecosystem service due to an HAB event appears to be the mussels (43% of events).
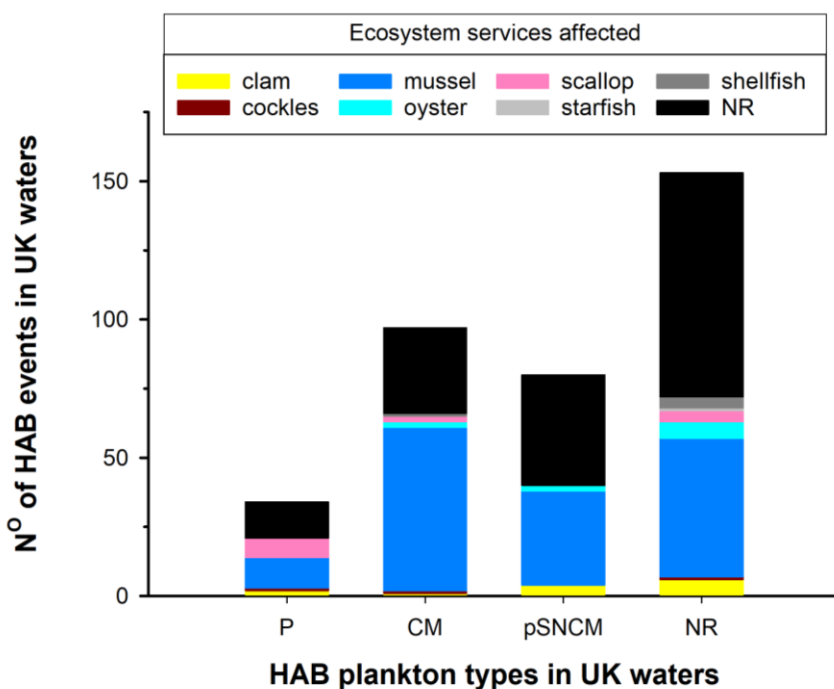
Figure 19. Attribution of HAB events in UK waters by affected ecosystem service since 1960. HAB events attributed to phytoplankton, CM, pSNCM and NR according to records from HAEDAT. NR – causative agent not recorded. P, phytoplankton; CM, constitutive mixoplankton; pSNCM, plastidic specialist non-constitutive mixoplankton. See also **Boxes 1** and **3**; **Table A6, Appendix.**

5.3 Asset valuation and mixoplankton

5.3.1 Why consider mixoplankton in natural capital asset valuation?

The report by Best et al. (2023) highlights the need to consider plankton within UK natural capital. The arguments put forward by Best et al. (2023) are rooted in the old paradigm with its emphasis upon the primary producing diatoms (protist phytoplankton) and their predators, notably the metazoan copepods (multicellular 'animal' zooplankton). Mixoplankton as a community, with a status akin to that of phytoplankton and zooplankton, are not considered within the Best et al. (2023) report. This situation could in part be attributed to the conduct of many plankton field studies around the spring bloom or autumnal bloom events. **Figure 20** provides a schematic of the temporal dynamics of plankton communities in temperate waters, such as the UK coastal and marine systems, over a calendar year. UK marine productivity is supported by phytoplankton primarily in the spring and autumn months; the contribution of mixoplankton occurs mainly post-spring bloom and during the summer months (e.g., **Figure 16**; Leles et al., 2018, 2021; Mitra et al., 2014a).

Summer months are crucial to the UK natural capital accounting for various reasons. Development and maturity of shellfish and finfish juveniles (nauplii, larvae) occur over the summer months (Mitra et al., 2014b). In the UK waters, the marine food web in the summer months are dominated by mixoplankton (**Figure 16**; Leles et al., 2018, 2021). Grazing by these mixoplankton on picoplankton could potentially upgrade food quality for higher trophic levels (Mitra et al., 2014a; Traboni, 2022; Flynn & Mitra, 2023). However, there is a lack of information and connectivity between the picoplankton, their predators and the higher trophic levels in monitoring and management of UK marine and coastal waters (Mulholland et al. 2021).

The health of UK coastal and marine water ecosystems, and thus water quality, is also of paramount importance during the summer holiday months. According to the Office for National Statistics (ONS):

"*Health benefits from recreation, valued at £445 billion in 2021, was the largest contribution to the total asset value of UK ecosystem services.*"

According to the [ONS data](#) published in 2023, ca. **22.38% of the asset value for health benefits from recreation is attributed to 'coastal and marine' habitats**. Further, **ca. 34.05% of the asset value for recreation and tourism (expenditure) is attributed to 'coastal and marine' habitats**.
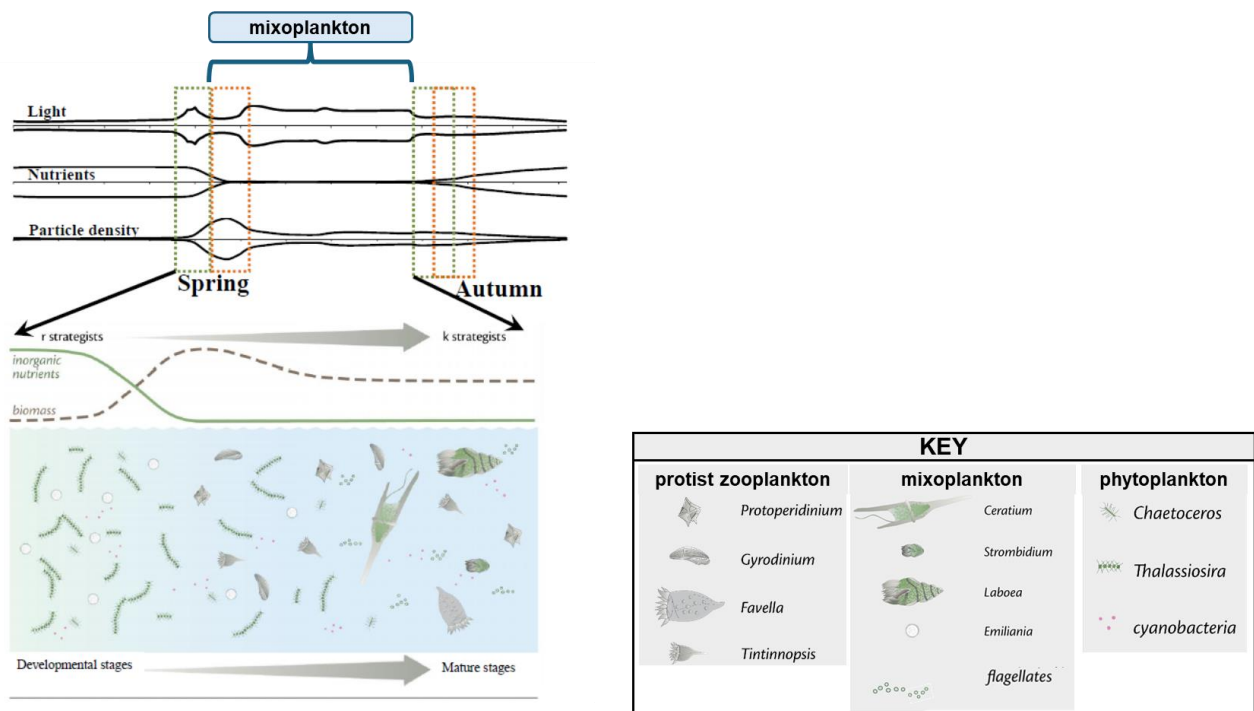
Figure 20. Diagrammatic portrayal of the changes to the planktonic food web over a year, in the temperate waters such as those of the UK waters, with transitions between ecosystem states. The upper panels show changing patterns of light, inorganic nutrients and particle density (i.e., total plankton biomass) over the temperate year. Transitions between developmental and mature stages of the ecosystem are as indicated; green and orange dashed lines indicate the developmental stages, where green represents conditions optimal for phytoplankton and orange for protist zooplankton. Later periods (transition to the more mature state) are suboptimal for phytoplankton and/or protist zooplankton, and more supportive for mixoplankton. The lower panel shows in detail the transition from developmental to mature stages, with changes in selection priorities from "r-selected" phytoplankton and protist zooplankton in the developmental phase of the ecosystem to a mature ecosystem with "K-selected" mixoplankton. For definitions and discussion of developmental vs. mature state, and r vs. K selection, see Odum (1969) and Parry (1981). Figure modified from Mitra et al. (2014a).

5.3.2 Assigning asset values to mixoplankton

Assigning an asset value to mixoplankton falls into two distinct categories:

(i) The **positive asset value** correlates directly with the critical role of mixoplankton in marine ecology especially during the late-spring – summer period when the growth of the juveniles of holoplankton and meroplankton metazoa depend on the presence of a good quality and varied diet (Mitra & Flynn, 2005). A healthy marine ecosystem, and especially a shelf-coastal system, depends greatly on the proliferation of mixed populations of mixoplankton over this period (**Figure 20**).

(ii) The flip side to the positive asset value is seen when conditions conspire to promote the proliferation and accumulation of noxious mixoplankton. These impose a **negative asset value**. That value is not just associated with toxic species (*Alexandrium*, *Dinophysis*, *Karlodinium*, *Prymnesium*, *Heterosigma* etc.) but also with species such as *Prorocentrum* and *Phaeocystis* that can produce copious amounts of mucus that

can form sea-snot foams (e.g., **Figure 11**) and otherwise hinder the flow of energy and materials up the food chain through the formation of ecosystem disruptive algal blooms (EDABs; Sunda et al., 2006).

The greatest challenge in judging and balancing positive versus negative asset values (noting that negating a negative gives a positive) is a lack of scientific understanding. Extant tools and interpretations used for ecosystem monitoring, management and policies are built upon a century-old misunderstanding of how plankton ecology works, based on the plant-animal-like phytoplankton-zooplankton dichotomy (**Figure 1a**). That historical view is ill-equipped to take into account organisms that combine multi-nutritional mechanisms and thus express multiple trophic levels within a single cell (**Figures 1b, 2b**). The challenge exists at both an international level and also at a UK level.

Logic dictates that the <u>positive asset valuation</u> associated with mixoplankton is calculated as the sum of the following:

- Wild fin- and shell- fisheries; these are all directly or indirectly dependant on plankton and thence upon mixoplankton (**Figure 20**);
- General marine ecosystem functioning (benthic as well as open water); the bulk of this is directly or indirectly dependant on plankton and thence upon mixoplankton (**Figure 1b**)
- Seabird and sea mammal populations etc; these are all directly or indirectly dependent on plankton and thence upon mixoplankton via linkages to fisheries (**Figures 1b** and **20**)
- Contributions of marine plankton to biogeochemistry and Earth homeostasis; mixoplankton play key roles in these processes (**Figure 16**).

The <u>negative asset valuation</u> associated with mixoplankton is calculated as the sum of the following:

- HABs impacting wild and aquaculture fisheries; mixoplankton include various important HAB species (**Table A5, Appendix**), some of which can cause widespread destruction of the aquatic ecosystem either directly via toxins or indirectly via promoting deoxygenation events (**Figure 19**).
- HABs and ecosystem disruptive algal blooms (EDABs) impacting seabirds, sea mammals etc.; mixoplankton include species associated with various generic water-health issues, including foams (**Figure 11**).
- Nuisance algal bloom events impacting amenity access and aesthetics; mixoplankton include species associated with sea foams, bad smells, water discolouration and similar.

It is not possible at this time to further calculate an asset valuation for the natural capital of mixoplankton. The positive valuation is shared with 'plankton' in general (Best et al., 2023). The negative valuation, for which the mitigation equates to a financial positive, is largely unique to mixoplankton (with only the HAB diatom *Pseudo-nitzschia* providing a non-mixoplankton marine component; **Figures 17-19**).

Application of the <u>precautionary principle</u> places an onus on regulators to take account of the existence of mixoplankton and of their diverse nutritional mechanisms and ecological interactions. This is required to optimise the healthy contributions (positive assets) and minimise the negatives. As a general rule, any factor that promotes the increased growth of mixoplankton, and especially events favouring development of essentially uni-species blooms, warrants consideration as one that increases the tendency towards negative asset valuations. These factors include:

i) <u>Increases to inorganic nutrient loading</u>: while this promotes phytoplankton growth as well, those phytoplankton species and also any bacterial growth can subsequently provide feed (prey) for mixoplankton (Anschütz et al., 2022).

ii) <u>Increases to organic nutrient loading</u>: this more likely promotes mixoplankton than phytoplankton proliferation (Ghyoot et al., 2017).

iii) <u>Decreased turbulence and/or decreased flushing rates, especially associated with salinity changes</u>: mixoplankton are generally (but not always) optimised for growth in low turbulent waters (Tillmann et al., 2023). Some species, notably *Prymnesium* and allies, are especially well adapted to growth in systems subjected to changes in salinity (Caron et al., 2023).

iv) <u>Increased temperature</u>: this promotes more rapid growth and also acts to stabilise the water column, favouring mixoplankton growth (Anschütz et al., 2022).

v) <u>Factors promoting ecosystem stability</u>: allelopathic interactions are common amongst mixoplankton – once a species begins to dominate, a positive feedback event can occur (Mitra et al., 2016).

The above factors are in turn also affected by climate change events which may promote flash floods that simultaneously bring additional inorganic and organic nutrients with low salinity into coastal zones. New harbour, dock and allied infrastructures affecting water flows, new sewage outfalls and changes to land usage, are all potential sources of changes to water quality that may promote harmful or nuisance mixoplankton growths and/or decrease the growth of good quality mixoplankton+phytoplankton communities.

6. Conclusions & Recommendations

Mixoplankton are not new members of the marine ecosystem. They have always been there; indeed, from an evolutionary standpoint they were members of that ecosystem before phytoplankton such as diatoms (**Figure 6**). What has changed is the belated realisation that these organisms, that combine primary production (photosynthesis) with grazing, simultaneously and synergistically in the one cell, are common and collectively abundant (**Tables 1, 2, A1-A5**; **Figures 13, 16**; Glibert & Mitra, 2022; Mitra et al., 2023).

Three overarching recommendations present themselves:

i. Normalise the usage of 'mixoplankton' in any/all discussions concerning plankton.

ii. Recognise the eco-physiological variation within mixoplankton types.

iii.   Recognise the challenges present in monitoring and managing the asset value of mixoplankton.

Each of these is considered in detail, below, followed by a policy recommendation associated with the management of risk associated with deleterious mixoplankton growths.

6.1 Clarity in terminology – normalise 'mixoplankton'

The most important, arguably the most obvious, first step is to ensure that in reference to plankton a clear distinction is made between 'phytoplankton' and 'mixoplankton' (**Figure 1**; **Box 1**). References to 'mixotrophic phytoplankton' must be avoided as that term is confusing and ambiguous; <u>all</u> phytoplankton are mixotrophic by coupling phototrophy and osmotrophy.

The use of 'mixoplankton' needs to be normalised. Any reference to 'phytoplankton' needs to be recognised as applying to a selection of marine organisms that can photosynthesize, and specifically to such organisms that are unable to consume prey. Allied to this, it should be recognised that phytoplankton support only a proportion of planktonic primary production (albeit a dominant part during the spring bloom; **Figures 1** and **20**). That mixoplankton are also grazers complicates things further; NCM can comprise $1/3^{rd}$ or so of organisms traditionally grouped together as (protist) microzooplankton (Bé et al., 1977; Anderson, 1983; Michaels, 1988; Gast & Caron, 1996; Stoecker et al., 2009).

In many ways the importance of correctly referencing phytoplankton vs mixoplankton mirrors that of the importance of differentiating between protist-zooplankton and metazoan-zooplankton. Referencing all types of zooplankton grazers as one group is well known as problematic in the extreme, not least as their sizes range from 2 µm nanoflagellates to 2 m jellies (Mitra et al., 2014b).

In short, reference to plankton must be made using appropriate labels and not historically convenient but scientifically flawed groupings. To not use the correct terminology to describe plankton functional types places those that use science evidence at risk of being called out as being out of touch with the latest developments.

6.2 Correct allocation of protist plankton to their trophic status

By extension to the need for clarity in overarching terminology (**Section 6.1**), it is important to recognise that the complexity of protist evolution (**Figure 6**) has given rise to different trophic abilities being expressed by members of a given taxonomic group. This results in each branch of the protist tree-of-life (**Figure 5**) containing multiple examples of contrasting physiological capabilities.

The exemplar for this is the dinoflagellate group, which contains protist-zooplankton, mixoplankton (CM, NCM) and phytoplankton species (and, also parasitic members). The placement of such groups into just a single plankton group is incorrect. For example, placing all dinoflagellates within the single functional type 'phytoplankton' or considering 'dinoflagellates' as a single functional group or lifeform with no differentiation between

zooplanktonic, mixoplanktonic and phytoplanktonic species (e.g., McQuatters-Gollop et al., 2019; Ostle et al., 2021) is inappropriate as such descriptors fail to provide indicators of the different roles of these organisms in ecology.

The diversity of mixoplankton and the capabilities of individual species (especially bloom and toxic species), needs to be recognised. Establishing ecological associations between species would likely be of benefit. An example is the essential linkage between the three mixoplankton species *Teleaulax*, *Mesodinium*, and *Dinophysis* (Park et al., 2006). In UK waters, according to the HAEDAT data, species belonging to the genus *Dinophysis* are responsible for ca. 22% of the HAB events.

Dinophysis spp. are plastidic-specialist NCM (pSNCM; **Box 3**). The different species within this genus require the photosynthetic apparatus manufactured by the cryptophyte *Teleaulax amphioxeia* to provide their acquired phototrophic potential (Wisecaver & Hackett, 2010). *Teleaulax amphioxeia*, is a constitutive mixoplankton (CM) with the innate capability to synthesise chloroplasts to support phototrophy. However, *Dinophysis* cannot directly ingest *Teleaulax*; they can acquire the *Teleaulax* plastids only from another pSNCM - *Mesodinium rubrum* (Park et al., 2006; **Figure 10**). After ingestion of *Teleaulax* cells, *Mesodinium* disassembles the *Teleaulax* cell, retaining the mitochondria, chloroplast and nuclear material within capture membranes for acquired phototrophy. The pSNCM *Dinophysis* feeds on the *Mesodinium* and obtains the photosynthetic apparatus originating from *Teleaulax*. Thus, pSNCM dinoflagellate *Dinophysis* require cellular components transferred from the CM cryptophyte *Teleaulax* via the pSNCM ciliate *Mesodinium* for their growth and proliferation (Johnson & Stoecker, 2005; Stoecker et al., 2017). Considerable efforts have been expended on research and monitoring of *Dinophysis* blooms. However, such efforts have concentrated on importance of physical oceanography in the proliferation of *Dinophysis* HAB events (e.g., Siemering et al., 2016). The complex ecological interactions between the *Teleaulax-Mesodinium-Dinophysis* leading to the potential for *Dinophysis* blooms and thus outbreaks of diarrhetic shellfish poisoning (DSP) impacting shellfish aquaculture has been rarely considered (Fiorendino et al., 2020; Anschütz et al., 2022).

6.3 Recognise the value of mixoplankton for natural capital and ecosystem management

At the most basic level, the natural capital of mixoplankton, and of plankton in general, equates to the sum of all the asset values of the organisms that feed directly or indirectly upon them, plus that of societal assets linked to the marine ecosystem (**Figures 1 and 20**). The absence of mixoplankton, or blooms of the 'wrong' mixoplankton, would result in the deterioration of those assets. Most importantly, and in contrast to most phytoplankton (exceptions being HAB phytoplankton such as *Pseudo-nitszchia*), various mixoplankton when present above threshold levels carry a negative asset value. Understanding how to mitigate their proliferation confers (re-establishes) a positive asset value to the whole ecosystem.

The complexity of the nutritional mechanisms and needs across protist plankton is greatest within the mixoplankton (**Figures 2, 3, 8**). This is clear at the species level from the Mixoplankton Database (Mitra et al., 2023). For certain this greatly complicates the collection and interpretation of plankton and nutrient data, and thence attempts to compute the natural capital value of mixoplankton.

In this context, it is important to allocate numeric abundance to as many members of the protist plankton as possible; such data need to be aligned with abiotic data over the seasons. And, the data need to be considered in light of the new understanding of plankton ecology, not through the lens of the old 'phytoplankton-zooplankton' dichotomy.

Environmental monitoring of nutrients should consider the potential roles of not only dissolved inorganic nutrients (e.g., nitrate, ammonium, phosphate) but also that of dissolved organics in plankton community structure and function. This is especially as dissolved organic nutrients can have substantial impact on the plankton community structure such as supporting blooms of picoplankton (i.e., heterotrophic bacteria and photosynthetic cyanobacteria). Proliferation of such picoplankton would in turn support growth and proliferation of nano-sized mixoplankton species (Flynn & Mitra, 2023; Mitra & Flynn, 2023).

Figure 21 provides a simple schematic of two alternate scenarios in a healthy coastal and marine ecosystem versus one subjected to pressures from human activities. The HAB event example provided in this figure is of harmful *Dinophysis* spp blooms. *Dinophysis* spp. are responsible for 22% of HAB events in the UK (**Table A6**, **Appendix**). DSP production by *Dinophysis* spp. leads to closures of shellfisheries. Recent studies have shown that temperature, nutrient load, mixed layer depth, and irradiance all greatly influence the trophic interactions between *Teleaulax*, *Mesodinium* and *Dinophysis* (**Section 6.2**) and thence, the timing and magnitude of *Dinophysis* blooms (Anschütz et al., 2022; Mitra, 2024).
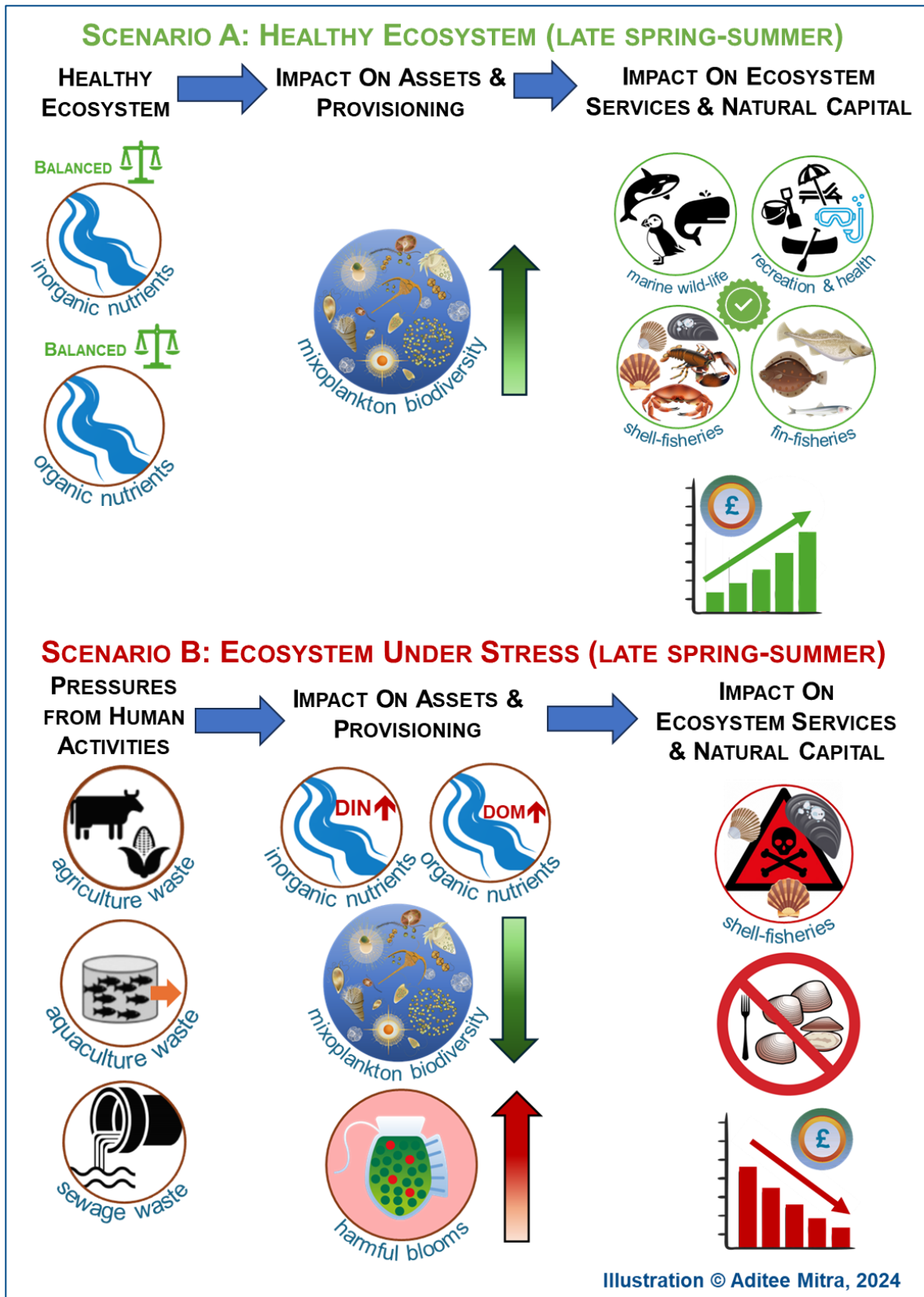
Figure 21. Contrasting scenarios of mixoplankton as positive versus negative assets. Scenario A depicts a healthy ecosystem where the dissolved inorganic and organic nutrients (DIN and DOM, respectively) support biodiversity in mixoplankton communities which in turn support the different ecosystem services. **Scenario B** is an example showing how pressures from human activities adversely impact nutrient status in the marine and coastal waters. Increasing nutrient concentrations leading to harmful bloom events and decline in plankton diversity. These have deleterious impact on ecosystem services and natural capital. The HAB event example provided here is of *Dinophysis* which are responsible for 22% of HAB events in the UK; DSP production by *Dinophysis* leads to closures of shellfisheries.

6.4 Policy recommendations

Application of the <u>precautionary principle</u> now places an onus on regulators to take account of the known existence of mixoplankton and of their diverse nutritional mechanisms and ecological interactions. The following recommendations provide a roadmap for this.

i) <u>Policies on monitoring and management of UK coastal and marine waters</u>: all monitoring and management tools are based on the old paradigm where plankton are identified as either primary producers or consumers. Mixoplankton are producers <u>and</u> consumers. This synergistic action of primary production <u>plus</u> prey consumption has different implications for food webs under different environmental conditions. It is recommended that monitoring and management methodologies and policies are revised such that the multi-trophic impacts of mixoplankton are recognised.

ii) <u>Policies on management of organic eutrophication</u>: wastes from sewage, agriculture and aquaculture include dissolved inorganic as well as organic nutrients. Currently, marine and coastal monitoring, management and policies focus on dissolved inorganic nutrients. It is recommended that concentration, types and sources of organic nutrients (sewage, farm, aquaculture) should be considered in policies relating to the management of eutrophication of marine and coastal waters. Such organic eutrophication can support the growth of mixoplankton, including HAB species.

iii) <u>Policies on management of removal of phosphorus and nitrogen from sewage</u>: the ratios of elements in inorganic nutrients – nitrogen, phosphorus and silica (N:P:Si) – have important implications. Heavily skewed ratios of N:P:Si select for deleterious mixoplankton growth and toxicity. It is recommended that removal of phosphorus from sewage and effluent treatment needs to be balanced by the removal of nitrogen.

iv) <u>Policies on building marine infrastructures</u>: the building of infrastructures affects turbulence (altering water column stability), flushing rates and salinity of the marine environment. These processes affect plankton community ecology and are potential promoters of deleterious mixoplankton blooms. It is recommended that planning policies should conduct assessments on how such constructions could risk marine ecosystem health through potentially supporting mixoplankton blooms.

The likelihood of these factors, alone or in combination, need to be considered in the context of climate change, with extremes in weather events.

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Appendix

- **Table A1**: List of Constitutive Mixoplankton (CM) species that occur in UK coastal and marine waters. Records obtained from the Ocean Biogeographic Information System (OBIS) database and Mixoplankton Database (MDB). Mixoplankton species listed according to indicative size (smallest to largest). Under the old 'phytoplankton-zooplankton' paradigm these species were all categorised as 'phytoplankton'.

- **Table A2**: List of Generalist Non-Constitutive Mixoplankton (GNCM) species that occur in UK coastal and marine waters. Records obtained from the Ocean Biogeographic Information System (OBIS) database and Mixoplankton Database (MDB). Mixoplankton species listed according to indicative size (smallest to largest). Under the old 'phytoplankton-zooplankton' paradigm these species were all categorised as 'protist-zooplankton' or 'microzooplankton' or 'protozooplankton'.

- **Table A3.** List of plastidic Specialist Non-Constitutive Mixoplankton (pSNCM) species that occur in UK coastal and marine waters. Records obtained from the Ocean Biogeographic Information System (OBIS) database and Mixoplankton Database (MDB). Mixoplankton species listed according to indicative size (smallest to largest). Under the old 'phytoplankton-zooplankton' paradigm these species were all categorised as 'zooplankton'.

- **Table A4.** List of endosymbiotic Specialist Non-Constitutive Mixoplankton (eSNCM) species that occur in UK coastal and marine waters. Records obtained from the Ocean Biogeographic Information System (OBIS) database and Mixoplankton Database (MDB). Mixoplankton species listed according to indicative size (smallest to largest). Under the old 'phytoplankton-zooplankton' paradigm these species were all categorised as 'zooplankton'.

- **Table A5.** List of mixoplankton harmful algal bloom (HAB) species that occur in UK coastal and marine waters. Records obtained from the Mixoplankton Database (MDB) with reference to the Ocean Biogeographic Information System (OBIS) database and the IOC-UNESCO Taxonomic Reference List of Harmful Micro Algae database. Mixoplankton species listed in alphabetical order. Under the old 'phytoplankton-zooplankton' paradigm, all CM species are categorised as 'phytoplankton' and all pSNCM and eSNCM species categorised as 'zooplankton'.

- **Table A6.** Records of Harmful Algal Bloom (HAB) events in UK coastal and marine waters. Records obtained from the Harmful Algal Event Database (HAEDAT). Events are listed according to date order. FT, functional type; HTL, higher trophic level; CM, constitutive mixoplankton; P, phytoplankton; pSNCM, plastidic non-specialist constitutive mixoplankton; NR, not recorded. CM* & pSNCM*, events where only the genus name of the causative organism is recorded. P**, events where neither the genus nor species names of the causative organism is recorded, plankton FT is attributed to P based on toxin records.

Table A1: List of CM species in UK waters

Table A1. List of Constitutive Mixoplankton (CM) species that occur in UK coastal and marine waters. Records obtained from the Ocean Biogeographic Information System (OBIS) database and Mixoplankton Database (MDB). Mixoplankton species listed according to indicative size (smallest to largest). Under the old 'phytoplankton-zooplankton' paradigm these species were all categorised as 'phytoplankton'. See also **Boxes 1** and **3**.

MFT, mixoplankton functional type. NR, not recorded. Size class: femto, <2 µm; pico, 0.2–2 µm; nano, 2–20 µm; micro, 20–200 µm; meso, 200 µm–20 mm. femto sized prey includes virus; pico sized prey includes bacteria and cyanobacterial prey. 'OBIS records' indicate the total number of observations per species in the OBIS database.

MFT	Mixoplankton indicative size	Mixoplankton Species Name	Mixoplankton Taxonomic Group	OBIS records	Prey indicative size	Prey taxonomic group
CM	pico	*Micromonas pusilla*	Chlorophyta	1940	pico	Bacteria
CM	nano	*Heterocapsa rotundata*	Dinoflagellata	21246	nano	Diatomeae, Bacteria
CM	nano	*Prorocentrum cordatum*	Dinoflagellata	7340	nano	Dinoflagellata, Cryptophyceae, Ochrophyta, Haptophyta, Cyanobacteria
CM	nano	*Dinobryon faculiferum*	Ochrophyta	5373	pico	Bacteria
CM	nano	*Emiliania huxleyi*	Haptophyta	3671	femto-pico	Bacteria
CM	nano	*Dinobryon balticum*	Ochrophyta	3339	pico	NR
CM	nano	*Phaeocystis globosa*	Haptophyta	1953	pico	Bacteria
CM	nano	*Karlodinium veneficum*	Dinoflagellata	983	pico-nano	Cryptophyceae, Bacteria
CM	nano	*Calcidiscus leptoporus*	Haptophyta	505	femto-pico	Bacteria
CM	nano	*Cymbomonas tetramitiformis*	Chlorophyta	491	pico	Bacteria
CM	nano	*Prymnesium polylepis*	Haptophyta	272	femto-pico	Bacteria
CM	nano	*Amphidinium carterae*	Dinoflagellata	180	nano	Diatomeae
CM	nano	*Nephroselmis pyriformis*	Chlorophyta	40	pico	Bacteria

CM	nano	*Haptolina hirta*	Haptophyta	34	femto-pico	Ochrophyta, Chlorophyta, Diatomeae
CM	nano	*Prymnesium parvum*	Haptophyta	19	femto-meso	Dinoflagellata, Chlorophyta
CM	nano	*Haptolina ericina*	Haptophyta	6	femto-pico	Chlorophyta
CM	nano	*Nephroselmis rotunda*	Chlorophyta	3	pico	Bacteria
CM	nano	*Chrysochromulina leadbeateri*	Haptophyta	2	femto-nano	NR
CM	nano-micro	*Chrysochromulina pringsheimii*	Haptophyta	24	femto-nano	NR
CM	nano-micro	*Chrysochromulina camella*	Haptophyta	1	femto-nano	Chlorophyta
CM	micro	*Tripos fusus*	Dinoflagellata	80719	NR	NR
CM	micro	*Tripos furca*	Dinoflagellata	56318	nano-micro	NR
CM	micro	*Tripos muelleri*	Dinoflagellata	53352	NR	NR
CM	micro	*Prorocentrum micans*	Dinoflagellata	23010	nano	Haptophyta, Ochrophyta, Cryptophyceae, Dinoflagellata, Cyanobacteria, Diatomeae
CM	micro	*Tripos longipes*	Dinoflagellata	19779	NR	NR
CM	micro	*Karenia mikimotoi*	Dinoflagellata	6680	pico-nano	Haptophyta
CM	micro	*Lingulodinium polyedra*	Dinoflagellata	4606	nano-micro	Diatomeae, Cyanobacteria
CM	micro	*Scrippsiella acuminata*	Dinoflagellata	3535	nano	Haptophyta, Cryptophyceae, Ochrophyta, Dinoflagellata, Cyanobacteria
CM	micro	*Gonyaulax spinifera*	Dinoflagellata	3451	pico	Cyanobacteria
CM	micro	*Protoceratium reticulatum*	Dinoflagellata	3002	NR	NR
CM	micro	*Akashiwo sanguinea*	Dinoflagellata	2676	nano-micro	Ciliophora, Haptophyta, Cryptophyceae, Dinoflagellata
CM	micro	*Alexandrium pseudogonyaulax*	Dinoflagellata	2054	nano-micro	Cryptophyceae

CM	micro	*Alexandrium minutum*	Dinoflagellata	1799	pico	Cyanobacteria
CM	micro	*Lepidodinium chlorophorum*	Dinoflagellata	1765	NR	NR
CM	micro	*Fibrocapsa japonica*	Ochrophyta	1147	pico	Cyanobacteria
CM	micro	*Alexandrium ostenfeldii*	Dinoflagellata	830	nano-micro	Ciliophora
CM	micro	*Prorocentrum lima*	Dinoflagellata	828	NR	NR
CM	micro	*Dissodinium pseudolunula*	Dinoflagellata	679	parasite	Copepoda
CM	micro	*Gymnodinium aureolum*	Dinoflagellata	638	pico-nano	Bacteria, Cyanobacteria
CM	micro	*Fragilidium subglobosum*	Dinoflagellata	572	micro	Dinoflagellata
CM	micro	*Mantoniella squamata*	Chlorophyta	501	pico	not recorded
CM	micro	*Gonyaulax polygramma*	Dinoflagellata	479	pico-nano	Cryptophyceae, Ochrophyta, Haptophyta, Dinoflagellata, Diatomeae
CM	micro	*Torodinium teredo*	Dinoflagellata	331	NR	NR
CM	micro	*Tripos teres*	Dinoflagellata	312	NR	NR
CM	micro	*Tripos declinatus*	Dinoflagellata	256	NR	NR
CM	micro	*Gymnodinium catenatum*	Dinoflagellata	141	pico-nano	Cyanobacteria, Dinoflagellata, Cryptophyceae, *Heterosigma akashiwo*, *Isochrysis galbana*, *Rhodomonas salina*, *Prorocentrum minimum*
CM	micro	*Levanderina fissa*	Dinoflagellata	50	micro	Ciliophora
CM	micro	*Thecadinium kofoidii*	Dinoflagellata	44	nano	Cryptophyceae, Dinoflagellata
CM	micro	*Gonyaulax alaskensis*	Dinoflagellata	35	NR	Ciliophora
CM	micro	*Alexandrium andersonii*	Dinoflagellata	34	nano	Chlorophyta, Cryptophyceae, Dinoflagellata
CM	micro	*Karenia brevis*	Dinoflagellata	31	pico	Cyanobacteria
CM	micro	*Gymnodinium impudicum*	Dinoflagellata	26	nano	Cyanobacteria, Cryptophyceae, Dinoflagellata

CM	micro	*Gonyaulax diegensis*	Dinoflagellata	21	NR	NR
CM	micro	*Gonyaulax diegensis*	Dinoflagellata	21	NR	NR
CM	micro	*Karenia papilionacea*	Dinoflagellata	18	NR	NR
CM	micro	*Margalefidinium polykrikoides*	Dinoflagellata	18	pico-nano	Cryptophyceae, Ochrophyta, Dinoflagellata
CM	micro	*Barrufeta resplendens*	Dinoflagellata	14	nano-micro	Dinoflagellata
CM	micro	*Biecheleria baltica*	Dinoflagellata	10	NR	NR
CM	micro	*Tripos lunula*	Dinoflagellata	5	NR	Dinoflagellata
CM	micro	*Alexandrium catenella*	Dinoflagellata	2	pico-nano	Cyanobacteria, Diatomeae
CM	micro	*Polykrikos lebourae*	Dinoflagellata	1	micro	Cryptophyceae, Dinoflagellata
CM	micro	*Tripos arcticus*	Dinoflagellata	1	NR	NR
CM	micro	*Spatulodinium pseudonoctiluca*	Dinoflagellata	221	nano-micro	NR
CM	micro	*Herdmania litoralis*	Dinoflagellata	20	femto-pico	Bacteria
CM	micro	*Amphidinium scissum*	Dinoflagellata	1	NR	NR
CM	micro	*Lepidodinium viride*	Dinoflagellata	1	NR	NR

Table A2: List of GNCM species in UK waters

Table A2. List of Generalist Non-Constitutive Mixoplankton (GNCM) species that occur in UK coastal and marine waters. Records obtained from the Ocean Biogeographic Information System (OBIS) database and Mixoplankton Database (MDB). Mixoplankton species listed according to indicative size (smallest to largest). Under the old 'phytoplankton-zooplankton' paradigm these species were all categorised as 'protist-zooplankton' or 'microzooplankton' or 'protozooplankton'. See also **Boxes 1** and **3**.

MFT, mixoplankton functional type. NR, not recorded. Size class: pico, 0.2–2 µm; nano, 2–20 µm; micro, 20–200 µm. "OBIS records" indicate the total number of observations per species in the OBIS database.

MFT	Mixoplankton indicative size	Mixoplankton Species Name	Mixoplankton Taxonomic Group	OBIS records	Prey indicative size	Prey taxonomic group
GNCM	nano	*Strombidium vestitum*	Ciliophora	58	nano	Chlorophyta
GNCM	nano	*Strombidium dalum*	Ciliophora	3	pico	NR
GNCM	micro	*Laboea strobila*	Ciliophora	2322	nano	Haptophyta, Chlorophyta, Dinoflagellata
GNCM	micro	*Strombidium conicum*	Ciliophora	582	nano	Haptophyta, Chlorophyta
GNCM	micro	*Strombidium reticulatum*	Ciliophora	19	nano	Chlorophyta
GNCM	micro	*Tontonia ovalis*	Ciliophora	7	nano	Ciliophora
GNCM	micro	*Pseudotontonia cornuta*	Ciliophora	6	nano	NR
GNCM	micro	*Pseudotontonia simplicidens*	Ciliophora	5	nano	Haptophyta, Stramenopiles
GNCM	micro	*Strombidium capitatum*	Ciliophora	3	nano	Haptophyta, Cryptophyceae
GNCM	micro	*Omegastrombidium elegans*	Ciliophora	1	nano	NR
GNCM	micro	*Paratontonia gracillima*	Ciliophora	1	pico-nano	Cyanobacteria
GNCM	micro	*Paratontonia poopsia*	Ciliophora	1	nano	NR
GNCM	micro	*Strombidium acutum*	Ciliophora	1	nano	Chlorophyta
GNCM	micro	*Strombidium chlorophilum*	Ciliophora	1	nano	Haptophyta, Chlorophyta
GNCM	micro	*Strombidium stylifer*	Ciliophora	1	nano	Chlorophyta

Table A3: List of pSNCM species in UK waters

Table A3. List of plastidic Specialist Non-Constitutive Mixoplankton (pSNCM) species that occur in UK coastal and marine waters. Records obtained from the Ocean Biogeographic Information System (OBIS) database and Mixoplankton Database (MDB). Mixoplankton species listed according to indicative size (smallest to largest). Under the old 'phytoplankton-zooplankton' paradigm these species were all categorised as 'zooplankton'. See also **Boxes 1** and **3**.

MFT, mixoplankton functional type. NR, not recorded. Size class: nano, 2–20 µm; micro, 20–200 µm; meso, 200 µm–20 mm. 'OBIS records' indicate the total number of observations per species in the OBIS database.

MFT	Mixoplankton indicative size	Mixoplankton Species Name	Mixoplankton Taxonomic Group	OBIS records	Prey indicative size	Prey taxonomic group
pSNCM	nano-micro	*Mesodinium rubrum*	Ciliophora	42031	nano	Cryptophyceae
pSNCM	micro	*Dinophysis acuminata*	Dinoflagellata	23474	micro	Ciliophora
pSNCM	micro	*Dinophysis norvegica*	Dinoflagellata	11815	micro	Ciliophora
pSNCM	micro	*Dinophysis acuta*	Dinoflagellata	6941	micro	Ciliophora
pSNCM	micro	*Amylax triacantha*	Dinoflagellata	1766	micro	Ciliophora
pSNCM	micro	*Dinophysis sacculus*	Dinoflagellata	1297	micro	Ciliophora
pSNCM	micro	*Dinophysis caudata*	Dinoflagellata	904	micro	Ciliophora
pSNCM	micro	*Kryptoperidinium foliaceum*	Dinoflagellata	548	NR	NR
pSNCM	micro	*Dinophysis tripos*	Dinoflagellata	465	micro	Ciliophora
pSNCM	micro	*Dinophysis fortii*	Dinoflagellata	188	micro	Ciliophora
pSNCM	micro	*Nusuttodinium latum*	Dinoflagellata	6	nano	NR
pSNCM	micro	*Amylax triacantha var. buxus*	Dinoflagellata	5	micro	Ciliophora
pSNCM	micro	*Phalacroma rapa*	Dinoflagellata	13	NR	NR
pSNCM	micro-meso	*Elphidium*	Foraminifera	184	micro-meso	Bacteria, Copepoda, Sarsostraca (*Artemia*)

Table A4: List of eSNCM species in UK waters

Table A4. List of endosymbiotic Specialist Non-Constitutive Mixoplankton (eSNCM) species that occur in UK coastal and marine waters. Records obtained from the Ocean Biogeographic Information System (OBIS) database and Mixoplankton Database (MDB). Mixoplankton species listed according to indicative size (smallest to largest). Under the old 'phytoplankton-zooplankton' paradigm these species were all categorised as 'zooplankton'. See also **Boxes 1** and **3**.

MFT, mixoplankton functional type. NR, not recorded. Size class: pico, 0.2–2 µm; nano, 2–20 µm; micro, 20–200 µm; meso, 200 µm–20 mm. 'OBIS records' indicate the total number of observations per species in the OBIS database.

MFT	Mixoplankton indicative size	Mixoplankton Species Name	Mixoplankton Taxonomic Group	OBIS records	Prey indicative size	Prey taxonomic group
eSNCM	micro	*Hexacontium pachydermum*	Radiolaria	31	pico-micro	Diatomeae
eSNCM	micro	*Phorticium pylonium*	Radiolaria	20	nano-micro	Diatomeae
eSNCM	micro	*Acrosphaera murrayana*	Radiolaria	12	pico-micro	Diatomeae, Ciliophora, Copepoda, Mollusca, Ostracoda
eSNCM	micro	*Actinomma boreale*	Radiolaria	7	pico-micro	Diatomeae, Ciliophora, Copepoda, Mollusca, Ostracoda
eSNCM	micro	*Strombidium purpureum*	Ciliophora	1	nano	Bacteria
eSNCM	micro	*Triposolenia truncata*	Dinoflagellata	1	NR	NR
eSNCM	micro	*Ornithocercus magnificus*	Dinoflagellata	15	NR	NR
eSNCM	micro	*Kofoidinium splendens*	Dinoflagellata	9	NR	NR
eSNCM	micro	*Podolampas bipes*	Dinoflagellata	3	NR	NR
eSNCM	micro-meso	*Globigerina bulloides*	Foraminifera	11492	micro-meso	Bacteria, Copepoda, Sarsostraca
eSNCM	micro-meso	*Globigerinita glutinata*	Foraminifera	8300	micro-meso	NR

eSNCM	micro-meso	*Globigerinoides ruber*	Foraminifera	5694	micro-meso	Ciliophora, Copepoda
eSNCM	micro-meso	*Globigerinella siphonifera*	Foraminifera	4797	micro-meso	Bacteria, Copepoda, Sarsostraca
eSNCM	micro-meso	*Orbulina universa*	Foraminifera	4500	micro-meso	Ciliophora, Copepoda
eSNCM	micro-meso	*Globigerina falconensis*	Foraminifera	4152	micro-meso	Bacteria, Copepoda, Sarsostraca
eSNCM	micro-meso	*Globorotalia hirsuta*	Foraminifera	2841	micro-meso	Bacteria, Copepoda, Sarsostraca
eSNCM	micro-meso	*Neogloboquadrina dutertrei*	Foraminifera	1947	micro-meso	Diatomeae
eSNCM	micro-meso	*Trilobatus sacculifer*	Foraminifera	1728	micro-meso	Bacteria, Copepoda, Sarsostraca
eSNCM	micro-meso	*Turborotalita humilis*	Foraminifera	865	micro-meso	Bacteria, Copepoda, Sarsostraca
eSNCM	micro-meso	*Globorotalia menardii*	Foraminifera	634	micro-meso	Diatomeae, Ochrophyta (Chrysophyceae)
eSNCM	micro-meso	*Globigerinoides conglobatus*	Foraminifera	557	micro-meso	Bacteria, Copepoda, Sarsostraca
eSNCM	micro-meso	*Pulleniatina obliquiloculata*	Foraminifera	503	micro-meso	Ochrophyta (Chrysophyceae)
eSNCM	micro-meso	*Acanthometron pellucida*	Radiolaria	184	pico-micro	Ciliophora
eSNCM	micro-meso	*Globorotalia tumida*	Foraminifera	108	micro-meso	NR
eSNCM	micro-meso	*Globigerinoides elongatus*	Foraminifera	70	micro-meso	Bacteria, Copepoda, Sarsostraca
eSNCM	micro-meso	*Globoquadrina conglomerata*	Foraminifera	46	micro-meso	Bacteria, Copepoda, Sarsostraca
eSNCM	micro-meso	*Acanthostaurus nordgaardi*	Radiolaria	12	pico-micro	Diatomeae, Ciliophora, Copepoda, Mollusca, Ostracoda
eSNCM	micro-meso	*Androcyclas gamphonycha*	Radiolaria	2	pico-micro	Diatomeae

eSNCM	micro-meso	*Amphilonche elongata*	Radiolaria	1	nano-meso	Diatomeae, Ciliophora, Copepoda, Mollusca, Ostracoda
eSNCM	meso	*Noctiluca scintillans*	Dinoflagellata	6379	nano-micro	Diatomeae, Dinoflagellata
eSNCM	meso	*Collozoum inerme*	Radiolaria	68	nano-meso	Diatomeae, Ciliophora, Copepoda, Mollusca, Ostracoda
eSNCM	meso	*Candeina nitida*	Foraminifera	59	micro-meso	Bacteria, Copepoda, Sarsostraca

Table A5: List of HAB mixoplankton species in UK waters

Table A5. List of mixoplankton harmful algal bloom (HAB) species that occur in UK coastal and marine waters. Records obtained from the Mixoplankton Database (MDB) with reference to the Ocean Biogeographic Information System (OBIS) database and the IOC-UNESCO Taxonomic Reference List of Harmful Micro Algae database. Mixoplankton species listed in alphabetical order. Under the old 'phytoplankton-zooplankton' paradigm, all CM species are categorised as 'phytoplankton' and all pSNCM and eSNCM species categorised as 'zooplankton'. See also **Boxes 1** and **3**.

MFT, mixoplankton functional type. NR, not recorded. Size class: femto, < 0.2 µm; pico, 0.2–2 µm; nano, 2–20 µm; micro, 20–200 µm; meso, 200 µm–20 mm. femto sized prey includes virus; pico sized prey includes bacteria and cyanobacteria. 'OBIS records' indicate the total number of observations per species in the OBIS database.

MFT	Mixoplankton indicative size	Species Name	Mixoplankton Taxonomic Group	OBIS records	Prey indicative size	Prey taxonomic group
CM	micro	*Akashiwo sanguinea*	Dinoflagellata	2676	nano-micro	Ciliophora, Haptophyta, Cryptophyceae, Dinoflagellata
CM	micro	*Alexandrium andersonii*	Dinoflagellata	34	nano	Chlorophyta, Cryptophyceae, Dinoflagellata
CM	micro	*Alexandrium catenella*	Dinoflagellata	2	pico-nano	Cyanobacteria, Diatomeae
CM	micro	*Alexandrium minutum*	Dinoflagellata	1799	pico	Cyanobacteria
CM	micro	*Alexandrium ostenfeldii*	Dinoflagellata	830	nano-micro	Ciliophora
CM	micro	*Alexandrium pseudogonyaulax*	Dinoflagellata	2054	nano-micro	Cryptophyceae
CM	nano	*Amphidinium carterae*	Dinoflagellata	180	nano	Diatomeae
CM	nano	*Chrysochromulina leadbeateri*	Haptophyta	2	femto-nano	not recorded
pSNCM	micro	*Dinophysis acuminata*	Dinoflagellata	23474	micro	Ciliophora
pSNCM	micro	*Dinophysis acuta*	Dinoflagellata	6941	micro	Ciliophora
pSNCM	micro	*Dinophysis caudata*	Dinoflagellata	904	micro	Ciliophora
pSNCM	micro	*Dinophysis fortii*	Dinoflagellata	188	micro	Ciliophora

pSNCM	micro	*Dinophysis norvegica*	Dinoflagellata	11815	micro	Ciliophora
pSNCM	micro	*Dinophysis sacculus*	Dinoflagellata	1297	micro	Ciliophora
pSNCM	micro	*Dinophysis tripos*	Dinoflagellata	465	micro	Ciliophora
CM	micro	*Fibrocapsa japonica*	Ochrophyta	1147	pico	Cyanobacteria
CM	micro	*Gonyaulax spinifera*	Dinoflagellata	3451	pico	Cyanobacteria
CM	micro	*Gymnodinium catenatum*	Dinoflagellata	141	pico-nano	Cyanobacteria, Dinoflagellata, Cryptophyceae, *Heterosigma akashiwo*, *Isochrysis galbana*, *Rhodomonas salina*, *Prorocentrum minimum*
CM	micro	*Karenia brevis*	Dinoflagellata	31	pico	Cyanobacteria
CM	micro	*Karenia mikimotoi*	Dinoflagellata	6680	pico-nano	Haptophyta
CM	micro	*Karenia papilionacea*	Dinoflagellata	18	NR	NR
CM	nano	*Karlodinium veneficum*	Dinoflagellata	983	pico-nano	Cryptophyceae, Bacteria
CM	micro	*Lingulodinium polyedra*	Dinoflagellata	4606	nano-micro	Diatomeae, Cyanobacteria
CM	micro	*Margalefidinium polykrikoides*	Dinoflagellata	18	pico-nano	Cryptophyceae, Ochrophyta, Dinoflagellata
eSNCM	meso	*Noctiluca scintillans*	Dinoflagellata	6379	nano-micro	Diatomeae, Dinoflagellata
CM	nano	*Phaeocystis globosa*	Haptophyta	1953	pico	Bacteria
CM	nano	*Prorocentrum cordatum*	Dinoflagellata	7340	nano	Dinoflagellata, Cryptophyceae, Ochrophyta, Haptophyta, Cyanobacteria
CM	micro	*Prorocentrum lima*	Dinoflagellata	828	NR	NR
CM	micro	*Protoceratium reticulatum*	Dinoflagellata	3002	NR	NR
CM	nano	*Prymnesium parvum*	Haptophyta	19	femto-meso	Dinoflagellata, Chlorophyta
CM	nano	*Prymnesium polylepis*	Haptophyta	272	femto-pico	Bacteria

Table A6: Records from HAEDAT of HAB events in UK waters

Table A6. Records of Harmful Algal Bloom events in UK coastal and marine waters. Records obtained from the Harmful Algal Event Database (HAEDAT). Events are listed according to date order. FT, functional type; HTL, higher trophic level; CM, constitutive mixoplankton; P, phytoplankton; pSNCM, plastidic non-specialist constitutive mixoplankton; NR, not recorded. CM* & pSNCM*, events where only the genus name of the causative organism is recorded. P**, events where neither the genus nor species names of the causative organism is recorded, plankton FT is attributed to P based on toxin records.

HAEDAT REF	event Year	UK nation	causative organism	toxin	plankton FT	HTL affected	HTL FT
GB-60-001	1960	England	*Microcystis spp.*		P		NR
GB-79-001	1979	Scotland			NR		NR
GB-80-001	1980	Scotland	*Gyrodinium aureolum*		CM		NR
GB-82-001	1982	Scotland			NR		NR
GB-82-002	1982	Scotland			NR		NR
GB-88-001	1988	NR	*Heterosigma akashiwo (Hada) Hada ex Hara et Chihara 1987*		CM		NR
GB-88-002	1988	NR	*Cladopyxis brachiolata Stein 1883*		P		NR
GB-88-003	1988	NR	*Heterosigma akashiwo (Hada) Hada ex Hara et Chihara 1987*		CM		NR
GB-88-004	1988	Scotland	*Chaetoceros wighamii*		P		NR
GB-88-005	1988	Scotland	*Chaetoceros debilis Cleve 1894*		P		NR
GB-90-002	1990	England & Wales	*Gymnodinium spp.*		CM*		NR
GB-90-003	1990	England & Wales	*Alexandrium tamarense*		CM		NR
GB-90-001	1990	England			NR		NR

GB-90-004	1990	Scotland		Saxitoxins	NR	*Mytilus edulis*	mussel
GB-90-005	1990	Scotland		Saxitoxins	NR	*Mytilus edulis*	mussel
GB-91-001	1991	Scotland	*Alexandrium sp.*		CM*		NR
GB-91-002	1991	Scotland	*Alexandrium sp.*	Saxitoxins	CM*	Mussels	mussel
GB-91-003	1991	Scotland	*Alexandrium sp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-91-004	1991	Scotland	*Heterosigma akashiwo*		CM		NR
GB-91-005	1991	England?	*Microcystis spp.*		P		NR
GB-92-003	1992	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-92-004	1992	Scotland	*Alexandrium spp.*		CM*		NR
GB-92-006	1992	England		Saxitoxins	NR	*Mytilus edulis*	mussel
GB-92-005	1992	England & Wales	*Phaeocystis pouchetii*		CM		NR
GB-92-001	1992	Scotland	*Dinophysis norvegica*		pSNCM		NR
GB-92-007	1992	Scotland		Okadaic Acid	NR	*Mytilus edulis*	mussel
GB-92-008	1992	England		Okadaic Acid	NR	*Mytilus edulis*	mussel
GB-92-009	1992	Scotland		Okadaic Acid	NR	*Mytilus edulis*	mussel
GB-92-010	1992	England			NR		NR
GB-93-002	1993	England & Wales	*Alexandrium tamarense*		CM		NR
GB-93-001	1993	Scotland		Saxitoxins	NR	*Mytilus edulis*	mussel
GB-93-003	1993	Scotland		Saxitoxins	NR	*Mytilus edulis*	mussel
GB-93-004	1993	England		Okadaic Acid	NR	*Mytilus edulis*	mussel
GB-93-005	1993	Scotland			NR		NR
GB-94-007	1994	England & Wales	*Gyrodinium aureolum*		CM		NR
GB-94-002	1994	England			NR	mussels & scallops	mussels & scallops
GB-94-004	1994	Scotland	*Alexandrium sp.*		CM*		NR
GB-94-005	1994	Scotland	*Alexandrium sp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-94-008	1994	Northern Ireland	*Dinophysis acuminata*		pSNCM		NR
GB-94-006	1994	Scotland	*Alexandrium sp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel

GB-94-001	1994	Scotland			NR		NR
GB-94-003	1994	Scotland	*Alexandrium spp.*		CM*	mussels, scallops, oysters	mussels, scallops, oysters
GB-94-009	1994	England			NR		NR
GB-94-010	1994	Scotland			NR		NR
GB-95-001	1995	England & Wales	*Alexandrium tamarense*		CM		NR
GB-95-002	1995	England		Saxitoxins	NR	*Mytilus edulis*	mussel
GB-95-003	1995	Scotland		Saxitoxins	NR	*Pecten maximus*	scallop
GB-95-004	1995	Scotland		Saxitoxins	NR	*Mytilus edulis*	mussel
GB-95-005	1995	Wales		Saxitoxins	NR	*Mytilus edulis*	mussel
GB-95-006	1995	Scotland			NR		NR
GB-95-007	1995	Scotland			NR		NR
GB-95-008	1995	England			NR		NR
GB-96-001	1996	Scotland			NR		NR
GB-96-002	1996	Scotland	*Dinophysis spp.*	Saxitoxins	pSNCM*	Mussel (May 13th)	mussel
GB-96-003	1996	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	Mussels	mussel
GB-96-004	1996	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-96-005	1996	Scotland	*Alexandrium sp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-96-006	1996	Scotland	*Gymnodinium sp.*		CM*		NR
GB-96-012	1996	Northern Ireland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-96-013	1996	England	*Alexandrium tamarense (Lebour) Balech 1985*		CM		NR
GB-96-011	1996	England & Wales	*Alexandrium tamarense*	Saxitoxins	CM	*Mytilus edulis*	mussel
GB-96-015	1996	Scotland			NR		NR
GB-96-016	1996	Scotland			NR		NR
GB-96-017	1996	England			NR		NR
GB-97-001	1997	Scotland	*Alexandrium tamarense*	Saxitoxins	CM	*Mytilus edulis*	mussel
GB-97-002	1997	England		Saxitoxins	NR	*Mytilus edulis*	mussel

GB-97-003	1997	Scotland			NR		NR
GB-97-004	1997	Scotland			NR		NR
GB-97-005	1997	Scotland			NR		NR
GB-97-006	1997	Scotland			NR		NR
GB-97-007	1997	Scotland	*Microcystis spp.*		P		NR
GB-98-014	1998	England & Wales	*Alexandrium tamarense*		CM		NR
GB-98-015	1998	England & Wales			NR		NR
GB-98-001	1998	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-98-003	1998	Scotland	*Pseudo-nitzschia spp.*	Domoic Acid	P	*Pecten maximus*	scallop
GB-98-006	1998	Scotland	*Pseudo-nitzschia spp.*	Domoic Acid	P	*Pecten maximus*	scallop
GB-98-007	1998	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-98-011	1998	Scotland	*Dinophysis spp.*		pSNCM*		NR
GB-98-012	1998	NR	*Pseudo-nitzschia spp.*		P		NR
GB-98-008	1998	Scotland	*Dinophysis spp.*		pSNCM*		NR
GB-98-004	1998	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	Blue mussels	mussel
GB-98-017	1998	Scotland		Saxitoxins	NR	*Mytilus edulis*	mussel
GB-98-013	1998	Scotland	*Prorocentrum lima*		CM		NR
GB-98-018	1998	Scotland			NR		NR
GB-98-019	1998	Wales			NR		NR
GB-99-012	1999	Scotland			NR	shellfish	shellfish
GB-99-013	1999	Scotland	*Dinophysis spp.*		pSNCM*		NR
GB-99-015	1999	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-99-014	1999	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-99-017	1999	Scotland		Saxitoxins	NR	*Mytilus edulis*	mussel
GB-99-018	1999	Scotland	*Gyrodinium aureolum*		CM		NR
GB-99-005	1999	Scotland	*Pseudo-nitzschia spp.*	Domoic Acid	P	*Mytilus edulis*	mussel
GB-99-019	1999	Wales			NR		NR
GB-99-020	1999	England			NR		NR

GB-00-001	2000	Scotland	Pseudo-nitzschia spp.	Domoic Acid	P	Pecten maximus	scallop
GB-00-002	2000	Scotland	Dinophysis acuta		pSNCM		NR
GB-00-014	2000	Scotland	Alexandrium spp.	Saxitoxins	CM*	Chlamys opercularis	scallop
GB-00-015	2000	Scotland		Saxitoxins	NR	Mytilus edulis	mussel
GB-00-016	2000	Scotland		Saxitoxins	NR	Chlamys opercularis	scallop
GB-00-024	2000	England		Saxitoxins	NR	Mytilus edulis	mussel
GB-00-025	2000	Wales		Saxitoxins	NR	Mytilus edulis	mussel
GB-00-026	2000	England			NR		NR
GB-00-027	2000	NR			NR		NR
GB-00-028	2000	England		Domoic Acid	P**	Mytilus edulis	mussel
GB-01-008	2001	Scotland	Pseudo-nitzschia spp.	Domoic Acid	P	Pecten maximus (gonad)	scallop
GB-01-001	2001	Scotland	Alexandrium spp.		CM*		NR
GB-01-003	2001	Scotland			NR		NR
GB-01-004	2001	Scotland	Alexandrium spp.		CM*		NR
GB-01-005	2001	Scotland			NR		NR
GB-01-006	2001	Scotland			NR		NR
GB-01-007	2001	Scotland	Alexandrium spp.		CM*		NR
GB-01-014	2001	Scotland	Dinophysis acuta Ehrenberg 1841		pSNCM		NR
GB-01-015	2001	Scotland	Dinophysis sp.		pSNCM*		NR
GB-01-016	2001	Scotland			NR		NR
GB-01-017	2001	Scotland	Dinophysis acuta		pSNCM		NR
GB-01-018	2001	Scotland	Dinophysis acuta		pSNCM		NR
GB-01-019	2001	Scotland			NR		NR
GB-01-020	2001	Scotland			NR		NR
GB-01-022	2001	England			NR		NR
GB-01-023	2001	Scotland	Microcystis spp.		P		NR
GB-01-024	2001	Scotland	Microcystis spp.		P		NR

GB-01-025	2001	Scotland	*Microcystis spp.*		P		NR
GB-01-026	2001	NR	*Heterocapsa triquetra*		CM		NR
GB-01-027	2001	Scotland	*Karenia mikimotoi*		CM		NR
GB-02-001	2002	Scotland			NR		NR
GB-02-002	2002	Scotland	*Dinophysis acuminata*		pSNCM		NR
GB-02-003	2002	Scotland	*Dinophysis acuta*		pSNCM		NR
GB-02-004	2002	Scotland	*Dinophysis acuta*		pSNCM		NR
GB-02-005	2002	Scotland			NR		NR
GB-02-006	2002	Scotland			NR		NR
GB-02-007	2002	Scotland	*Dinophysis acuminata*		pSNCM		NR
GB-02-008	2002	Scotland	*Dinophysis acuta*		pSNCM		NR
GB-02-009	2002	Scotland			NR	Shellfish	shellfish
GB-02-010	2002	Scotland	*Dinophysis acuta*		pSNCM		NR
GB-02-011	2002	Scotland			NR		NR
GB-02-012	2002	England		Saxitoxins	NR	*Mytilus edulis*	mussel
GB-02-013	2002	England		Saxitoxins	NR	cockles	cockles
GB-02-014	2002	England			NR		NR
GB-02-015	2002	England			NR		NR
GB-02-016	2002	Scotland		Domoic Acid	P**	*Pecten maximus*	scallop
GB-03-008	2003	Isle of Man			P**		NR
GB-03-001	2003	Scotland	*Alexandrium spp.*		CM*		NR
GB-03-002	2003	Scotland	*Alexandrium spp.*		CM*		NR
GB-03-003	2003	England			NR		NR
GB-03-004	2003	England			NR		NR
GB-03-006	2003	Scotland	*Dinophysis spp.*		pSNCM*		NR
GB-03-007	2003	Scotland	*Karenia mikimotoi*		CM		NR
GB-03-005	2003	Scotland	*Pseudo-nitzschia spp.*	Domoic Acid	P	*Pecten maximus*	scallop
GB-04-001	2004	England			NR		NR
GB-04-002	2004	Scotland	*Pseudo-nitzschia spp.*	Domoic Acid	P	*Pecten maximus*	scallop
GB-04-003	2004	Scotland	*Dinophysis spp.*		pSNCM*		NR

GB-05-001	2005	Northern Ireland			NR		NR
GB-05-002	2005	England		Saxitoxins	NR	*Mytilus edulis*	mussel
GB-05-006	2005	Scotland			NR		NR
GB-05-003	2005	Scotland	*Phaeocystis spp.*		CM*		NR
GB-05-004	2005	Scotland			NR		NR
GB-05-005	2005	Scotland			NR		NR
GB-05-007	2005	Scotland		Saxitoxins	NR	*Pecten maximus*	scallop
GB-06-001	2006	Scotland	*Alexandrium spp.*		CM*	Shellfish	shellfish
GB-06-002	2006	Scotland	*Alexandrium spp.*		CM*		NR
GB-06-003	2006	Scotland			NR		NR
GB-06-004	2006	Northern Ireland			NR		NR
GB-06-005	2006	Northern Ireland			NR		NR
GB-06-006	2006	England		Saxitoxins	NR	*Mytilus edulis*	mussel
GB-06-007	2006	England			NR		oyster
GB-06-008	2006	Scotland	*Dinophysis spp.*		pSNCM*		NR
GB-06-009	2006	Scotland	*Dinophysis spp.*		pSNCM*		NR
GB-06-010	2006	Scotland	*Karenia mikimotoi*		CM		NR
GB-06-011	2006	England	*Dinophysis spp.*		pSNCM*		NR
GB-07-001	2007	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-07-003	2007	Scotland		Saxitoxins	NR	*Mytilus edulis*	mussel
GB-07-004	2007	Scotland			NR		NR
GB-07-005	2007	Northern Ireland			NR		NR
GB-07-006	2007	Northern Ireland			NR		NR
GB-07-007	2007	Northern Ireland			NR		NR
GB-09-007	2007	Northern Ireland			NR		NR
GB-07-008	2007	England			NR		NR
GB-07-009	2007	England			NR		NR
GB-07-010	2007	Wales			NR		NR
GB-07-011	2007	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-07-012	2007	Scotland	*Dinophysis spp.*		pSNCM*		NR

GB-07-013	2007	Scotland	*Dinophysis spp.*		pSNCM*		NR
GB-07-014	2007	Scotland	*Dinophysis spp.*		pSNCM*		NR
GB-07-015	2007	Scotland	*Dinophysis spp.*		pSNCM*		NR
GB-07-016	2007	Scotland	*Pseudo-nitzschia spp.*		P		NR
GB-07-017	2007	Scotland	*Dinophysis spp.*		pSNCM*		NR
GB-07-002	2008	Scotland			NR	shellfish	shellfish
GB-08-001	2008	England		Saxitoxins	NR	*Mytilus edulis*	mussel
GB-08-002	2008	England & Wales			NR		NR
GB-08-003	2008	England			NR		NR
GB-08-004	2008	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Spisula solida*	clam
GB-08-005	2008	Scotland	*Dinophysis spp.*		pSNCM*		NR
GB-08-006	2008	Scotland	*Dinophysis spp.*		pSNCM*		NR
GB-08-007	2008	Scotland	*Dinophysis spp.*		pSNCM*		NR
GB-08-008	2008	Scotland	*Dinophysis spp.*		pSNCM*		NR
GB-08-009	2008	Scotland	*Dinophysis spp.*		pSNCM*		NR
GB-08-010	2008	Scotland	*Dinophysis spp.*		pSNCM*		NR
GB-08-011	2008	Scotland			NR		NR
GB-08-012	2008	Scotland			NR		NR
GB-08-013	2008	Scotland	*Pseudo-nitzschia spp.*	Domoic Acid	P	*Mytilus edulis*	mussel
GB-08-014	2008	Scotland			NR		NR
GB-08-015	2008	England		Saxitoxins	NR	*Mytilus edulis*	mussel
GB-09-001	2009	Scotland	*Dinophysis spp.*		pSNCM*		NR
GB-09-002	2009	Scotland			NR		NR
GB-09-003	2009	Scotland			NR	shellfish	shellfish
GB-09-004	2009	Scotland	*Alexandrium sp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-09-005	2009	Scotland			NR		NR
GB-09-006	2009	Scotland	*Alexandrium spp.*		CM*		NR
GB-09-008	2009	Northern Ireland			NR		NR
GB-09-009	2009	Northern Ireland			NR		NR

GB-09-010	2009	England		Saxitoxins	NR	*Mytilus edulis*	mussel
GB-09-011	2009	England & Wales			NR		NR
GB-09-012	2009	England			NR		NR
GB-09-013	2009	England			NR		NR
GB-09-014	2009	England	*Karenia mikimotoi*		CM		NR
GB-10-001	2010	England	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-10-002	2010	England			NR		NR
GB-10-003	2010	England			NR		NR
GB-10-004	2010	England			NR		NR
GB-10-005	2010	England			NR		NR
GB-10-006	2010	Northern Ireland	*Dinophysis acuminata*		pSNCM		NR
GB-10-007	2010	Northern Ireland			NR		NR
GB-10-008	2010	Scotland	*Dinophysis spp.*		pSNCM*		NR
GB-10-009	2010	Scotland	*Dinophysis spp.*		pSNCM*		NR
GB-10-010	2010	Scotland	*Dinophysis spp.*		pSNCM*		NR
GB-11-001	2011	Scotland			NR		NR
GB-11-002	2011	Scotland		Azaspiracids	NR	*Mytilus edulis*	mussel
GB-11-003	2011	Scotland		Yessotoxins	NR	*Mytilus edulis*	mussel
GB-11-005	2011	Scotland		Saxitoxins	NR	*Mytilus edulis*	mussel
GB-11-006	2011	Scotland	*Dinophysis spp.*		pSNCM*		NR
GB-11-007	2011	Scotland			NR		NR
GB-11-008	2011	Scotland	*Dinophysis spp.*		pSNCM*		NR
GB-11-009	2011	Scotland	*Dinophysis spp.*	Okadaic Acid	pSNCM*	*Mytilus edulis*	mussel
GB-11-010	2011	Scotland			NR		NR
GB-11-011	2011	Scotland	*Dinophysis spp.*	Okadaic Acid	pSNCM*	*Mytilus edulis*	mussel
GB-11-015	2011	Northern Ireland	*Dinophysis acuminata*		pSNCM		NR
GB-11-016	2011	England			NR		NR
GB-11-017	2011	Wales		Saxitoxins	NR	*Mytilus edulis*	mussel
GB-11-018	2011	England		Okadaic Acid	NR	*Mytilus edulis*	mussel

GB-11-019	2011	Wales		Okadaic Acid	NR	*Mytilus edulis*	mussel
GB-11-020	2011	England			NR		NR
GB-11-004	2011	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-11-021	2011	Scotland		Saxitoxins	NR	*Mytilus edulis*	mussel
GB-12-001	2012	Scotland		Domoic Acid	P**	*Mytilus edulis*	mussel
GB-12-002	2012	Scotland		Saxitoxins	NR	*Mytilus edulis*	mussel
GB-12-003	2012	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-12-004	2012	Scotland		Saxitoxins	NR	*Mytilus edulis*	mussel
GB-12-005	2012	Scotland		Saxitoxins	NR	*Mytilus edulis*	mussel
GB-12-006	2012	Scotland		Saxitoxins	NR	*Mytilus edulis*	mussel
GB-12-007	2012	Scotland	*Dinophysis spp.*	Okadaic Acid	pSNCM*	*Mytilus edulis*	mussel
GB-12-008	2012	Scotland	*Dinophysis spp.*	Okadaic Acid	pSNCM*	*Ensis arcuatis (razor clam)*	clam
GB-12-009	2012	Scotland	*Dinophysis spp.*	Okadaic Acid	pSNCM*	*Mytilus edulis*	mussel
GB-12-010	2012	Scotland		Okadaic Acid	NR	*Mytilus edulis*	mussel
GB-12-011	2012	Scotland	*Dinophysis spp.*	Okadaic Acid	pSNCM*	*Mytilus edulis*	mussel
GB-12-012	2012	Scotland	*Dinophysis spp.*	Okadaic Acid	pSNCM*	*Myilus edulis*	mussel
GB-12-013	2012	Scotland	*Dinophysis spp.*	Okadaic Acid	pSNCM*	*Mytilus edulis*	mussel
GB-12-014	2012	Scotland		Okadaic Acid	NR	*Mytilus edulis*	mussel
GB-12-015	2012	Scotland	*Protoceratium spp.*	Yessotoxins	CM*	*Mytilus edulis*	mussel
GB-12-016	2012	Scotland		Yessotoxins	NR	*Mytilus edulis*	mussel
GB-12-017	2012	Scotland		Azaspiracids	NR	*Mytilus edulis*	mussel
GB-12-018	2012	Scotland		Azaspiracids	NR	*Spisula solida*	clam
GB-12-019	2012	Scotland			NR		NR
GB-13-001	2013	England	*Dinophysis sp.*	Okadaic Acid	pSNCM*	*Mytilus edulis*	mussel
GB-13-002	2013	England		Okadaic Acid	NR	*Crassostrea gigas*	oyster
GB-13-004	2013	England	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-13-005	2013	England	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-13-003	2013	England		Saxitoxins	NR	*Crassostrea gigas*	oyster
GB-13-006	2013	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel

GB-13-007	2013	Scotland		Saxitoxins	NR	*Spisula solida*	clam
GB-13-008	2013	Scotland		Saxitoxins	NR	*Mytilus edulis*	mussel
GB-13-009	2013	Scotland		Domoic Acid	P**	*Cerastoderma edule*	cockles
GB-13-010	2013	Scotland	*Dinophysis acuminata*	Okadaic Acid	pSNCM	*Mytilus edulis*	mussel
GB-13-011	2013	Scotland		Azaspiracids	NR	*Crassostrea edulis*	oyster
GB-14-002	2014	England	*Dinophysis spp.*	Okadaic Acid	pSNCM*	*Mytilus edulis*	mussel
GB-14-003	2014	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-14-004	2014	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-14-005	2014	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-14-006	2014	Scotland	*Alexandrium sp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-14-007	2014	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-14-009	2014	Scotland	*Dinophysis acuminata*	Okadaic Acid	pSNCM	*Mytilus edulis*	mussel
GB-14-010	2014	Scotland	*Dinophysis spp.*	Okadaic Acid	pSNCM*	*Mytilus edulis*	mussel
GB-14-011	2014	Scotland	*Dinophysis spp.*	Okadaic Acid	pSNCM*	*Ensis*	clam
GB-14-012	2014	Isle of Man			P**		NR
GB-14-001	2014	Scotland	*Pseudo-nitzschia spp.*	Domoic Acid	P	*Mytilus edulis*	mussel
GB-14-008	2014	Scotland	*Alexandrium sp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-15-002	2015	England		Okadaic Acid	NR	*Mytilus edulis*	mussel
GB-15-003	2015	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-15-004	2015	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-15-005	2015	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-15-006	2015	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-15-007	2015	Scotland	*Dinophysis spp.*	Okadaic Acid	pSNCM*	*Mytilus Edulis*	mussel
GB-15-008	2015	Scotland	*Dinophysis spp.*	Okadaic Acid	pSNCM*	*Mytilus edulis*	mussel
GB-15-009	2015	Northern Ireland	*Pseudo-nitzschia spp.*	Domoic Acid	P	*Mytilus edulis*	mussel
GB-15-010	2015	England		Azaspiracids	NR	*Mytilus edulis*	mussel
GB-16-005	2016	Scotland	*Pseudo-nitzschia spp.*	Domoic Acid	P	*Ensis*	clam
GB-16-011	2016	Scotland		Domoic Acid	P**	*Mytilus edulis*	mussel
GB-16-001	2016	Wales	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel

GB-16-002	2016	England	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-16-003	2016	England	*Dinophysis spp.*	Okadaic Acid	pSNCM*	*Mytilus edulis*	mussel
GB-16-004	2016	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-16-006	2016	Scotland		Domoic Acid	P**	*Ensis*	clam
GB-16-007	2016	Scotland	*Dinophysis spp.*	Okadaic Acid	pSNCM*	*Mytilus edulis*	mussel
GB-16-008	2016	Scotland	*Dinophysis spp.*	Okadaic Acid	pSNCM*	*Mytilus edulis*	mussel
GB-16-010	2016	Scotland	*Karenia mikimotoi (Mikaye et Kominami ex Oda) Hansen et Moestrup 2000*		CM	cockles	cockles
GB-16-009	2016	Scotland		Okadaic Acid	NR	*Mytilus edulis*	mussel
GB-17-001	2017	Scotland		Saxitoxins	NR	*Mytilus edulis*	mussel
GB-17-002	2017	Scotland		Saxitoxins	NR	*Crassostrea gigas*	oyster
GB-17-003	2017	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-17-004	2017	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-17-005	2017	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-17-006	2017	Scotland	*Dinophysis spp.*	Okadaic Acid	pSNCM*	*Crassostrea gigas*	oyster
GB-17-007	2017	Scotland	*Dinophysis spp.*	Okadaic Acid	pSNCM*	*Mytilus edulis*	mussel
GB-17-008	2017	Scotland	*Dinophysis acuminata*	Okadaic Acid	pSNCM	*Mytilus edulis*	mussel
GB-17-009	2017	Scotland	*Dinophysis spp.*	Okadaic Acid	pSNCM*	*Mytilus edulis*	mussel
GB-17-010	2017	England	*Alexandrium spp.*	Saxitoxins	CM*	*Crassotera gigas*	oyster
GB-17-011	2017	England		Okadaic Acid	NR	*Mytilus edulis*	mussel
GB-17-012	2017	England		Saxitoxins	NR	*Asterias rubens*	starfish
GB-18-001	2018	Scotland	*Dinophysis spp.*	Okadaic Acid	pSNCM*	*Crassostrea gigas*	oyster
GB-18-002	2018	Scotland	*Dinophysis spp.*	Okadaic Acid	pSNCM*	*Mytilus edulis*	mussel
GB-18-003	2018	Scotland	*Dinophysis spp.*	Okadaic Acid	pSNCM*	*Spisula solidissima*	clam
GB-18-004	2018	England	*Dinophysis spp.*	Okadaic Acid	pSNCM*	*Mytilus edulis*	mussel
GB-18-005	2018	Northern Ireland	*Dinophysis spp.*	Okadaic Acid	pSNCM*	*Mytilus edulis*	mussel
GB-18-006	2018	Scotland		Saxitoxins	NR	*Mytilus edulis*	mussel
GB-18-007	2018	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel

GB-18-008	2018	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-18-009	2018	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-18-010	2018	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-19-005	2019	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-19-005	2019	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-19-003	2019	Scotland	*Dinophysis spp.*	Okadaic Acid	pSNCM*	*Mytilus edulis*	mussel
GB-19-004	2019	Scotland	*Dinophysis spp.*	Okadaic Acid	pSNCM*	*Mytilus edulis*	mussel
GB-19-002	2019	England	*Dinophysis spp.*	Okadaic Acid	pSNCM*	*Mytilus edulis*	mussel
GB-19-001	2019	England	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-19-006	2019	Northern Ireland	*Dinophysis parvula (Schütt) Balech*	Okadaic Acid	pSNCM	*Mytilus edulis*	mussel
GB-20-001	2020	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-20-002	2020	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-20-003	2020	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-20-004	2020	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-20-005	2020	Scotland	*Alisphaera spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-20-006	2020	Scotland		Domoic Acid	P**	*Mytilus edulis*	mussel
GB-20-007	2020	Scotland	*Dinophysis spp.*	Okadaic Acid	pSNCM*	*Mytilus edulis*	mussel
GB-20-008	2020	Scotland	*Dinophysis spp.*	Okadaic Acid	pSNCM*	*Spisula solidissima*	clam
GB-20-009	2020	Scotland	*Dinophysis spp.*	Okadaic Acid	pSNCM*	*Mytilus edulis*	mussel
GB-21-001	2021	Scotland		Saxitoxins	NR	*Mytilus edulis*	mussel
GB-21-002	2021	Scotland		Saxitoxins	NR	*Crassostrea gigas*	oyster
GB-21-003	2021	Scotland		Saxitoxins	NR	*Ensis sp.*	clam
GB-21-004	2021	Scotland		Okadaic Acid	NR	*Mytilus edulis*	mussel
GB-21-005	2021	Scotland		Okadaic Acid	NR	*Spisula solidissima*	clam
GB-21-006	2021	Scotland		Okadaic Acid	NR	*Spisula solidissima*	clam
GB-21-007	2021	Scotland		Okadaic Acid	NR	*Spisula solidissima*	clam
GB-21-008	2021	England	*Dinophysis spp.*	Okadaic Acid	pSNCM*	*Mytilus edulis*	mussel
GB-22-001	2022	Scotland	*Pseudo-nitzschia spp.*	Domoic Acid	P	*Mytilus edulis*	mussel
GB-22-002	2022	Scotland	*Pseudo-nitzschia spp.*	Domoic Acid	P	*Mytilus edulis*	mussel

GB-22-003	2022	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-22-004	2022	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-22-005	2022	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-22-006	2022	Scotland	*Alexandrium spp.*	Saxitoxins	CM*	*Mytilus edulis*	mussel
GB-22-007	2022	Scotland	*Dinophysis acuminata*	Okadaic Acid	pSNCM	*Mytilus edulis*	mussel
GB-22-008	2022	Scotland	*Dinophysis acuminata*	Okadaic Acid	pSNCM	*Mytilus edulis*	mussel
GB-22-009	2022	Scotland	*Dinophysis spp.*	Okadaic Acid	pSNCM*	*Mytilus edulis*	mussel