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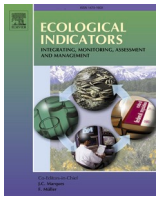

Review

Undesirable river biofilms: The composition, environmental drivers, and occurrence of sewage fungus

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ABSTRACT

Sewage fungus is a classic bioindicator of organic pollution in streams and rivers. However, it has received limited scientific interest in recent decades, despite persistent occurrence in lotic ecosystems. The aim of this review is to provide an up-to-date assessment of sewage fungus, its composition and structure, and the environmental factors that influence its growth to support future research and mitigation interventions. We advocate for the term "undesirable river biofilm" (URB) to more accurately characterise the composition, location, and environmental consequences of sewage fungus. These filamentous or gelatinous growths found on the banks and beds of flowing watercourses are composed predominantly of bacteria, not fungi. Based on modern genomic analyses, we now know that URBs are composed of a diversity of microbial taxa, including those that have long been associated with sewage fungus (e.g. *Sphaerotilus*, *Beggiatoa*, and *Zoogloea*) and newer associated taxa (e.g. *Rhodoferax* and *Thiothrix)*. While organic pollution is generally considered the main trigger, this review highlights the importance of other environmental factors, such as water velocity, river substrate, pollutant composition and loading, and shading, in the occurrence and persistence of URBs. To illustrate the widespread and continued presence of URBs in rivers, environmental surveillance data for England's rivers were analysed. Between 2000 and 2020, environment officers documented 6,025 occurrences of URBs as part of a wider water quality incident reporting programme. Thus, URBs persist even in countries with stringent water quality standards and comprehensive wastewater infrastructure, suggesting they may continue to be a significant issue globally, despite limited public or scientific focus. We argue that in addition to tackling point discharge of organic pollutants, greater emphasis should be placed on understanding the impact of intermittent and diffuse pollution and altered environmental conditions on river ecosystems. To safeguard river ecosystems, a holistic approach is needed that considers pollution in combination with wider river functioning (e.g. river hydrology, geomorphology, biogeochemical processing, and riparian zones) and climate change. Future areas for study into the URB phenomenon are suggested, including more comprehensive monitoring of URBs specifically and river biofilm health generally.

1. Introduction

Sewage fungus is a classic bioindicator of poor water quality for rivers (Harrison and Heukelekian, 1958; Quinn and Mcfarlane, 1985). The term describes gelatinous and filamentous growths found on the riverbed and other submerged substrates in flowing waters, particularly those impacted by organic pollution (i.e. saprobic conditions). Research conducted in the mid-20th century provided essential information on the composition and environmental drivers of sewage fungus growth. It identified key taxa that comprise the 'fungus' (Curtis, 1969), named the cause of occurrence as insufficiently treated wastewater effluent (Curtis and Harrington, 1971), and described its impacts on river ecosystems (Gray, 1987). As wastewater treatment improved from the 1960 s and 1970 s in many countries, sewage fungus growths decreased in occurrence and the topic disappeared slowly from the scientific literature (Whelan et al., 2022). However, sewage fungus has not disappeared from rivers; it continues to grow even in countries with advanced wastewater treatment systems, suggesting that organic pollution continues to be a problem.

The presence of sewage fungus is widely accepted to be a robust and easily identifiable indicator of a highly degraded riverine ecosystem (Fig. 1). The high biological demand of organic pollution drives a

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positive feedback loop that enables the establishment and proliferation of sewage fungus, at the expense of much other aquatic life (Curtis et al., 1971; Gray, 1985; Hickey, 1988a, 1988b). Sewage fungus uptakes dissolved organic carbon readily and tolerates the low dissolved oxygen (DO) concentrations caused by high microbial respiration rates. Through its rapid growth, it also creates an aquatic environment that is less conducive to other organisms. Sewage fungus uptakes DO at a rate 10–20 times higher than aquatic macrophytes of equivalent mass (Gray, 1987) resulting in a high biomass. Thus, sewage fungus can drive and maintain DO concentrations below minimal thresholds for other aerobic organisms. Even when organic pollution events end, the ecological and biochemical impacts of sewage fungus can persist for long periods (Hartwell et al., 1995; Pillard, 1995; Pillard and DuFresne, 1999). Studies have shown that sewage fungus outcompetes native periphyton (Gray, 1985), degrades benthic habitat quality (impacting, for example, invertebrates (Hirsch, 1958; Hynes, 1960; Lemly, 1998) and fish spawning (Curtis, 1969; Curtis et al., 1971; Smith and Kramer, 1963)), affects riverbank filtration and hyporheic exchange flows (Ahmed and Marhaba, 2017; Hiscock and Grischek, 2002), outcompetes native periphytons (Gray, 1985), and concentrates heavy metals and other toxic compounds (Flemming et al., 2016; Flemming and Wingender, 2010; Geng et al., 2019; Wuertz et al., 2000).

The scientific understanding of sewage fungus, though, has not kept pace with other disciplines. The rapid advancements seen in the biological, biochemical and biophysical characterization of microbial communities and biofilms have only very recently been applied to sewage fungus. These studies suggest that sewage fungus is considerably more diverse, complex and responsive that previously thought. For example, metagenomic approaches have been used to quantify their microbial community composition, finding a greater diversity than in past studies using culture-based methods and documenting important shifts in the biofilm community composition when it becomes a sewage fungus (Exton et al., 2023; Nott et al., 2020). Other studies have shown how the community composition of the river biofilm changes in response to water quality and environmental factors, including wastewater effluent (Freixa et al., 2020; Sabater-Liesa et al., 2019); pesticides (Mahler et al., 2020); pharmaceuticals (Hagberg et al., 2021); diffuse urban pollution, (Gorbarán et al., 2022), and river flow velocity (Huang et al., 2022; Waite et al., 2019). An improved understanding of sewage fungus and the factors influencing its establishment and growth is essential to the development of more sensitive and responsive indicators of water quality, e.g. intermittent or diffuse pollution that is difficult to detect with current monitoring (Exton et al., 2023; Murray-Bligh and Griffiths, 2022) or holistic river health (Waite et al., 2019).

The aim of this review is to provide an up-to-date reassessment of sewage fungus as a bioindicator of organic pollution in rivers and streams, which has not been the subject of a review since the 1980′s (Gray, 1987; Quinn and Mcfarlane, 1985). To achieve this aim, a new name is proposed first, as sewage fungus is neither a fungus nor solely associated with sewage. Secondly, the existing knowledge on sewage fungus is consolidated and extended by leveraging recent advancements in biofilm research and genomics. Thirdly, the water quality and environmental factors that contribute to or limit sewage fungus growth are summarized, highlighting the importance of an integrated river processes perspective on the bioindicator. Lastly, new data on the occurrence of sewage fungus in rivers at national scale are presented to illustrate the continued persistence of sewage fungus linked to numerous human activities. A better understanding of its composition and the environmental factors affecting its growth are essential to the development of improved indicators of organic pollution to drive continued improved in river ecosystem health. Furthermore, visible indicators of water quality degradation, such as the presence of sewage fungus, influence public perceptions and their interactions with rivers, often deterring recreational activities alongside other ecosystem services (Curtis and Harrington, 1971; Gray, 1985).

2. Methods

This multidisciplinary review involved (i) the collation and critical review of research on sewage fungus and related topics (e.g. stream biofilms) and (ii) the visualization of sewage fungus occurrence data provided by a national regulator to provide new evidence of its continued presence in rivers at national scale.

2.1. Literature search and filtering

Literature was identified using keyword searches in online databases that was expanded through a manual search of cited references in key papers, which was particularly important to find older articles. The initial literature search was conducted in Scopus with the search term “sewage fungus”, which identified 52 documents. Further literature was identified using Google Scholar as some of it pre-dates accurate Scopus discoverability. Most of the research on sewage fungus was conducted prior to 1990 so, to advance our understanding of URBs, additional literature on biofilms was incorporated to review URBs as a biofilm. The search was expanded to include the search terms “stream biofilm” and “river biofilm”, which identified 415 documents. These documents were filtered to exclude literature pertaining to organismal biology or medicine, yielding 301 papers. The search was not limited to any specific period, and research articles, books, technical papers, and review papers were included. Finally, highly cited papers on the “biofilm matrix”, limited to the years 2002 – 2022, were reviewed to provide insights into the biophysical structure of sewage fungus.

2.2. Sewage fungus occurrence at national scale

To illustrate the continued presence of sewage fungus in rivers, even in a country with strong wastewater treatment regulation, data on the recorded incidences of sewage fungus in England were analysed and visualised. Occurrence data were obtained from the Environment

Fig. 1. Sewage fungus (i.e., undesirable river biofilm (URB)) growth in the River Crane, London (UK) linked to the use of de-icers at an adjacent airport from (a) the entire river width (approximately 7.5 m channel width), to (b) a small section of the channel, to (c) a close-up of the sewage fungus (approximately 30 cm width).

Agency (EA, England) via a standard data request. Whilst sewage fungus is not formally monitored by the EA, environment officers log a record if it is present when they attend a pollution incident (Geatches et al., 2014). The EA provided records of all recorded incidents of sewage fungus for the years 2000 – 2020. For data protection reasons, no identifying information was included with the dataset (i.e. pollution source, river or administrative district); it listed solely the date and coarse spatial location (10 x 10 km grid). A heatmap was constructed by plotting coordinates and frequency of occurrences and subsequent analysis was performed in Microsoft Excel.

3. Sewage fungus is an undesirable river biofilm (URB)

The term "sewage fungus" has been used for almost a century, introduced to the scientific community in 1932 by R.W. Butcher. It was used to describe the filamentous growths present in polysaprobic and eutrophic rivers. Interestingly, even at its inception, Butcher suggested that the term was a misnomer (Butcher, 1932). This review suggests a renaming of sewage fungus to undesirable river biofilm (URB) on account of its ecosystem impacts, environmental context, and diverse microbial assembly.

There are two primary reasons that the term sewage fungus is misleading. First, its composition is not majorly fungal. Instead, it is a diverse polymicrobial biofilm, bound within a matrix of extracellular polymeric substances (EPS) (Gray, 1987, 1985). Second, while it has been predominantly observed near sources of untreated or inadequately treated sewage (Chonova et al., 2018; Curtis and Harrington, 1971; Forbes and Richardson, 1913; Hammond et al., 2021; Harrison and Heukelekian, 1958), its presence is not confined to these regions. Numerous other sources, such as industries and varied organic pollution outlets including airport de-icers, papermill effluents and agricultural runoff, have also been identified as contributors to its occurrence. Historically, several alternative names have surfaced, including heterotrophic biocoenosis (Wuhrmann, 1954); slime infestation (Harrison and Heukelekian, 1958); heterotrophic slime (Gray, 1985); and biological floc (Phaup, 1968). However, none of these names have been universally accepted or consistently used. Moreover, they do not accurately capture the unique composition and ecology of the sewage fungus phenomenon.

We introduce and advocate the term "undesirable river biofilm" (URB) to replace sewage fungus, as it more precisely captures the essence of these polymicrobial assemblies that proliferate in organically enriched conditions in rivers. Starting with the term "undesirable", biofilms can be broadly categorised as beneficial, desirable, undesirable, or disastrous (Glasenapp et al., 2019; Lewandowski and Beyenal, 2013). Even though URBs have detrimental effects on ecosystems, they serve an essential ecological role by utilising excess dissolved organic carbon. This function, while important, can have negative implications, making "undesirable" a fitting descriptor. The term "river" brings the habitat specificity of URBs into focus. They predominantly colonise flowing waters, as they are reliant on a certain water velocity thresholds to ensure the uptake of oxygen and nutrients (Harrison and Heukelekian, 1958). While "stream biofilms" is a term often used to encompass a general class of environmental biofilms (Battin et al., 2016), URBs are a subset that emerge due to elevated organic loading in fluvial systems. Lastly, the term "biofilm" addresses the inherent nature of URBs. At their core, URBs are biofilms – communities of microorganisms bound together in an EPS matrix and adhering to surfaces or interfaces, such as riverbeds or outfall aprons (Costerton et al., 1995). The incorporation of "biofilm" in the name underscores this fundamental characteristic. In summary, the new term (i) addresses the common misunderstanding about the dominant biological community, (ii) identifies the ecosystem in which they are found, (iii) describes their morphology, and (iv) highlights that while biofilms, including URBs, are nearly ubiquitous in nature (Curtis, 1969; Harrison and Heukelekian, 1958), they become problematic and ecologically damaging when growth is extensive.

In the following section, we summarise the existing knowledge about microbial composition of URBs and drawn on the current understanding of biofilm elucidating the structural and functional attributes of a typical biofilm with relevance to URBs, considering the latest advances in biofilm research to refine comprehension of URBs, and highlighting the competitive edge and adaptive strengths of URBs within complex river ecosystems.

4. The composition and structure of URBs

The physical manifestation of an URB can differ substantially based on its particular environment and microbial constitution. Factors such as water chemistry, hydrodynamics, and the nature of the riverbed substrate influence its appearance. The URB morphology (described as "cotton wool like" or as more of a "slime") and colour (e.g., grey, brown, or white with occasionally pink or yellow tints) is dynamic and shaped by its unique environment (Fig. 1). While the diverse visual characteristics of URBs have been well-documented (Geatches et al., 2014) there is limited research connecting these variations to specific environmental conditions, the nature of the organic pollution, or the makeup of the microbial community and the composition and structure of the EPS matrix.

4.1. *What microorganisms create URBs?*

Historical perceptions of URB microbial composition derive primarily from studies conducted between the 1950 s and 1980 s using culturing-based microbiological techniques (Bahr, 1953; Curtis, 1969; Mulder and van Veen, 1963, 1962; Phaup, 1968; Schade, 1940; Schade and Thimann, 1940; van Veen et al., 1978; Waitz and Lackey, 1958). These studies identified various genera, yet recent advancements in microbiological and genetic methodologies have highlighted additional complexity to the dynamics of the URB (Gray, 1985; Hall-Stoodley et al., 2004). Most notably, the genera *Sphaerotilus*, with particular emphasis on the species *Sphaerotilus natans*, emerged as pivotal components of URBs. For decades, *Sphaerotilus* spp. became the model organisms for experimental studies, and its presence in rivers was equated to an URB event (Curtis, 1969; Phaup, 1968).

Characteristically, *S. natans* exhibits a filamentous bacterial structure, comprising non-sporing, Gram-negative, rod-shaped cells with rounded ends (Gray, 1987). These cells are ensconced within a robust sheath (Harrison and Heukelekian, 1958; Lackey and Wattie, 1940), but upon extrication, exhibit motility courtesy of their subpolar flagella (Kämpfer and Spring, 2015). The metabolic adaptability of *Sphaerotilus* spp. enables them to utilise a diverse range of carbon sources– especially growth substrates of glucose and acetate (Curtis et al., 1971) – encompassing alcohols, organic acids, sugars (e.g., mono- and disaccharides), glycerol's, and amino acids (Gray, 1987, 1982; Harrison and Heukelekian, 1958; Phaup and Gannon, 1967) while assimilating ammonium and nitrates for nitrogen supply. Despite being obligate aerobes, these bacteria have the capacity to proliferate even in environments with minimal DO concentrations (below 0.1 mg/L) (Kämpfer and Spring, 2015), which is common in rivers with elevated organic loads. The recurrent detection of URBs in organically enriched river waters (Bryce-Cooper, 1983; Curtis and Harrington, 1971; Demoll and Liebmann, 1952; Dondero, 1961; Gray, 1987; Mulder, 1964) supports their role as indicators of pronounced organic pollution (Gray, 1985; John and Johnson, 1991). Other *Sphaerotilus* species, like *S. tenue* and *S. montanus,* have reported but as less documented components of URBs (Gray, 1985; John and Johnson, 1991).

The genera *Zoogloea* and *Beggiatoa* have also been reported as important taxa in URBs (Curtis and Curds, 1971; Geatches et al., 2014). *Zoogloea* are rod-shaped bacteria with a single polar flagellum forming gelatinous biofilm (Unz, 2015). Such biofilms typically inhabit freshwaters subjected to organic pollution, predominantly appearing in waters with relatively slow flows (Geatches et al., 2014), or on exposed surfaces within wastewater treatment plants (Hattingh, 1962; Unz,

2015). Metabolically, *Zoogloea* function via an aerobic metabolic pathway, but demonstrate substantial versatility with respect to organic carbon use (Unz, 2015; Unz and Farrah, 1976) but they favour organic acids, alcohols, and aromatic salts. For nitrogen assimilation, *Zoogloea* prefer organic nitrogen compounds and ammonia, but notably, they cannot utilise nitrate (Unz, 2015).

Beggiatoa is a genus of filamentous, sulphur metabolising bacteria which forms long filaments, ranging from 5 to 10 cm in length. Freshwater strains typically have cell diameters of less than 5.0 μm and re located at the interface of anoxic and oxic zones within sediments. that play a significant role in sulphur cycling. They utilise hydrogen sulphide (H_2S) as an energy source through the process of chemolithotrophic sulphur oxidation (Strohl, 2015). *Beggiatoa* is a facultative anaerobe. It uses oxygen as an electron acceptor in aerobic conditions and switches to nitrate in anaerobic environments. It thrives primarily at the interface between oxygen-rich and sulphide-rich zones, enabling it to utilise both metabolic pathways. *Beggiatoa* also displays greater selectivity and oxidises a smaller pool of carbon compounds than *Sphaerotilus* or *Zoogloea*, but it is reported to grow primarily on $C_{2\text{-}4}$ organic acids and sometimes amino acids serve as a less favoured substrate (Strohl, 2015). Both freshwater and marine strains of *Beggiatoa* possess the ability to fix N_2 and utilise various nitrogen sources, including nitrate, nitrite, ammonia, and specific amino acids (Strohl, 2015). Other bacterial species *Thiothrix II*, *Flavobacterium* spp., and *Flexibacter* spp., have also been linked with URBs (Geatches et al., 2014) but there is a dearth of data on their abundance, distribution, and contribution to URBs in rivers affected by organic pollution.

The microbial composition of URBs has more recently been tested using next-generation sequencing approaches in the context of airport de-icer contaminated runoff. Nott et al. (2020) utilised PhyloChip G3 DNA microarrays and conducted whole genome sequencing (Nott et al., 2020); whereas Exton et al. (2023) used amplicon sequencing of 16S rRNA (Exton et al., 2023). Both investigations highlighted the significance of *Sphaerotilus*, which constituted up to 14 % of the URB taxa based on relative abundance (Exton et al., 2023). Nott et al. (2020) further conducted metagenomic analyses, identifying a unique *S. montanus* isolate with intermittent detection of *Thiothrix* (Nott et al., 2020). Whereas Exton et al. (2023) identified members of the family Comamonadaceae (64 % of relative abundance) including *Zoogloea* as the most frequently detected taxa within URBs (Exton et al., 2023). Within this family, the genus *Rhodoferax* (32.8 % relative abundance) was identified in high abundance for the first time, suggesting a potential avenue for more focused genomic studies (Exton et al., 2023). Further genomic studies are needed to better elucidate how URB influences and is influenced by the natural streambed microbiome. *Rhodoferax* are typical freshwater bacteria (Okafor, 2011) coincident to environments enriched with elevated levels of degradable organic content (Imhoff, 2006). Some species within *Rhodoferax* are facultative photoheterotrophs (Imhoff, 2006), some facultative anaerobes (Finneran et al., 2003), and some fully anaerobic (Imhoff, 2006).

Other microorganisms are potentially significant components of URBs, yet current empirical evidence regarding their prevalence and functions is limited. For instance, fungi have been detected in URBs, including *Leptomitus lacteus* (Geatches et al., 2014; Riethmüller et al., 2006; Schade and Thimann, 1940). This fungus exhibits branching hyphae and has a distinct flocculant, plumose appearance. Discovered in freshwater environments, *L. lacteus* serves as an indicative species for waters containing organic refuse from sugar processing (Coker et al., 1937; Riethmüller et al., 2006; Schade, 1940). Notably, it can metabolize low molecular weight organic acids but not sugars, which are generally more bioavailable (Schade, 1940). *Leptomitus lacteus* can proliferate in acidic waters and grows well using high M_W organic nitrogen compounds (such as amino acids but not ammonium, nitrate or nitrate) (Harrison and Heukelekian, 1958; Schade, 1940). Other associated fungi include *Geotrichium candidum*, *Fusarium aquaeductuum*, and *Achyla* spp. (Geatches et al., 2014). Additionally, algae such as *Cladophora glomerata* (Geatches et al., 2014), are also present in URBs though their roles within this context remain less studied. In stream biofilms, algae can produce a significant audit of organic substrate for heterotrophic biofilm microorganisms (Besemer, 2015) and may also play a role in the structure and organization of the biofilm matrix (Battin et al., 2007). Algal strands provide a scaffolding for *S. natans'* growth (Quinn and Mcfarlane, 1985). Archaea and protozoa (e.g., *Carchesium polypinum* (Geatches et al., 2014)) make up a smaller fraction of the taxonomy of benthic stream biofilms (Battin et al., 2016; Besemer et al., 2012), viruses, although detected, are not believed to significantly affect URB growth (Battin et al., 2016). However, the knowledge gap as to how factors, such as source water microbiome, available nutrients (Olapade and Leff, 2005) and environmental conditions (Fierer et al., 2007; Hall-Stoodley et al., 2004), determine the specific and unique URB microbiome remains.

URBs are complex and diverse polymicrobial biofilms with varying composition. Whilst the taxonomic and functional focus of sewage fungus has been primarily skewed to bacteria, and to a lesser extent fungi and algae, there has been an underrepresentation of other microbial taxa that have been used as bioindicators of freshwater quality (Foissner, 2006; Parmar et al., 2016; Zaghloul et al., 2020). For example, protozoa are integral components of river periphyton and URBs and are well established indicators of poor water quality (Foissner, 1988; Kazmi et al., 2022; Nicolau et al., 2001).

Therefore, protozoa and other microbial communities – including fungi and algae – should be included in studies on the microbial composition and functions of URBs. Whilst 16S sequencing is a well-established and cost-effective method, it is restricted in scope, only analysing bacterial components of these complex, mixed microbial ecosystems. Furthermore, future URB research stands to gain from the considerable progress in the broader area of freshwater microbial indicators, as the majority of its investigations have yet to fully leverage these advancements (Parmar et al., 2016; Zaghloul et al., 2020). These advancements have been particularly significant in monitoring the impacts of faecal pollution, enabling more accurate assessment of water quality and health risks associated with microbial contaminants (Holcomb and Stewart, 2020; Korajkic et al., 2018; Some et al., 2021). This progress aligns with the One Health approach, emphasizing the interconnected health of humans, animals, and environments (Aslam et al., 2021; Botturi et al., 2021; One Health Commission, 2008; World Health Organisation, 2008), and is increasingly relevant given heightened standards for recreational and bathing water quality (World Health Organisation, 2021). An illustrative example of the importance of incorporating advancements in microbial bioindicator analysis into URB research is the capacity to determine the origin and age of sewage contamination in surface waters. This capability enhances risk assessment and management strategies for waters designated for recreational and bathing uses (Boehm et al., 2018). Analogously, wastewater-based epidemiology for tracking disease dynamics, which entails analysing sewage for bacterial or viral traces, enables public health officials to monitor the spread of diseases like COVID-19 across communities without depending on individual testing (Farkas et al., 2020; Hassard et al., 2022). This methodology has been implemented worldwide to offer early alerts for infection surges, track epidemiological trends, and detect new viral variants, thereby supporting precise public health interventions and policy-making (Wade et al., 2022). Such progress underscores a broader movement towards integrating bioindicators into standard environmental water quality assessments (Jackson et al., 2016; Sagova-Mareckova et al., 2021). These advancements in source and time indication of faecal contamination should be leveraged and applied to the study of URBs, with significant implications for both routine and specific event-based freshwater monitoring for organic pollutants. For example, a significant shift in periphyton composition towards URB-specific taxa was observed two weeks prior to a visible manifestation of URBs (Exton et al., 2023). This early detection of changes within the microbial community suggests that incorporating routine monitoring of

URB indicator taxa could effectively identify organic pollution, offering insights into its source and age. This enables the management of potential point or diffuse pollution sources to prevent further ecological damage. The highlighted deficiencies in existing URB research underscore the urgent need for future studies to enhance taxonomic and functional understanding, fully recognizing the complexity of microbial communities within URBs. Specifically, this points to the importance of more comprehensive research efforts that include protozoans and other non-bacterial taxa.

4.2. The biofilm matrix in the context of URBs

The microbiological community of an URB are found within a matrix, which accounts for the majority of mass in a biofilm (Flemming and Wingender, 2010). The matrix is primarily composed of EPS and provides the scaffold for the biofilm, facilitating substrate adhesion and providing a 3-D polymer network that acts as an external digestive system of extracellular enzymes (Flemming and Wingender, 2010) This matrix in the URB forms unique microhabitats with varied physical attributes (Caldwell et al., 1992; Costerton et al., 1994; de Beer et al., 1994; Korber et al., 1993; Lens et al., 1993), such as oxygen and substrate gradients. These variances directly influence the metabolic activities present within the biofilm (Billings et al., 2015; Caldwell et al., 1992; Costerton et al., 1994; de Beer et al., 1994; Korber et al., 1993; Lens et al., 1993; Persat et al., 2015; van Loosdrecht et al., 1990). Consequently, URBs exhibit efficient nutrient utilisation (Mulcahy et al., 2010; Pinchuk et al., 2008; Zrelli et al., 2013), enabling them to swiftly assemble and dominate a river's biosphere. Once established, these biofilms can often rely on their matrices and the contents of lysed cells for sustenance, even when external nutrient sources are depleted (Mulcahy et al., 2010; Pinchuk et al., 2008; Zrelli et al., 2013). The impact of sporadic organic pollution events, as well as the persistence of URBs during phases of variable organic input requires additional research.

Biofilms are highly responsive to environmental cues, providing their constituent organisms with significant competitive and survival benefits. Their adaptability is evident in several ways: rapid adaptation through phenotypic plasticity (Costerton et al., 1995); tolerance to desiccation and washout (Ophir and Gutnick, 1994; Whitton, 2012; Wright et al., 1989); and the capacity for active biofilm dispersal by partial matrix degradation (Petrova and Sauer, 2016). This behaviour suggests that the highly structured biofilm is not a terminal stage but continually evolves (Whitfield et al., 2015), adapting to maintain its ecological fitness advantage. Therefore, URBs must not be considered static entities. Their matrix architecture and microbial composition can adjust swiftly to changing environments, encompassing variations in available nutrients and other environmental or hydrological factors. The diverse and unique characteristics of biofilms bestow upon them competitive advantages, making the management of URBs in natural aquatic systems difficult.

4.3. Implications of advancements in biofilm analyses for UBRs

We have already outlined several pivotal methodological advancements in the study of biofilms, but it is crucial to re-emphasize their significance for future research on URBs. These advancements encompass techniques that have reshaped our understanding of biofilm composition and functions (Azeredo et al., 2017). Notably, these include next-generation sequencing (Romaní et al., 2014; Timoner et al., 2014; Zeglin, 2015) to better appreciate the microbial composition; growth kinetics measurements to study response rates to intermittent or variable loads of organic pollution (Azeredo et al., 2017). In addition, EPS measurements to explain matrix biochemical composition and function; mesocosm scale experiments to preserve the 3D structure of environmental biofilms. Finally, fluorescence *in situ* hybridisation techniques coupled with microscopy can add to ecological interaction models, composition and structure of the biofilm and thus better inform systems level models (Neu and Lawrence, 2014a, 2014b). Azeredo et al. (2017) (Azeredo et al., 2017) provided a comprehensive summary of these methods. To elucidate fundamental drivers of how URBs initiate growth, thrive, influence their surroundings, exploit available nutrients or pollutants, and to inform strategies to mitigate their ecological harm, it is imperative that these advancements are systematically applied in the context of URB research.

5. Factors affecting URB growth

The conditions that affect where URBs reside and their morphology include (i) water quality, especially the macro- and micro-nutrients required for microbial growth, and (ii) the various environmental factors that can affect the growth of URBs.

5.1. Water quality

URBs serve as natural indicators of organic pollution (Evans, 2018; Quinn and Mcfarlane, 1985), with their growth and microbial composition closely tied to the availability of organic carbon (Gray, 1985; Olapade and Leff, 2005). While past studies have demonstrated that URB organisms utilise many of the degradable organic compounds present in sewage – the intricacies of organic carbon bioavailability remain water type and taxa specific (Sun et al., 1997), especially when considered within the URB framework. The precise carbon sources that different URB taxa can access and their preferences when faced with a diverse and intricate substrate pool have not been investigated with sufficient depth (Behrends et al., 2009; Erbilgin et al., 2017). Though methodologies to investigate bioavailability and nutrient preference exist, they should be deployed in the study of URBs (Artz et al., 2006; Egli, 2010; Marius et al., 2010). Future work should aim to examine nutrient utilisation in URB taxa and common pollutants associated with their growth.

Nitrogen is a fundamental macronutrient for URB growth (Mulder and van Veen, 1962; Okrend and Dondero, 1964), and its various forms – like organic nitrogen, ammonium, nitrate, and nitrite – are all potential sources for growth. *Sphaerotilus* can metabolize ammonium and nitrate (Kämpfer and Spring, 2015) but the role of vital nutrients like nitrogen and phosphorus is less important compared to organic carbon (Hattingh, 1962). Available sources of nitrogen are generally found in adequate amounts for URB proliferation in natural freshwaters (Curtis and Harrington, 1971). Yet, the concentration of such nutrients can be influenced by outputs from specific industrial effluents discharging into receiving waters. Dairy factory effluents, for instance, have been identified as marginally nitrogen-deficient for optimal URB growth (Marshall, 1976), whereas effluents from sources such as slaughterhouses have been reported to generally contain sufficient nitrogen sources to prevent any limitation (Cooke et al., 1980; Cooper, 1981). Depending on the extent of the pollution, background water quality may offset nutrient deficiencies in effluents from becoming limiting.

Phosphorus, predominantly available as phosphate in freshwaters, is seldom a limiting factor for URB growth. Phosphate concentration as low as 0.05 mg/L was found to support substantial URB growths (Curtis et al., 1971). Some studies have reported that phosphate concentrations of < 0.04 mg/L may limit growth (Amberg and Cormack, 1959; Gaudy and Wolfe, 1961), while others noted that at 0.01 mg/L growth was not supported (Ormerod et al., 1966). However increasing phosphate concentrations above 0.05 mg/L did not enhance growth in another study (Curtis and Harrington, 1971). *S. natans* can reportedly be a dominant species over a wide range of phosphate concentrations of 0.01 – 1.5 mg/L, which encompasses the typical phosphate levels in most UK rivers (Eichenberger and Wuhrmann, 1966; Ormerod et al., 1966; Wuhrmann et al., 1966).

Specific micronutrients are important for the growth of URB taxa, for example, calcium is reportedly an important micronutrient requirement

for *S. natans* to develop its sheath, in turn allowing filamentous growth to become a biofilm (Gray, 1987). Vitamin B_{12} or methionine has also been reported as important for *S. natans* growth (Harrison and Heukelekian, 1958), though other studies suggest that vitamins are rarely at levels where they inhibit URB development (Curtis and Harrington, 1971; Mulder and van Veen, 1962). Certain chemical conditions in the river environment can also promote certain taxa, for example, high sulfide concentrations results in an URB that is dominated by *Beggiatoa* sp. (Bryce-Cooper, 1983; Liebmann, 1951).

5.2. Environmental drivers of growth

Whilst the availability of nutrients, especially dissolved carbon, is essential to microbial growth and composition, environmental determinants exert a significant influence on URB presence, growth rates, and the eventual composition and morphotype of the biofilm. Such factors include flow velocity, substrate types, exposure to sunlight, temperature, and pH.

Water velocity is an important factor influencing URB presence and decisively shaping the biofilm's structure and morphotype (Battin et al., 2007). URB growth requires a minimum velocity to replenish essential nutrients like DO (Curtis, 1969; Phaup, 1968; Quinn and Mcfarlane, 1985), and, thus, they are not found in stagnant waters (Gray, 1987). The minimum water velocity to support filamentous growth of *Sphaerotilus* spp. has been reported as 0.19 m/s. Velocities below this threshold can still support single-cell forms of the bacteria, but not URB growths (Amberg and Cormack, 1959). However, if water velocity is too fast, URBs are scoured away, as they get dislodged by high shear environments. This upper limit has been reported as 0.6 m/s (Gray, 1987; Harrison and Heukelekian, 1958; Quinn and Mcfarlane, 1985), though more research is needed to determine how species composition and morphology influence maximum velocity thresholds. Similarly additional research is needed on the effects of river flow and water quality variations on the temporal dynamics of URBs. For example, research has shown that benthic biofilm biomass reduces following flooding events (Power and Stewart, 1987), through erosion and burial of parts of the biofilm (Piqué et al., 2016). However, high river flows are often associated with elevated organic loads (i.e., flood events and heavy rainfall-induced stormwater overflows (Abrahams et al., 2013)) that could promote recovery and growth of URBs once flows decrease to normal levels. Additional is research is needed to determine the minimum and maximum flow velocities for the different species, their morphologies and the substrate.

URBs colonise submerged surfaces in rivers, including natural material (e.g. riverbed sediment, submerged trees and wood) and artificial structures and debris (e.g. plastics, rubble, and litter). Large sediment grain sizes (i.e. cobble and gravel) and large wood are inherently more stable than smaller sized ones, as they require higher river velocities to initiate transport (Knighton, 1998), making them ideal substrates for URB. Their entrainment velocity is higher than the upper threshold for URB growth. Similar, artificial structures (e.g. river banks reinforced with concrete) or riverbeds with poorly sorted sediment (e.g. fine sediment ingress into a coarse bed) also have very high thresholds for erosion and transport (Wharton et al., 2017). In many degraded rivers, multiple types of stable substrate are present along with elevated organic loads (e.g. artificial banks, artificial or poorly sorted riverbeds, anthropogenic debris), increasing the available habitat for URB colonisation and growth. Contrastingly, fine sediment (i.e. sand and silt) is a less stable substrate for URBs, as it more readily mobilised at lower velocities (Ahilan et al., 2019; Poleto et al., 2009; Taylor and Owens, 2009). However, the EPS within biofilm matrices considerably enhances the biostabilisation of riverbed sediments (Black et al., 2002; Piqué et al., 2016; Vignaga et al., 2013) – i.e., the cohesion of sediments and biofilm to the substratum (Gerbersdorf et al., 2008) – thus ensuring the bed remains relatively stable even under stronger water flows, provided an established biofilm exists (Grabowski et al., 2011; Grant and Gust, 1987; Vignaga, 2012). Furthermore, biofilms also alter the bed's hydraulic dynamics (Fang et al., 2020; Salant, 2011; Vignaga, 2012) further influencing bed mobilisation. Though this knowledge is grounded in studies on general river biofilms, specific research directly connecting sediment stabilisation and river hydraulics to URBs remains sparse. From the available literature on river biofilms and observations by the authors, it can be inferred that both river velocity and substrate types are crucial influences on URB growth. While stable, immobile substrates are ideal for URB colonisation, the biofilm's ability to solidify finer, more mobile sediments also enhances the prospects for URB expansion.

URB forming species exhibit growth over a relatively broad temperature range (Pellegrin et al., 1999). For instance, *S. natans* has been documented to grow within a 5 – 40 °C range (Cawley, 1958; Mulder and van Veen, 1974; Phaup, 1968). Some research, however, suggests a tighter span from 15 to 40 °C (Stokes, 1954), with an optimum growth of 25 – 30 °C (Curtis, 1969). Several URB species present analogous temperature spans. Zoogloea ramigera thrives between 9 and 37 °C, peaking at 20 – 25 °C (Unz and Dondero, 1967), while *Beggiatoa* spp. are known to grow from 0 to 40 °C (Strohl, 2015). Given these temperature parameters, it might be surmised that URBs would struggle to establish and endure during winter. Yet, observations reveal URB growth in temperate rivers tainted by airport de-icer runoff during frigid winters and low temperatures (ACRP, 2014; Exton et al., 2023; Nott et al., 2020).

URB occurrences can vary significantly in duration and extent. While some are seasonal, others exhibit stronger resilience in particular seasons (Gray, 1987). Sunlight exerts significant influence on URB composition; as the balance of chemical nutrients and sunlight determines the heterotroph to phototroph ratio within the URB (Lock et al., 1984). Factors such as seasonal light changes, shade from overhead vegetation, river depth, and turbidity also play a part (Wuhrmann, 1974). At their core, URB outbreaks persist provided there is ample nutrient supply and favourable environmental conditions (Gray, 1987). Whilst environmental conditions are undoubtedly important to the composition and proliferation of URBs, there is contention over the contributions of genetics, nutrient, and environmental conditions to the development of biofilm structure (Hall-Stoodley and Stoodley, 2002; Kjelleberg and Molin, 2002) – but this should not imply that any are mutually exclusive.

6. Frequency of URBs detection in England (UK)

URBs remain a problem in rivers and streams globally, despite improvements in wastewater treatment and environmental and water quality regulation, but their reporting remains poor, even in countries with robust environmental reporting practices – such as the USA and countries in the EU. However, URB incidences are reported in England as part of evidence gathering to document the impact of pollution events in rivers (Geatches et al., 2014; Water Briefing, 2018). Thus, these pollution records are a unique opportunity to use primary data from a national environmental regulator to (i) provide new empirical evidence on the widespread occurrence of URBs, (ii) examine what industries are implicated; and (iii) explore in more detail an industry and activity that is frequently linked with URB outbreaks, commercial airport de-icing.

Data obtained from the Environment Agency document 6025 incidents of URBs across all counties (administrative regions) in England, 2000 – 2020 (Fig. 2). Whilst the reduced spatial resolution of the dataset does not allow the identification of individual rivers with recurring URB incidences, it demonstrates the widespread nature of the problem and broad spatial patterns. On average, 7 occurrences were reported per grid square (10 x 10 km) over the two decades, though this average is influenced by high numbers of reported incidences in several regions of the country. Approximate one quarter of grid squares (22.6 %) had greater than 10 URB occurrences. URB events were particularly frequent in the southwest and north of England, including the counties of Devon, Lancashire, and Tyne and Wear (Fig. 2**a**). Nine catchments contained

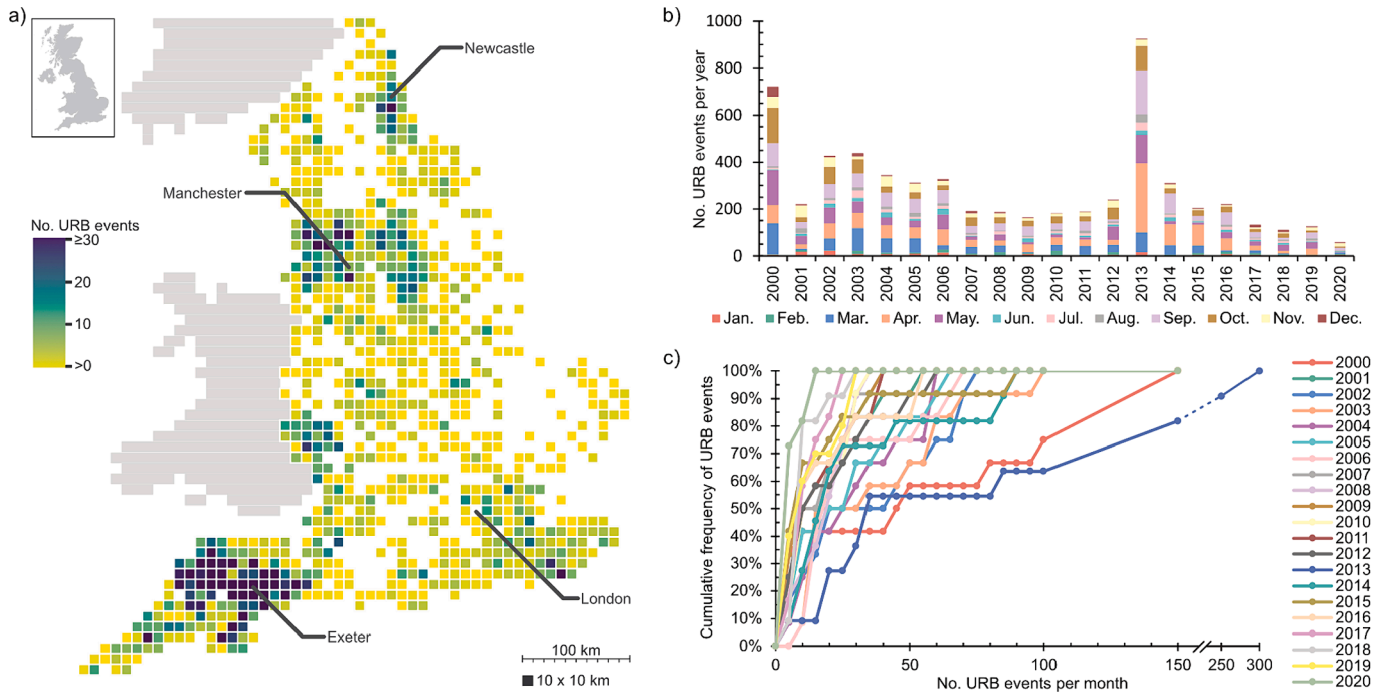

Fig. 2. Spatial-temporal analysis of undesirable river biofilm (URB) occurrences in England from 2000 to 2020, recorded by the Environment Agency. (a) Heatmap detailing the density of occurrences per 10x10 km^2; (b) Stacked bar chart delineating the annual distribution of URB events, segmented by month; and (c) Cumulative frequency distribution depicting the monthly accumulations of URB events. Using data provided with permission by the Environment Agency (Defra, England).

greater than 100 recorded URB events: Exe (618), Taw (400), Torridge (377), English parts of the Wye (226), Axe (Devon) (162), Tamar (146), Teign (129), Don (104), and Aire (103). Notably these regions and catchments include a mixture of urban and rural land cover.

The temporal distribution of URB occurrences highlights a higher frequency of URBs in spring (March – May, $\overline{X} = 36 - 55$ occurrences per month) and autumn (September – November, $\overline{X} = 22 - 48$ occurrences per month) (Fig. 2**b**). The greater detection of URBs in spring could be indicative of warming temperatures better facilitating microbial growth. It could also be related to greater visibility of the riverbed in spring due to lower riparian and in-channel vegetation growth and/or more pollution reporting activity by officers or citizen scientists. Evaluating this on an annual basis, there are consistently 200 – 400 URB occurrences per year, with the years 2000 and 2013 having the highest numbers of reported URB occurrences (722 and 926 occurrences respectively). Furthermore, cumulative frequency distribution of annual data demonstrates that, in the vast majority of years, there are less than 100 URB occurrences recorded per month in England (Fig. 2**c**). However, 2000 and 2013 had an abnormally high number of recorded incidents (>150 and > 300 detections per month) with no clear distribution or driver. Further research is needed to determine the factors influence URB growth and reporting.

In incorporating primary data from regulatory bodies into this review, we acknowledge inherent limitations that may influence the interpretation of findings. For example, the triaging process for pollution incidents can lead to a skewed representation, potentially underrepresenting less visible incidents. This approach introduces a potential selection bias, focusing on reported incidents and possibly overlooking unreported environmental impacts (Cassidy and Jordan, 2011), however this is also a limitation for other types of river monitoring (Vilmin et al., 2018). Variability in investigation methods across regions and operators, coupled with fluctuating resources for incident response, can introduce inconsistencies in data collection, affecting analysis (Rode and Suhr, 2007). Furthermore, the spatiotemporal patterns observed in incident reports prompt a consideration of data representativeness, indicating the possibility of biases in how data is collected and reported. Despite its limitations, the unique dataset presented provides important insights into river pollution impacts.

The dataset demonstrates the prevalence of URBs and their negative impacts on benthic ecosystems, underscoring the consequences of compromised river water quality. While specifically detailing occurrences in England, its significance extends globally due to the scarcity of such detailed data elsewhere. This gap indicates that URB challenges may be even more acute in regions without effective wastewater management, emphasizing the global necessity for enhanced water quality monitoring to fulfil Sustainable Development Goal 6 (SDG6) across all nations, not just those with developed wastewater conveyance and treatment infrastructure. It underscores the importance of comprehensive efforts to enhance freshwater quality, especially in high-income countries with established wastewater treatment infrastructures.

Given the increasing awareness of the levels of organic pollution in rivers worldwide, it is evident that an increased understanding of the drivers (chemical and environmental – for example, specific pollutants) that cause URBs, the implicated industries for regulation, and restoration approaches to increase a rivers resilience to URBs. Within the data presented here, additional information about each occurrence, such as the implicated industry, was not provided and no microbial community analyses were performed. This is indicative of the wider picture where there is limited recent regulatory or research data on the specific industries, pollutants and taxa responsible for URB growth. Existing scientific literature details implicated industries including: farming (especially dairy effluents), wastewater, power plants, refuse liquors, and a range of industrial effluents (Curtis and Harrington, 1971). However, with improving wastewater treatments and tighter regulations, the industries causing URBs may have changed in recent years. Therefore, herein we rely on national and local news, reports by community groups and Government press releases to outline current pollution sources linked to URBs (Table 1) to help build a comprehensive, up-to-date understanding of industries causing URB outbreaks, whilst appreciating that the links between them and URBs have not been explicitly proven.

One industry that has received recent and well-documented

Table 1
Reports of "sewage fungus" outbreaks showing the putatively implicated pollutants in (a) UK news, (b) UK Government reports, and (c) scientific literature.

(a) UK media coverage	Implicated pollutant	River	Date (of article)	Reference
Fermanagh business fined for water pollution offences	Chicken shed washings (agriculture)	unnamed tributary of the Arney River, Northern Ireland	17 Feb 2023	(Yahoo Sports, 2023)
Thames Water's real-time map confirms raw sewage discharges	Raw sewage	Colwell brook (River Windrush), Witney, UK	23 Jan. 2023	(The Guardian, 2023)
England's rivers pay the price for hollowed-out Environment Agency	Airport de-icer	River Trent (& its tributaries), UK	04 Nov. 2022	(Financial Times, 2022)
Giant fungus spreading into rivers near East Midlands Airport being investigated	Airport de-icer	River Trent (& its tributaries), UK	09 Jun. 2022,01 Jun. 2022	(Fish Legal, 2022; Live, 2022a; Live, 2022b)
Water firm fined £240,000 over County Durham sewage discharges	Raw sewage	Coundon Burn, Bishop Auckland, UK	19 Jan. 2022	(GB News, 2022; The Guardian, 2022)
Sewage fungus sighted in West Oxfordshire after heavy rain	Raw sewage	Colwell Brook (River Windrush), UK	06 Jan. 2021, 13 Jan. 2021,21 Apr. 2021	(BBC News, 2021; ITV News, 2021; Oxford Mail, 2021)
Sewage warning for Witney stream after heavy rainfall	Raw sewage	Colwell Brook & Queen Emma's Dyke (River Windrush), Witney, UK	26 Dec. 2019	(BBC News, 2019a)
River Almond polluted by de-icer from Edinburgh Airport	Airport de-icing	River Almond, Edinburgh, UK	05 Dec. 2019	(BBC News, 2019b)
Fungal blooms on the River Crane may be caused by pollution from Heathrow outfall	Airport de-icing	River Crane, Hounslow, UK	19 Feb. 2019	(AirportWatch, 2019)
Farmer fined after 'sewage fungus' contaminated stream which feeds 'important' Somerset fishery	Agricultural wastes	Sedgemoor Old Rhyme, Stoke St Gregory, UK	04 Jan. 2019	(Somerset Live, 2019)
Stoborough Heath sewage spill: Wessex Water pays £35,000 for restoration works	Raw Sewage	Stoborough Heath, UK	23 Jan. 2018 (pollution occurred)	(BBC News, 2020)

(b) UK government reports	Implicated pollutant	River (UK)	Date (of event)	Reference
Somerset supplier to national supermarkets fined for polluting watercourse	Farm manure runoff (agriculture)	tributary of the Congresbury Yeo near Cheddar	28 Jun. 2019	(Environment Agency, 2021)
Negligent farmer fined for fouling SSSI	Agricultural runoff (inc. cattle waste)	tributary of the River Great Ouse, Salcey Forest	April 2018	(Environment Agency, 2019a)
Wessex Water pays for polluting Dorset nature reserve	Sewage discharges	ditch in Stoborough Heath, Dorset	23 Jan. 2018	(Environment Agency, 2020)
Somerset farmer ordered to pay nearly £4,000 for stream pollution	Farm silage & slurry (agriculture)	stream near Stoke St. Gregory, Somerset	04 Dec. 2017	(Environment Agency, 2019b)
Company admits polluting Fenland watercourses	Silage liquor	Little Racy Drain, Emneth Hungate, Norfolk	07 Feb. 2017	(Environment Agency, 2019c)

(c) Journal articles	Implicated pollutant(s)	River	Year published	Reference
Polybacterial shift in benthic river biofilms attributed to organic pollution – prospect of a new biosentinel?	Airport de-icers	River Crane, UK	2023	(Exton et al., 2023)
Stream pollution causes aggregation of wintering insectivorous birds through increased aquatic emergence	Sewage	Vedeggio, Switzerland	2022	(Lepori, 2022)
Detection of untreated sewage discharges to watercourses using machine learning	Sewage	(anonymous) UK	2021	(Hammond et al., 2021)
Acute riverine microplastic contamination due to avoidable releases of untreated wastewater	Untreated urban wastewater	River Tame, UK	2021	(Woodward et al., 2021)
Advanced biofilm analysis in streams receiving organic deicer runoff	Airport de-icers	Edgerton Channel & Wilson Park Creek, Milwaukee, Wisconsin, USA	2020	(Nott et al., 2020)
River biofilm community changes related to pharmaceutical loads emitted by a wastewater treatment plant	Pharmaceuticals (from WWTP)	Arve River, France	2018	(Chonova et al., 2018)
Understanding Microbial Biofilms in Receiving Waters Impacted by Airport De-icing Activities	Airport de-icing effluents	Kinnickinnic River & Thornapple River	2014	(ACRP, 2014)
Morphological and Biochemical Properties of a *Sphaerotilus* sp. Isolated From Paper Mill Slimes	Paper mill effluent	(unknown)	1999	(Pellegrin et al., 1999)
The impact of livestock-farming on Welsh streams: The development and testing of a rapid biological method for use in the assessment and control of organic pollution from farmsAssessment and Control of Farm Pollution	Livestock farming (agriculture)Farm pollution (agriculture)	(various) West WalesEastern Cleddau catchment, west Wales	19931992	(Rutt et al., 1993) (Seager et al., 1992)
Effects of slaughterhouse and dairy factory wastewaters on epilithon: A comparison in laboratory streams	Slaughterhouse & dairy wastewaters (agriculture)	Manawatu River, New Zealand	1989	(Quinn and Gilliland, 1989; Quinn and Mcfarlane, 1989a, 1989b)
Sewage fungus growth in rivers receiving paper mill effluent	Paper mill effluent	(*unknown*) UK	1977	(Roberts, 1977)
The occurrence of sewage fungus in rivers in the United Kingdom	Industrial effluents, food & drinks industries, domestic sewage	(*various*) UK	1971	(Curtis and Harrington, 1971)
Slime Infestation: Literature Review	Various industrial wastewaters	(*various*)	1958	(Harrison and Heukelekian, 1958)

association with URBs is aviation, in particular as a consequence of airports anti- and de-icing activities. URB outbreaks are commonly observed during winter months in watercourses that receive surface runoff from airports, which has been linked to the use of chemical anti- and de-icers (ACRP, 2014; Exton et al., 2023; Nott et al., 2020). Such incidents have been documented across various international airports, including Milwaukee Mitchell Airport (Wisconsin, USA), Bishop International Airport (Michigan, USA), Gerald R. Ford International Des Moines International Airport (Iowa, USA), Cincinnati/Northern Kentucky International Airport (Kentucky, USA), Pittsburgh International Airport (Pennsylvania, USA), T. F. Green Airport (Rhode Island, USA), Heathrow Airport (London, UK), Edinburgh Airport (Edinburgh, UK), East Midlands (Leicestershire, UK) (ACRP, 2014; AirportWatch, 2019; BBC News, 2019b; Citizen Crane, 2020; Fish Legal, 2022; Nott et al., 2020; Live, 2022b; Ricardo, 2018). To ensure safe operations during colder months (Heathrow Airport Ltd., 2018), aircraft and other airport surfaces are coated with vast quantities of anti- and de-icing fluids annually (Freeman, 2016). Typically, these fluids are composed of propylene glycol, ethylene glycol, or acetate/formate salts. This results in the release of surface runoff with high organic loading, which, after treatment (ACRP, 2013; Freeman et al., 2015; Switzenbaum et al., 2001), is legally discharged into water bodies, often leading to the proliferation of URBs (Fig. 1) (ACRP, 2014). Specific research on airport de-icer implicated URBs has thus far been limited to DNA sequencing of periphyton and URBs in rivers receiving runoff from (Exton et al., 2023; Nott et al., 2020) (taxonomic findings are outlined in **Section 4.1**). For example, Exton et al. (2023) found there was a dramatic shift in the periphyton composition in response to suspected airport de-icer contaminated runoff from a highly diverse consortia (Shannon's diversity = 4.3) to a biofilm dominated by members of the Comamonadaceae family (62.7 – 64.1 % relative abundance) and a substantially reduced diversity (3.2). Yet, the exact mechanisms underpinning the influence of these chemicals – such as the thresholds of de-icer discharge, primary URB species, nutrient utilisation and growth kinetics, and the role of environmental conditions – remain nebulous. There is a clear and pressing need to deepen our understanding of the precise conditions and mechanisms triggering URB growth, such as a consequence of airport de-icing related discharges. Building on the strides made in related sectors, a rejuvenated emphasis must be given to this ongoing challenge. Only with a refined understanding can we devise and implement effective management strategies to mitigate this environmental concern.

7. Conclusions and future direction

Bacterial communities and biofilms are integral components of rivers (Curtis, 1969; Harrison and Heukelekian, 1958; Toner and O'Connell, 1971). URBs are a natural part of aquatic life, appearing at times and locations of excess organic loading (Gray, 1987, 1985). As a component of the self-purification processes in rivers, their presence on the riverbed is a sign that the watercourse remains aerobic and excess organic load is being processed. However, URB growth often and quickly becomes extensive or persistent and has profound impacts on the river ecosystem.

The relevance of URBs is clearly demonstrated by the findings presented here and the ubiquity of URBs in UK rivers is evident. URBs have significant ecological impacts within rivers by substantially depleting DO, outcompeting other more sensitive species, and smothering riverbeds. The microbial composition of URBs needs further investigation but the presence of *S. natans* is prominent. The specific microbial composition and morphotype of an URB are defined by the nutrients present (most significantly organic carbon) and environmental conditions (e.g., flow rate, substrate, temperature, and other water chemistry) for each occurrence. Improving wastewater treatment has undoubtedly improved the quality of our rivers and reduced the frequency and extent of URBs. However, Fig. 2 highlights, yet still underestimates, the extent of URBs in UK rivers and indicates that a renewed focus is required so that we can address pollution at source and improve other self-purification mechanisms (e.g., hyporheic zone) (Lewandowski et al., 2019). We recommend that more comprehensive monitoring is undertaken for URBs specifically but river biofilm and river health generally.

This review provides the basis for a renewed focus on URBs using developments in more general biofilm research to improve our understanding of sources of pollution, the diversity and composition of URBs, how water chemistry and physical processes affect the microbial composition, and how this can be used to better address organic river pollution. Specifically, future research needs to address:

- Genomic data on URBs across different continents, seasons and in response to various point and diffuse pollution sources.
- Detailed work on the physiological and ecological mechanisms that cause the shift from a stream biofilm to an URB and back.
- Growth kinetics for a wider-range of URB taxa and a wider range of organic compounds.

In this UN Decade on Ecosystem Restoration, emphasis should be placed on addressing the underlying reasons for the decline in natural ecosystems. Rivers are hotspots of biodiversity and essential to ecosystem functioning and recovery. However, they are still suffering from the old, persistent problem of organic pollution. By better understanding the water quality and environmental conditions that trigger URB growths in rivers, we can support the development of more effective, integrated ecosystem management and restoration.

CRediT authorship contribution statement

Ben Exton: Writing – review & editing, Writing – original draft, Data curation. **Francis Hassard:** Writing – review & editing, Supervision. **Angel Medina-Vaya:** Writing – review & editing, Supervision. **Robert C. Grabowski:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availabilitya)

The government monitoring data used to create Figure 2 was uploaded in the 'attach file' step (DOI: 10.17862/cranfield.rd.25135037)b)

Sewage Fungus Monitoring Data - England (Reference data) (Figshare)

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Data access statement.

No new data were created or analysed for this article. Data on sewage fungus occurrence were visualized for Fig. 2. This dataset was obtained via a standard data request to the Environment Agency. It is available in the Cranfield University data repository, DOI: 10.17862/cranfield.rd.25135037.

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