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Challenges to Managing Microbial Fecal Pollution in Coastal Environments: Extra-Enteric Ecology and Microbial Exchange Among Water, Sediment, and Air

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Abstract Human population growth, especially in coastal urban cities, increases the potential for fecal pollution of adjacent waterways, requiring continued advances in pollution monitoring and management. Infections remain the largest health risk from contact with fecal- and sewage-polluted waters, and a small number of fecal indicator bacteria (FIB) are used as primary pollution assessment tools. While FIB continue to be useful tools, some of the assumptions about the behavior of FIB in the environment, and the associated pathways for pathogen exposure, have come into question. Research into the extra-enteric ecology of these indicators has identified management-relevant complexities including particle association, prolonged environmental persistence, and multidirectional microbial exchange among water, sediment, and air. These complexities provide opportunities for improving current monitoring and modeling strategies and to better understand exposure pathways for sewage-related infections.

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Introduction

Fecal pollution of the coastal environment is the focus of substantial management attention to minimize public health risks from contact with contaminated water and to maximize aquatic ecosystem function. Patterns of recent global population increase have resulted in expanded urbanization and coastal development [1], increasing the potential for degradation of coastal water quality from sewage [2]. Even in countries with extensive wastewater treatment facilities, the stormwater and sanitary sewer delivery systems are often combined, and precipitation events can lead to combined sewer overflow (CSO), releasing large volumes of untreated sewage to waterways [3–5, 6•, 7]. Since coastal and estuarine waters are not typically used for drinking water, the primary health concerns related to sewage contamination in these waterways are the risk of illness from fecal pathogens through water contact and shellfish consumption [8, 9]. The most common water contact infections are of the skin, ear, eye, respiratory system, and gastrointestinal system [10–14]. Although uncertainties are very high, it has been estimated that more than 50 million cases of severe respiratory disease and 120 million cases of gastrointestinal disease occur globally each year from contact with sewage-polluted coastal waters [8].

Detecting and managing sewage contamination in water relies primarily on assessing the abundance of a few commonly used fecal indicator bacteria (FIB), including enterococci (ENT) and *Escherichia coli*, generally following recommendations and protocols from the World Health Organization [15] and the US Environmental Protection Agency [16, 17].

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In the USA alone, thousands of beaches are tested weekly during the recreational season, resulting in tens of thousands of beach closure days in a typical year [18]. The abundance of these FIB has generally been found to positively correlate with an increasing risk of infection from recreational contact with polluted water [10, 13, 14, 19–22], especially in children [23]. However, as research in this area has progressed, many of the assumptions upon which management and regulatory decisions are based, such as the behavior of FIB in the environment and the pathways for pathogen exposure, have been questioned. Accounting for the complexities in the extra-enteric ecology of FIB (the ecology of FIB once they leave the gut) could improve current management approaches [24–29, 30••]. Understanding the ecology of FIB also highlights opportunities for the use of new tools (e.g., DNA-based fecal source tracking) and new management actions (e.g., management of beach sand) beyond the constraints of current regulations and methodologies [31, 32]. This review will focus on a subset of prominent complexities and their implications for microbial fecal pollution monitoring and management in rivers, estuaries, and the coastal zone.

Four overarching concepts and linked complexities (Table 1), each related to the extra-enteric ecology of FIB and fecal pathogens, will be discussed in this review: (1) the importance of microbial particle association; (2) the potential for prolonged environmental persistence; (3) microbial exchange among water, sediment, and air; and (4) exposure pathways beyond direct contact with water. While none of these concepts are newly identified, and some have had extensive discussion in the literature, they are rarely fully

Table 1 Common water quality over-simplifications and management relevance of understanding the associated complexities

Over-simplifications	Complexities	Linked management relevance
1. Fecal microbes and FIB are free-living and conservatively transported with water	Particles are hotspots for microbial colonization, activity, and persistence; particles can sink rapidly, and transport of particle-associated cells will therefore diverge from their original water mass	1. Water quality models may be improved by adding particle sinking and differential persistence on particles 2. Changes in the relative importance of turbulence, particle sinking, and resuspension may cause the dynamics of FIB to differ seasonally and from nearshore to offshore in predictable ways
2. Fecal microbes are only viable for a few days in the coastal environment; their fate can be described by characterizing initial inputs and uniform decay rates	The extra-enteric ecology of microbial contaminants matters, including differential growth and persistence responses for different species; traditional indicators may be decoupled from the diverse fecal microbial community in some environments	3. FIB and fecal pathogens may persist for weeks/months based on factors such as temperature, organic content, and light intensity 4. FIB may not be appropriate indicators of risk in all environments; decoupling of indicators and pathogens can occur under some conditions 5. Community indicators provide some advantages over traditional FIB in discriminating fecal sources and their environmental persistence 6. Seasonal disinfection may be a flawed practice in many systems
3. Flow is unidirectional, with microbial fecal pollution originating from a concentrated terrestrial source and moving to an oceanic sink with a diluted concentration	Multidirectional flow occurs; microbes are exchanged among water, sediment, and air; nearshore environmental reservoirs of microbial pollutants occur and can be transported back to the terrestrial environment	7. Sediment and sand often act as environmental reservoirs of FIB 8. Resuspension may influence water quality in shallow water systems 9. Aerosols may connect water and air quality and may transport viable bacteria back to land 10. Flooding (e.g., tides, storms) can deliver contaminated water/sediment onshore
4. Public health concerns are restricted to direct contact with, or ingestion of, contaminated water	Diverse vectors for sewage-associated microbial contaminants occur in coastal environments, including sediment/sand and aerosols	11. Sediment and beach sand may be sources of illness, even for non-swimmers. Beach sand management actions may reduce health risk 12. Aerosols from sewage-polluted urban waterways may be related to the high incidence of urban respiratory illness 13. Waterway aeration for dissolved oxygen remediation may have unintended consequences for air quality

incorporated into coastal water quality monitoring or the management of sewage pollution. Each of these concepts has relevance for improving interpretation of monitoring data and better informing sewage pollution management decisions.

Background on Sources of FIB and Associated Allochthonous Microbes

Aquatic environments, even when lacking fecal or sewage pollution, contain diverse autochthonous microbial communities composed of both free-living and particle-associated bacteria [33], with compositions influenced by environmental conditions (e.g., salinity gradients) [34, 35], and abundances often exceeding a million cells per milliliter of water [34, 36, 37]. These autochthonous bacteria represent the background microbial community context into which fecal pollutants are discharged. This background microbial community context matters, as substantial competition among autochthonous microbes and allochthonous FIB can occur with the potential to significantly alter the persistence of FIB in environmental samples [38, 39]. The community of bacterial predators can also influence the persistence of FIB in the environment. For example, protistan predators have been shown to play a large role in decay rates of FIB [40, 41], and rates of predation of FIB may be higher than those on the background bacterial community [42]. However, the relative importance of predation to decay of FIB may differ between sand and water [38, 41].

The delivery of allochthonous fecal-associated microbes to an aquatic environment can occur during dry or wet weather via direct deposition, runoff, or conveyance via wastewater infrastructure such as a sewer pipe (Fig. 1). FIB, such as *E. coli* and ENT, comprise only a small fraction of the total allochthonous bacteria delivered with untreated fecal waste but are readily measurable and coupled by shared source and co-occurrence with the broader community of fecal bacteria including the subset of pathogenic microbes capable of causing human illness [10, 12–17]. FIB are also associated with non-human sources of fecal waste, usually delivered directly to the waterway through runoff containing agricultural [43, 44], wildlife [45–48], and domesticated animal waste [49–51].

Because both health risk and mitigation approaches differ based upon the source of fecal microbes [28], the field of microbial source tracking (MST) has emerged as an effort to differentiate animal versus human signatures in fecal microbial assemblages and to develop species-specific assays for fecal contaminants [52–54, 55••, 56]. While some MST approaches target a single taxonomic group of indicators, similar in concept to the use of traditional FIB, other MST approaches target broader groups of indicator or pathogen taxa. For example, high-throughput sequencing of DNA from the feces of multiple animal species and geographically isolated untreated

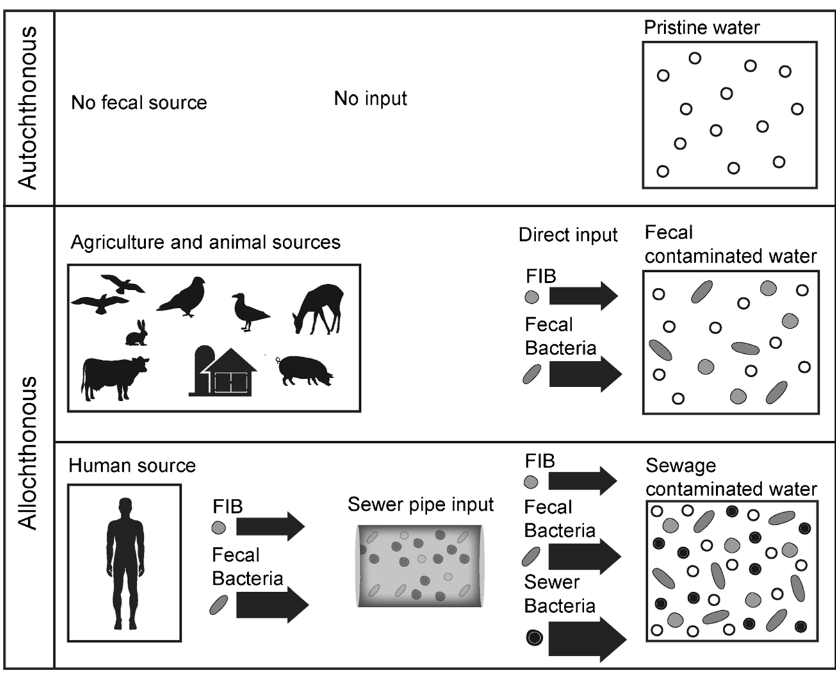

Fig. 1 Sources of microbes to water. Natural aquatic environments contain abundant and diverse autochthonous microbes (*open circles*), even in the absence of fecal input (*top panel*). Animal and human sources of allochthonous fecal microbes are delivered in addition to the autochthonous microbes in contaminated waterways (*two bottom panels*). FIB (*gray round circles*) represent a small portion of the allochthonous microbes (*size of arrow* indicates differing concentration), delivered together with more diverse fecal bacteria (*gray rods*) that often include pathogens. In the case of human waste delivered via a sewer, there are additional microbes originating in the sewer pipe (*black circles*) input to the waterway. Although FIB are delivered with both animal and human inputs, other allochthonous microbes vary by source and this information can be used to assess source and extent of contamination and can therefore be used to improve management and mitigation

wastewater samples allowed the identification of a fecal microbial community signature, based on multiple, rather than a single, species of fecal-associated bacteria [57, 58, 59•]. A major limitation of community-based indicators is that, unlike traditional indicators (e.g., ENT and *E. coli*), they are not currently used for regulatory decisions. Instead, the use of community-based indicators is primarily for source identification and to optimize mitigation actions. An advantage of the community signature approach is that combined taxa generally have orders of magnitude of greater abundance than traditional indicators such as *E. coli* and ENT, allowing even trace levels of sewage contamination to be detected [59•].

Microbial community-based source tracking can provide an insight into common delivery pathways for allochthonous microbes, because not all microbes found in untreated wastewater originate from fecal material. For example, some microbial groups inhabit sewer infrastructure (e.g., sewer pipes) and thus represent a microbial signature that is only found coupled with fecal contamination if delivered via wastewater infrastructure [58, 59•, 60] (Fig. 1). When combined with emerging chemical source tracking approaches [61–65], the continued development of MST approaches provides one of the greatest opportunities in the coming decade for research advances in monitoring and mitigation of fecal contamination in aquatic environments. The microbial community-based source tracking approach will be used conceptually to illustrate many of the complexities addressed in this review.

Complexity 1: Particle Association and Particle Sinking

It is widely recognized that particles can act as hotspots for microbial activity and ecology in aquatic environments [66–68], supporting both microbial communities and biogeochemical pathways that differ from particle-free, bulk portions of the water column [33, 69–71]. Despite this, until recently, most water quality models have assumed that FIB are free-living, moving with the water and exposed to stressors consistent with bulk water conditions [72]. In the last decade, there has been an increased focus on characterizing the frequency of the particle association of FIB (Table 2). Many sources of allochthonous FIB, including human and animal feces, enter the aquatic environment associated with high particle loading [73, 74, 78, 80] either by direct delivery of feces or in stormwater and sewage. For example, Walters et al. [73] found that 91% of *E. coli* and 83% of ENT in urban wastewater were associated with small (<12 μm) sewage particles. Therefore, it is not surprising that a large portion of FIB within estuaries have also been found to be particle-associated. In the Hudson River Estuary, Suter et al. [76•] found that FIB were approximately twice as frequently associated with particles (ENT 52.9 ± 20.9%) as total heterotrophic bacteria (23.8 ± 15.0%). Similarly, Mote et al. [77] found that up to 95% of estuarine FIB were particle-attached, often to detritus and phytoplankton cells. Understanding the dynamics of FIB and fecal pathogens in the water column therefore requires considering the role of particles in altering their environmental conditions and ecological interactions relative to those experienced by free-living cells.

Particle attachment modifies the environmental fate of associated microbes by influencing both transport and exposure to environmental stressors in the natural system. While free-living cells essentially lack a sinking flux and will therefore be transported as passive tracers within water masses, particle-attached cells can have a significant sinking flux, altering surface water concentrations, environmental context, and horizontal transport of these bacteria. Ultimately, sinking can deliver the cells to benthic sediments where environmental conditions are very different than the water column (e.g., light, temperature, dissolved oxygen) [72, 74, 79, 82, 83, 88]. A large percentage of sewage- and stormwater-associated allochthonous particles, based on size and density, can be deposited rapidly to sediment in close proximity to the point source, while smaller and less dense particles (such as free-living cells) remain suspended and can be transported further away from the point source [89, 90]. Control measures that take advantage of the larger effective size and sinking flux of particle-associated bacteria include constructed wetlands and pollution control ponds (which reduce microbial loads by allowing colonized particles to settle) [91]. The effectiveness of these systems in mitigating FIB has been linked primarily to their efficiency, or inefficiency, in removing the small end of the particle-sized spectrum, as FIB are often found to be disproportionally associated with smaller particle size fractions [73, 77, 84, 92].

In addition to altering the transport of FIB, particle loading and particle attachment can influence the exposure of FIB to environmental stressors. It is well known that particle-associated bacteria often have higher activity rates than free-living bacteria and increased access to organic matter [66, 68, 93, 94], which can lead to increased environmental persistence. Bacterial protection from UV inactivation through the physical effects of high concentrations of suspended material has been documented in wastewater [95] as well as in estuarine surface waters [96]. In combination, higher activity rates and stressor protection can lead to substantially enhanced persistence of FIB. For example, particle-attached *E. coli* were found to persist for twice as long as free-living *E. coli* in river water mesocosms [82] and some species of particle-attached ENT were found to have enhanced persistence when associated with plankton suspensions [77].

Levels of particle-associated FIB correlate with turbidity in surface waters of some estuaries [74, 75, 76•] and the coastal zone [97••], and both parameters have been found to be higher near sewage inputs (e.g., CSOs) and tributary mixing zones, when compared to mid-channels of estuaries [74, 75, 76•] or

Table 2 Summary of particle-associated percentages of FIB measured in prior studies

FIB	Sampled environment	Sampling condition	Average (%) particle association	Range (%) of particle association	Sampling method	Reference
ENT	Wastewater	Attached to particle <12 µm	83 ± 2.7 (SE)		Filtration	[73]
	Estuary—Neuse River Estuary, NC	Wet weather	38 ± 4 (SE)		Centrifugation	[74]
		Dry weather	60		Centrifugation	[74]
			30 ± 10 (SE)		Centrifugation	[75]
	Estuary—Hudson River Estuary, NY		52.9 ± 20.9 (SD)	13–89	Filtration	[76•]
	Estuary—Skidaway Island, GA			1–95	Filtration	[77]
	Streams—NC		37	<1–70	Centrifugation	[78]
		Wet weather, stormwater influenced	45 ± 7 (SE)	Approx. 20–65	Centrifugation	[79] (as reviewed by [74])
		Dry weather	20–35	<1–approx. 55	Centrifugation	[79]
	Streams—NY		15–30	<1–approx. 68	Centrifugation	[80]
	Lake Pontchartrain, LA			8.3–11.5	Filtration	[81]
E. coli	Wastewater	Attached to particle <12 µm	90.6 ± 7.1 (SE)		Filtration	[73]
	Estuary—Neuse River Estuary, NC	Wet weather	38 ± 4 (SE)		Centrifugation	[74]
		Runoff dominated	14 ± 7 (SE)		Centrifugation	[75]
		Re-suspension dominated	68 ± 12 (SE)		Centrifugation	[75]
	Rivers—Seine, France; Meuse and Scheldt, Belgium			<1–approx. 90	Filtration	[82]
	Stream—Grand River watershed, Ontario	Re-suspension experiment		20–44	Filtration	[83]
	Streams—NC		40	<1–68	Centrifugation	[78]
		Wet weather, stormwater influenced	25 ± 9 (SE)	Approx. 5–65	Centrifugation	[79] (as reviewed by [74])
		Dry weather	20–35	<1–approx. 65	Centrifugation	[79]
	Streams—NY		15–30	<1–approx. 78	Centrifugation	[80]
	Lake Pontchartrain, LA			21.8–30.4	Filtration	[81]
FC	Streams—NC		46	Approx. 22–68	Centrifugation	[78]
		Wet weather, stormwater influenced	30–55	Approx. 25–85	Centrifugation	[79] (as reviewed by [74])
		Dry weather	20–35	Approx. 15–40	Centrifugation	[79]
	Onondaga Creek and Lake, NY	particles <10 µm	90		Filtration	[84]
	Stormwater outfall pipe, Lake Michigan	Direct stormwater	17		Filtration	[85]
	Estuary and rivers, CA	During stormflow	10		Filtration	[86] (as reviewed by [87])
	Streams—NY		15–30	<1–approx. 68	Centrifugation	[80]
	Lake Pontchartrain, LA			9.8–27.5	Filtration	[81]

in offshore coastal waters [92]. The concentration of FIB in sediments also appears to vary inversely with the distance from sewage point sources [98] and to peak in urban waterways near CSOs [99]. The source of particle-associated FIB has been found to change temporally, in response to weather, as well as spatially. Following rain events, and especially in lower volume waterways exposed to stormwater flows (e.g., tributaries leading into estuaries), many of the particles in a water column can originate from particles associated with stormwater or CSO inputs [78, 90]. In contrast, resuspension of bottom sediments often dominates particle source during periods of dry weather and in regions less impacted by stormwater inputs [90] or more exposed to water column turbulence [92, 100–103]. By accounting for the particle association of FIB and ensuing sedimentation and resuspension dynamics, management models can better predict patterns of water contamination [72, 92, 104–108].

Complexity 2: Differential Persistence and Growth

The idealized assumptions for *E. coli* and ENT as indicator organisms included that they were abundant in fecal material and absent in aquatic environments that lacked recent fecal contamination, due in part to their inability to persist in the environment beyond a few days [109–111]. Stressors encountered in aquatic environments, including high salinity, high light, and low nutrient conditions, were known to differ from the enteric environment [112, 113], acting to limit growth and enhance decay of FIB. However, it is now recognized that the extra-enteric ecology of FIB can differ substantially from the idealized assumption of rapid environmental decay, with FIB able to persist for weeks or even months in some cases [25, 114].

Physical, chemical, and biological conditions in the water column have been found to influence the environmental persistence of FIB and have become a common area of research to better understand the environmental dynamics of FIB. Lower temperatures [114–116] and nutrient additions [115, 117–121] have commonly been found to extend the persistence of FIB, while predation [114, 116], elevated salinity [26, 122, 123], and exposure to sunlight [124–130] have typically been found to decrease environmental persistence. Other factors, such as suspended particle concentration, may have divergent effects on different groups of FIB [96]. While individual factors such as temperature, organic carbon concentration, and intensity of sunlight can be important to the understanding of persistence of FIB, it is not surprising that the environmental fate of FIB is often determined by the interaction of these physical, chemical, and biological factors. For example, sunlight and temperature [131], sunlight and salinity [124, 132], and temperature and predation [133] are just a few of the factors found to interact in determining the persistence of FIB in the water column and demonstrate the complexity of predicting the dynamics of FIB in the environment.

Deviation from idealized assumptions for the behavior of FIB is even more pronounced in the sediment than in the water column. Although it has been demonstrated for decades that surface sediments can contain higher volumetric, or mass-normalized, concentrations of FIB than water [98, 99, 117, 134–136], there has recently been increasing awareness that FIB generally persist for much longer in sediment than in water. This awareness has highlighted the potential function of freshwater and coastal sediments as a meaningful reservoir for FIB within the environment [26, 72, 115, 137–139]. The highest concentrations and longest persistence of FIB are generally found in sediments with small grain size, high organic content, and low temperatures [115, 117, 118, 140–143].

Another fundamental assumption behind the use of FIB in monitoring programs is that the commonly used indicators are correlated with the occurrence of pathogens that cause infection risk, as discussed above. The risk of illness should decrease with a decreasing concentration of fecal pathogens, which are assumed to be tightly coupled to the concentration of FIB and to originate from the same source (Fig. 2). However, the coupling of FIB and pathogens (and therefore, the risk indicated by a given concentration of FIB) may be complicated by factors that cause the differential persistence of FIB or pathogens in the environment. The epidemiological studies supporting the coupling of FIB and pathogens have typically targeted waterborne illnesses and used only water column sampling for indicators [13]. Extrapolating the connection between FIB and pathogenicity from the water to other environmental settings, such as in sediments, may not be appropriate. It is therefore unclear if the enhanced persistence of FIB in sediments (described above) also reflects the enhanced persistence of other fecal pathogens (Fig. 2, sediment scenario 1), or if instead, FIB become decoupled from both fecal pathogens and the associated health risk (Fig. 2, sediment scenarios 2, 3, and 4). If FIB found in sediments become decoupled from pathogens and the risk of illness, then it brings into question their usefulness for effective environmental monitoring and management in locations where sediments could be an important reservoir of FIB.

An added complication to the coupling between FIB and pathogens is that environmental persistence can also vary among types of FIB, e.g., *E. coli* vs ENT [140], and even at the strain level within a given type of FIB [26, 77]. For example, while some *Enterococcus* species are widely distributed in animal feces (e.g., *Enterococcus faecalis* and *Enterococcus faecium*), others have been associated with plant and soil sources (e.g., *Enterococcus casseliflavus* and *Enterococcus mundtii*) [144], suggesting that some strains of FIB may persist as epiphytes or in association with sediment and detritus [26, 77]. The most extreme manifestation of prolonged persistence is naturalization of allochthonous microbes. In some environments, often tropical and temperate streams, *E. coli*

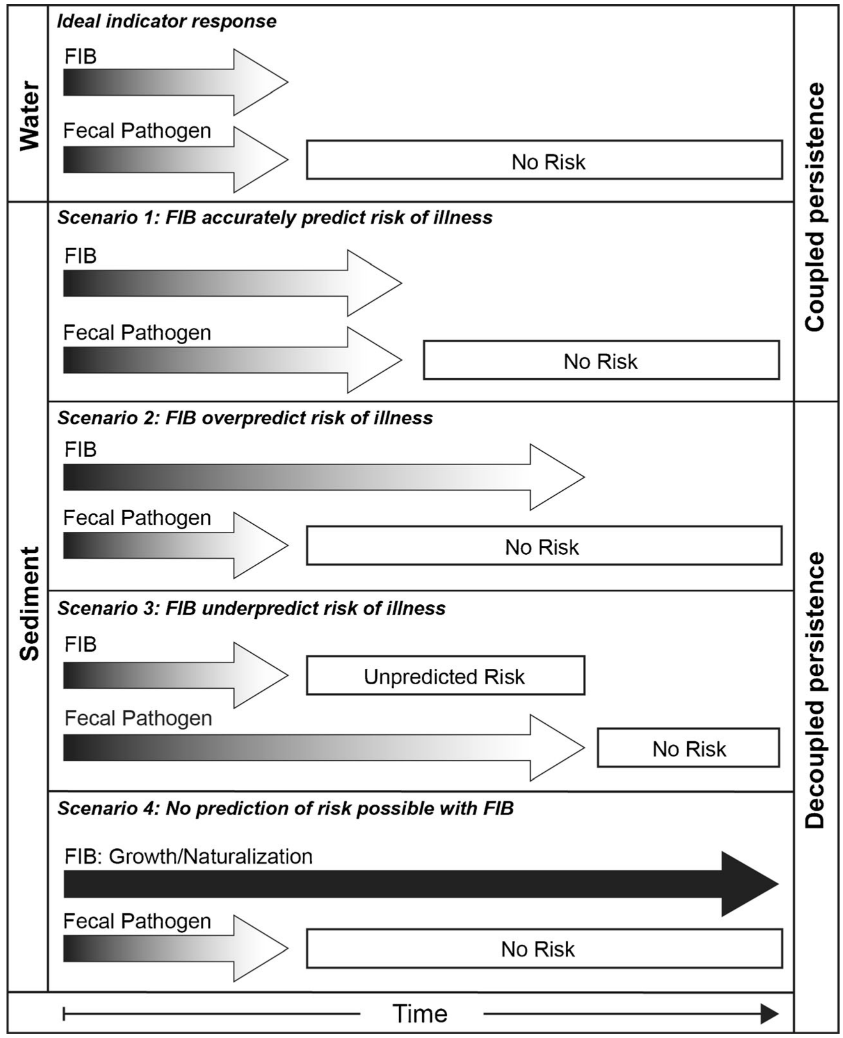

Fig. 2 Coupling of FIB to risk in the environment. Under idealized conditions, FIB in water (*top panel*) are assumed to correlate with the abundance of fecal pathogens, and the concentration of both groups decreases (*shading of arrow* indicating concentration) over time (to the *right*). When fecal pathogens die, there is no longer risk of illness. In sediment (*bottom panels*), the abundance of FIB may be coupled or decoupled from the abundance and persistence of fecal pathogens and therefore risk. The relationship can be described by at least four scenarios in sediment, leading to risk being well predicted by FIB (*scenario 1*), over-predicted (*scenarios 2 and 4*), or under-predicted (*scenario 3*). In the case of scenario 4, the FIB grow in sediment and are no longer a useful indicator of fecal contamination or risk

and ENT have been found to grow within sediment or soil, creating a naturalized population persisting at least seasonally [25, 28, 31, 145–150] (Fig. 2, sediment scenario 4).

Despite complexities such as these, a recent large-scale survey of estuarine sediment found FIB and other pathogenic indicators to be correlated [151]. Questions surrounding the persistence of FIB in sediment and the extent of their coupling, or decoupling, with fecal pathogens, and therefore illness risk, highlight the importance of emerging analytical approaches, including MST and community-based microbial signature techniques to assess fecal contamination [55••], as well as the need to re-evaluate human health risk in sediment-influenced systems [27, 28]. Furthermore, the potential for long-term, even seasonal, persistence of FIB in sediment also calls into question some common management practices, such as disinfection (e.g., chlorination) only during the recreational season at some wastewater treatment plants [152]. If FIB and pathogens are assumed to persist in the environment only for a few days, then disinfection would not be a priority in the non-recreational season. However, if sediments act as a long-term reservoir, failing to disinfect in the winter and spring months could build up sediment FIB and pathogen reservoir that could impact water and sediment quality in the following summer season. As our understanding of the environmental dynamics of fecal contaminants changes, management practices should also change.

Complexity 3: Microbial Exchange Among Water, Sediment, and Air

When concentrated sewage is delivered from a terrestrial source into a river or the coastal environment, it is often assumed that the contamination is carried away with the water, rapidly diluting and decaying during transport toward an oceanic sink. The limitations of simple dilution and rapid decay-based models have been identified in the last decade along with calls for the development of next-generation mechanistic or deterministic models [24, 72, 104, 105, 153, 154]. When considered in more detail, it becomes clear that the assumptions of unidirectional and passive water movement of FIB do not result in a comprehensive understanding of risk. Rather, multidirectional transport occurs through exchange of complex materials among water, sediment, and air, which, in some cases, can result in microbial contaminants being carried back to the terrestrial environment.

As already described above, when sewage-contaminated water enters an aquatic environment, a large percentage of the FIB, and fecal pathogens, are particle-associated with a significant sinking flux that reduces concentrations in surface waters over time. Sinking delivers FIB and fecal pathogens to deeper water where sunlight inactivation decreases and to benthic sediments where they may persist for an extended period of time (Fig. 3). These sediments often store a wide variety of pollutants, including microbial pollutants, as a signal of past human activities and associated contamination [155]. Turbulence in the nearshore environment caused by tides, wind, waves, or even recreational activity can cause resuspension of bottom sediments into the water column, re-introducing FIB [92, 97••, 101, 103, 156, 157]. Resuspension can therefore decouple levels of FIB in the water from recent inputs of allochthonous bacteria from terrestrial sewage sources, modifying the utility of water column FIB as an indicator of recent fecal contamination.

By incorporating the multidirectional exchange among water and sediment as well as the altered persistence that occurs due to the ecological responses of FIB to environmental conditions, it is possible to better predict patterns in monitoring data and to improve prediction tools based on a mechanistic understanding of the system. For example, sediment resuspension may lead to elevated FIB in turbulent nearshore environments (e.g., tributary mixing zones, wave-influenced beaches) and may provide a source of FIB even during periods of dry weather when sewage discharge may be limited. Because sediment resuspension will usually vary with water depth, spatial differences in FIB often occur as a function of water depth, rather than just proximity to known sewage point sources. These mechanisms of FIB redistribution are consistent with FIB patterns observed in many environments and can aid in the interpretation of monitoring data. As an example, in the Hudson River Estuary, the concentration of FIB and levels of turbidity are both greater in the shallow, nearshore environment than in the mid-channel [76•]. There are multiple mechanisms contributing to this pattern. The concentrations of FIB in the lower estuary are influenced by untreated sewage discharges following precipitation [6•, 158], and proximity to sewer overflow pipes is one explanation for nearshore elevations in FIB [6•, 76•]. Tributaries of the Hudson and tributary mixing zones also have consistently elevated concentrations of FIB and particle-associated FIB, relative to the mid-channel [76•, 159], suggesting that turbulent conditions in the nearshore environment resuspend FIB even during dry weather. Not coincidentally, sediment resuspension in nearshore and

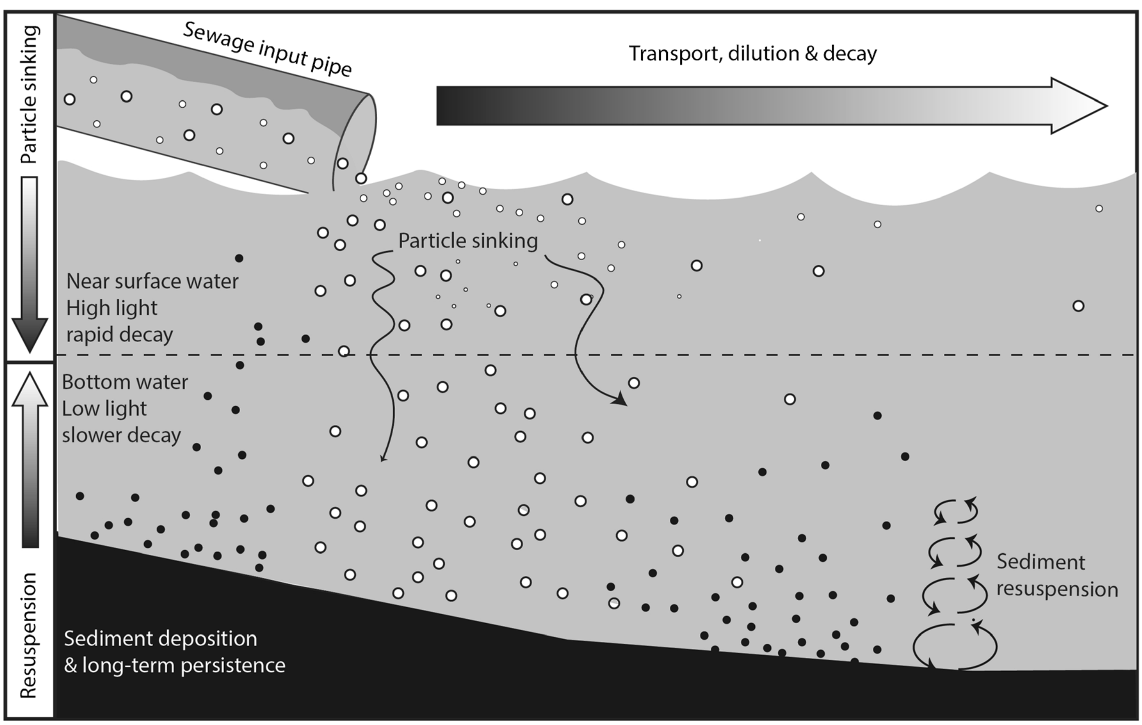

Fig. 3 Mechanisms altering spatial patterns of FIB. Sewage-associated microbes can be delivered to a waterway via a pipe and include free-living (*small open circles*) and particle-associated (*larger open circles*) microbes. Transport, dilution, and decay occur as water moves away from the point source, decreasing the concentration of sewage microbes. Particle sinking delivers microbes to the sediment where they may persist and, over time, sediment microbes may be resuspended into the water column. These processes alter spatial distributions of microbes and change their interaction with environmental conditions, including factors such as light level that can alter environmental persistence

near-bottom waters is also the most likely explanation for abundance patterns of other particle-associated microbial groups (e.g., amoebae) [160].

More broadly, the importance of sediment interactions has also been clearly documented in shallow stream systems where it has been a topic of extensive modeling efforts [83, 88, 107, 154, 161–163]. Thus, the potential for sediment contributions to water column FIB measurements [83, 88, 90, 105, 139, 164, 165] (Figs. 3 and 4) raises questions about the extent of FIB-pathogen coupling (Fig. 2) in the coastal nearshore environment [75, 139], especially in tributary and tributary mixing zones [29, 147, 166].

Intertidal beach environments are hotspots for recreational activity and are known to be heavily influenced by the sediment-water exchange of FIB. Recreational activity itself (e.g., wading into water or boats passing a beach) can influence water quality due to the disturbance of sediment-associated fecal bacteria in shallow water environments [156, 157]. Wave and tidal action can cause sediment and sand, colonized with FIB, to be mobilized [102, 103, 164, 167], influencing coastal water quality and exchanging FIB-colonized sand between the aquatic and terrestrial environments, especially at intertidal beaches [100, 168–170]. Similar to patterns found in high organic content benthic sediment, FIB have also been found to persist on low organic content beach sand and to often have higher concentrations of FIB than in water [149, 170, 171]. Therefore, beach sand can act as an environmental reservoir and dry weather source of FIB to adjacent waters [169, 170, 172, 173].

While exchange of bacteria is commonly considered in the beach environment, coastal flood events are another mechanism for the exchange between aquatic and terrestrial environments. Flooding, which occurs as frequently as the tides and, more dramatically, though less frequently with storms, carries water and sediment onto the shore, increasing the likelihood of human contact. Flooding from major storms (e.g., hurricanes Katrina and Superstorm Sandy) can transport large quantities of water and sediment into highly populated areas, creating the potential for humans to interact with fecal-associated bacteria [174–178]. Some of these microbes can persist on surfaces long after the flood waters recede [179].

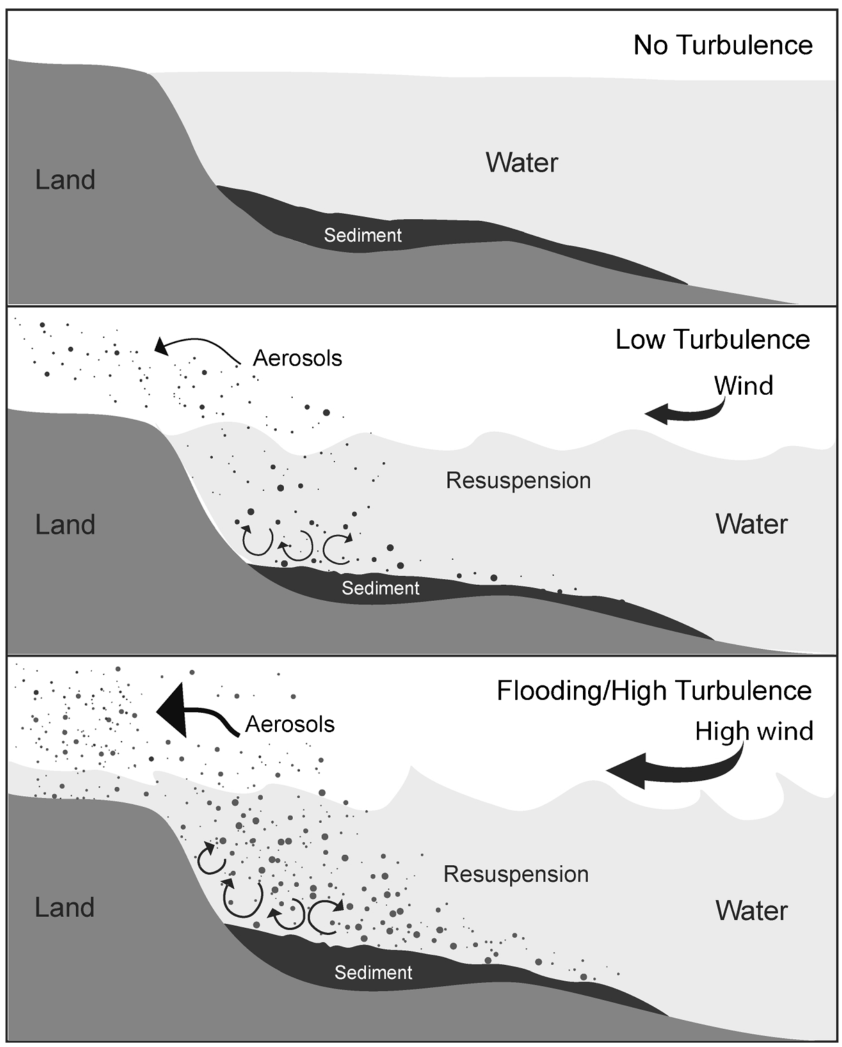

Fig. 4 Microbial exchange among sediment, water, and air. Turbulence, for example from tides and wind, alters the exchange of microbes among sediment, water, and air. Without turbulence, very little exchange occurs; however, with increased turbulence, sediment resuspension and aerosol formation occur. Under onshore wind conditions, viable microbes can be transported with aerosols back onto land. Under high turbulence, the extent of exchange increases and even coastal flooding may occur, representing an extensive multidirectional exchange of microbes

Other microbial transport pathways include water-to-air connections. Turbulence in the nearshore environment can cause the transport of bacteria from the water surface into air through aerosol formation [180–183]. Factors disturbing the water surface such as elevated wind [184], mechanical aeration [183], and breaking waves [182] can increase aerosol formation. Viable microbial aerosols can then be transported to the terrestrial environment with onshore winds and deposited on land [185–188, 189•, 190], creating a connection, still poorly understood in detail, between water, sediment, and air quality [27, 183, 189•, 191].

Complexity 4: Pathways for Exposure Beyond Direct Contact with Water

In the future, research and management of microbial fecal pollution must account for the multidirectional exchanges among water, sediment, and air, while incorporating more diverse pathways of exposure and health outcomes. The vast majority of epidemiological studies considering fecal contamination in the coastal environment have focused on direct contact with water and gastrointestinal illnesses [10, 13]. However, direct contact with river and estuarine sediment [192] and especially with beach sand [170, 193, 194•] is an emerging area of epidemiological research and management discussion [31, 32]. For instance, one criticism of the most recent (2012) update to the USEPA Recreational Water Quality criteria is the lack of criteria for beach sand [30••]. Many researchers have initiated studies of the microbial communities, including pathogens, in beach sand [97••, 195, 196], and recent epidemiological studies have found an increased risk of gastrointestinal illness, especially in children, after direct contact with beach sand [170, 193, 194•, 197]. Others have suggested that more research is needed before regulatory standards can be developed [173]. Despite the lack of regulations, there have been actions developed to mitigate beach sand contamination including grooming, UV and chlorine treatment, and animal control methods [31, 198, 199].

There is a need to expand microbial risk assessment to include a broader range of activities (e.g., swimming, surfing, kayaking, wading, boating, and general proximity to contaminated waterways) as the risk varies with the level of contact [200] and also to include additional pathways for exposure (e.g., contact with sand, contact with sea spray, mechanical aeration remediation). The production of aerosols from fecal-contaminated water sources is an emerging area of applied study and of public health concern that relates to non-swimmers. Although, as discussed above, aerosols have been demonstrated to deposit viable and culturable bacteria from coastal water sources back on to land, there is a very limited understanding of the associated health risk. Some prior studies have suggested linkages of aerosol pathogen transport to health risk in natural, agricultural, and engineered environments [201–206] and, in some cases, even from water sources [191, 203, 207, 208, 209•], but much more research is needed. Until these pathways are better understood, it would be difficult to regulate bacteria (concentrations or type) in outdoor air. Recent studies are also attempting to improve bioaerosol sampling methods to facilitate the exploration of the public health consequences [210–213]. However, given the known occurrences of pathogen and toxin aerosol transport, it remains important to consider the potential for unintended consequences of management actions (e.g., aeration remediation of waterways or control measures in wastewater treatment), especially in heavily polluted and highly populated urban environments, even if the risk remains poorly constrained. As we better understand microbial exchange among sediment, water, and air, this research will help expand and better inform management practices and regulations for microbial pollution.

Conclusions

The study of microbial sewage pollution in the coastal environment is not restricted to routine monitoring but is instead an active research field in need of continued innovation. Improved understanding of the extra-enteric ecology of both FIB and fecal pathogens will allow for greater optimization of pollution mitigation and prediction. In the future, these efforts must better account for multidirectional exchange among water, sediment, and air, while incorporating more diverse pathways of exposure and health outcomes. The potential for diverse health and ecological impacts of sewage and fecal pollution justify the expanded investment in research, monitoring, sewage infrastructure, and pollution mitigation.

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Compliance with Ethical Standards

Conflict of Interest The authors declare no conflicts of interest.

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- • Of importance
- •• Of major importance

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