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OPINION PIECE

Megafauna: the ignored bioturbators

Alessandra L. Vallim*, Stefano Schenone, Simon F. Thrush

Institute of Marine Science, University of Auckland, Auckland 1142, New Zealand

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ABSTRACT: Bioturbation is a process caused by animals that move particles and water in sediments. This influences gas and solute exchange, and organic matter concentrations through the sediment column. Bioturbators play an important role in biogeochemistry and ecosystem functioning. To date, bioturbation research has focused on the invertebrate macrofauna present in the sediment. However, many larger marine animals (e.g. rays, sharks, whales) display foraging behaviours that disturb the sediment and thus potentially affect sediment biogeochemistry. We propose a categorization of vertebrate megafauna bioturbation based on their reworking behaviours, classifying them as 'pit creators', 'bulldozers', and 'trench diggers'. These categories underscore the diversity of impacts on sediment structure and biogeochemical processes. The need to investigate the topic comes from the limited knowledge surrounding the extent to which sediment biogeochemistry is influenced by megafauna activities. Additionally, the declining population of vertebrate megafauna due to climate change, overfishing, bycatch, and habitat loss and modification makes discerning the functional roles of these animals in the sediment a pressing issue. Understanding the ecological implications of megafauna bioturbation will be critical to support conservation strategies and protect marine ecosystems and the animals that shape them.

KEY WORDS: Bioturbation · Megafauna · Foraging · Benthic · Ecosystem functioning

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1. INTRODUCTION

Studies of biogeochemical processes that strongly affect global cycles of oxygen, carbon, and nitrogen (Glud 2008, Arndt et al. 2013) often undervalue the potential contribution of vertebrate megafaunal bioturbation to these cycles (Snelgrove et al. 2018). Bioturbators cause changes in the sedimentary environment and alter resource availability for other species (Jones et al. 1994, Herringshaw et al. 2017). This process therefore influences heterogeneity of the seafloor landscape. Seafloor habitats, especially coastal soft sediments, are highly productive and contribute about half of the nutrients needed for primary production in coastal seas (Falkowski et al. 1998, Solan et al. 2004).

Ongoing research on soft sediments has been focusing on benthic invertebrate biodiversity and ecosystem functions (Walker 1992, Usseglio-Polatera et al. 2000, Norling et al. 2007). Functional traits of invertebrate macrofaunal organisms in marine sediments are often associated with location in the sediment, movement patterns, and feeding mechanisms (Hewitt et al. 2008, Kristensen et al. 2012), which can influence bioturbation rates (Bernard et al. 2019). Changes in invertebrate macrofauna population density and animal behaviour associated with environmental stress (e.g. marine heatwaves) can also influence bioturbation (Kauppi et al. 2023). While we are gradually uncovering the influence of invertebrate macrofauna on sediment, our understanding of the effect of vertebrate megafauna remains limited.

The definition of megafauna often varies between individual studies. Here we adopt a criterion based on size, relative to other organisms inhabiting soft sediment, and we focus our attention on larger organisms,

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*Corresponding author:
alessandra.vallim.lima@auckland.ac.nz

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primarily vertebrates, that interact with sediments and sediment processes through distinctive foraging mechanisms (Moleón et al. 2020). For megafauna, some functional traits have been characterised (e.g. feeding mechanisms) (Nelson et al. 1987, Nakaoka et al. 2002, Crook et al. 2022). Early studies addressed the pressures of megafauna in sediments in terms of disturbance and patch dynamics (VanBlaricom 1982, Thrush et al. 1991). However, the consequences of megafaunal bioturbation are poorly understood, hence the connection with biogeochemistry is still lacking. The urgency to fill this knowledge gap comes from the change in megafauna populations, with anthropic activities such as climate change, overfishing, bycatch, and habitat loss and modification affecting conservation (Dulvy et al. 2021, Alves et al. 2022, Braulik et al. 2023).

In this opinion piece, we aim to (1) describe the importance of soft sediment bioturbation, (2) characterise the nature of megafauna bioturbation through sediment reworking, (3) highlight the lack of knowledge on how those processes affect sediment biogeochemistry, and (4) stress the importance of understanding those processes to best conserve those animals and the ecosystem.

2. BIOTURBATION AND THE ROLE OF SEAFLOOR ANIMALS IN BIOGEOCHEMICAL CYCLES

Bioturbation was first described by Darwin (1881) and is defined as the altering of sediment though vertical or lateral movement of sediment particles caused by infauna motility (Mermillod-Blondin 2011). It also leads to transport of solutes through bioirrigation (Volkenborn et al. 2019). Therefore, bioturbation is now considered as an 'umbrella' term for both processes (Kristensen et al. 2012). Bioturbation affects sediment characteristics leading to mixing of sediment and changing the depth of oxic/anoxic layers (Teal et al. 2008, Adamek & Marsalek 2013). Bioturbation also has indirect effects, with tubes, pits, and mounds influencing sediment topography and benthic boundary layer flows (Eckman et al. 1981, Carey 1983). These biogenic structures and the sediment disturbances generated by bioturbation affect recovery processes and influence the diversity, abundance, and recolonization of seafloor communities (Thrush et al. 1991, Ajemian et al. 2012). Consequently, bioturbation influences many important processes from microphytobenthic primary productivity (Levinton 1995, Kristensen et al. 2012) to the transport of pollutants and greenhouse gasses (N_2O, CH_4) across the water–sediment interface (Mermillod-Blondin 2011, Bergman & Bump 2014).

Bioturbation is one of the most significant processes associated with faunal diversity. In the Ediacaran (635–538.8 million years ago), chemical exchanges between the sediment and water were driven by microbial activity and diffusion, but the biodiversity explosion of the Cambrian (538.8–485.4 million years ago) led to animals invading the sediment, profoundly changing both the rate and nature of fluxes (Meysman et al. 2006). In some coastal environments, remineralisation and soluble nitrogen release from the sediment is believed to be responsible for the entire nitrogen requirement for primary production in the water column (Welsh 2003). Current estimates of the global volume of sediment bioturbated in the oceans are over 20 000 km^3 yr^{-1}, over 8 times the volume of Mount Everest (Teal et al. 2008). This estimate is based on the role of invertebrate macrofauna, but as will be demonstrated below, the overall effect of bioturbation is a product of the size and density of bioturbators as well as the specific effects bioturbators have on the sediment (Braeckman et al. 2010, Bernard et al. 2019).

While invertebrate macrofauna generally exhibit higher density compared to vertebrate megafauna, the latter are capable of disturbing larger amounts of sediment, often delving deep into the sediment layers and accelerating biogeochemical processes (Malhi et al. 2016). For example, a single California gray whale *Eschrichtius robustus* contributes to sediment turnover at a rate of 1.2×10^9 m^3 yr^{-1} on the seafloor of the Bearing Sea while feeding (Johnson & Nelson 1984). One loggerhead turtle *Caretta caretta* moves up to 3 m^3 of sand per feeding event (Preen 1996). The size and permanence of the pits in the sediment are variable, remaining discernible from a few tidal cycles to several weeks (Thrush et al. 1991, Nakaoka et al. 2002). These differences depend on the sediment type and the hydrodynamic regime (Yager et al. 1993).

Generally, bioturbators that move the largest amount of sediment are assumed to be the most effective ecosystem engineers (Herringshaw et al. 2017). While the majority of vertebrate megafauna have been observed to actively engage in bioturbation, the impact of this activity on sediment biogeochemical processes has received little attention to date. This prompts us to question the significance of megafauna bioturbation. If megafauna indeed turn over more sediment, in terms of either quantity or depth, compared to invertebrate macrofauna, then they may serve as equally effective ecosystem engineers, particularly in areas characterised by high foraging activities.

3. MARINE MEGAFAUNA AS BIOTURBATORS: DELINEATING NEW FUNCTIONS

Megafauna bioturbation has a broad impact on various habitats across the globe. Rays (elasmobranchs) are possibly the most ubiquitous bioturbators, with diverse foraging behaviours that generate pits of various sizes (Thrush et al. 1991, Crook et al. 2022). Green sturgeons *Acipenser medirostris* engage in infaunal feeding in estuaries, creating as many as 1000 pits ha^{-1} (Moser et al. 2017). In tropical waters, dugongs *Dugong dugon* and hammerhead sharks, such as bonnetheads *Sphyrna tiburo*, are primarily benthic feeders leaving distinctive marks on the sediment surface (Nakaoka et al. 2002, Plumlee & Wells 2016). Similarly, in sub-Arctic environments, the Atlantic walrus *Odobenus rosmarus rosmarus* has a narrow ecological niche, feeding in the sediment for invertebrates (Gebruk et al. 2021). Furthermore, in shallow regions (<50 m) of the Bearing Sea, side-scan sonar has been used to detect the distinctive marks left by California gray whales over a survey area exceeding 22 000 km^2 (Nelson & Johnson 1987).

The reworking mechanism for invertebrate macrofauna has been categorized into functional groups (e.g. 'biodiffusors', upward and downward 'conveyors', and 'bulldozers') according to the amount, distance, or direction of sediment transported (Kristensen et al. 2012). Building upon this framework, we propose a similar division for megafauna (Fig. 1). Firstly, we identify 'pit creators', characterised by round depressions in the sediment, often associated with animals such as rays, dolphins, and sea otters (Thrush et al. 1991, Rossbach & Herzing 1997, Traiger et al. 2016). Pits are often deep enough to affect the oxic/anoxic layer in the sediment but may vary in size and depth. Secondly, 'bulldozers' engage in more disruptive sediment disturbances. These disturbances can extend from 30 cm deep or remain relatively shallow but covering a larger area. Bulldozers resuspend and destabilise a large amount of sediment. Here, examples such as gray whales cause the most significant disruptions, and bonnethead sharks contribute to more surface-level disturbances (Nelson & Johnson 1987, Plumlee & Wells 2016). Lastly, we classify 'trench diggers' as those capable of creating elongated marks exceeding 10 m in length. These marks are typically attributed to the activities of animals such as the Pacific walrus *O. rosmarus divergens* (Nelson et al. 1987).

The disturbances caused by megafauna are typically not singular, but a result of broader actions where large areas of the seafloor present patches of sediment excavated contingent upon prey availability (Johnson & Nelson 1984, Thrush et al. 1991). While these behaviours have been observed for several megafauna (see Table 1), our knowledge of the full range of animals that bioturbate the sediment and their reworking modalities remains limited. More importantly, how these activities influence sediment

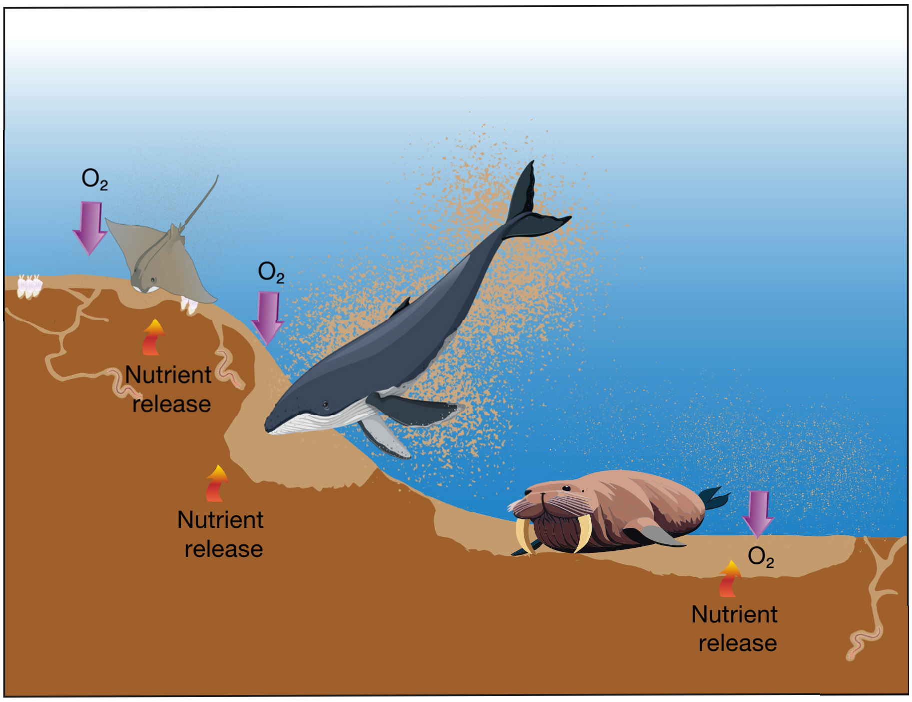

Fig. 1. Bioturbation caused by marine megafauna. Rays create pits in the sediment through different feeding methods such as suction or water jetting. Whales bulldoze by excavating patches of sediment in the seafloor, disrupting large amounts of sediment. Walruses excavate the sediment, creating long trenches. Light brown sediment colour represents oxic sediments, while dark brown represents anoxic sediments. As shown by sediment dispersal, bulldozers disturb larger amounts of sediment. All disturbance allows for penetration of oxygen and release of nutrients from the sediment (purple arrows indicate oxygen intake; orange arrows indicate nutrient release)

biogeochemistry has not yet fully been elucidated. Hence, this classification system serves not only to distinguish the various sediment-reworking behaviours exhibited by megafauna, but also to delineate their different influence on seabed roughness and biogeochemical processes.

4. DISCUSSION

Bioturbation by invertebrate macrofauna influences ecosystem productivity by enhancing transport of solutes and affecting nutrient cycling and sediment stability (Kristensen et al. 2012). Vertebrate bioturbation, primarily occurring during feeding, varies in intensity among species. This contrasts with the near-continuous bioturbation of invertebrate macrofauna. Despite lower density and lower frequency of bioturbation events, vertebrate megafauna individually and collectively disturb larger areas, raising the question of their significance to ecosystem functions linked to bioturbation (e.g. carbon and nitrogen cycling). Unfortunately, the lack of emphasis on vertebrate megafauna as bioturbators has resulted in a scarcity of such data. However, in cases where a seasonal pattern is evident, the disturbance intensity can reach levels sufficiently high to affect a substantial areal turnover within a given year (Table 1). For instance, when examining bioturbation activities by rays in regions such as Australia and New Zealand, a high excavating potential has been observed (Thrush et al. 1991, O'Shea et al. 2012, Crook et al. 2022). In a single harbour in New Zealand, for example, New Zealand eagle rays *Myliobatis tenuicaudatus*, through pit creation, turn over sediment within an area of 700–800 m^2 every 70 d (Thrush et al. 1991).

The location and nature of reworking mechanisms can result in distinct impacts on the vertical distribution of organic matter, particle arrangement, and sediment grain size distribution. Illustratively, 2 co-occurring Australian stingrays, *Himantura australis* and *Pastinachus ater*, exhibit different foraging behaviours while creating pits in similar sediment characteristics. *H. australis* engages in intense, localized bioturbation through sediment excavation, whereas *P. ater* prefers nondisruptive feeding, or may alternatively utilize a water jetting strategy if required. While *P. ater* forms fewer feeding pits, it forages over a broader sandflat area, likely promoting nutrient dispersal across a larger region (Crook et al. 2022). In contrast, within the Bering Sea, the feeding activities of gray whales and walruses on the seafloor lead to varied impacts attributed to differences in sediment types at each location. The fine sand disturbed by whales tends to resuspend to greater heights and travel longer distances with currents, while the coarse sediment and gravel excavated by walruses settle back onto the seabed more rapidly (Nelson & Johnson 1987).

Regardless of whether megafauna bioturbation events are episodic or more frequent than previously thought, there is no denying that they affect the sediment. The presence of the disturbances will affect the horizontal structure of the seabed and therefore of the benthic boundary layer, altering water flow and thus nutrient exchange (Richards 1990, Boudreau & Jørgensen 2001). The disturbance also allows larger particles from the water column to settle within the pits faster than in areas of the same size in the seabed (Yager et al. 1993). The effectiveness of the disturbance on fluxes will be modified by water flow and sediment particle size (Thrush et al. 1991, Yager et al. 1993, Townsend & Fonseca 1998). This is important for invertebrate macrofauna remaining in the pits and their recolonization, and their food availability, thus generating secondary bioturbation effects associated with megafaunal activity. It is imperative to emphasize that human-induced disturbances, such as dredging and trawling, differ from megafauna bioturbation. Whilst the latter is a natural occurring process, the former are notable for their large scale and heightened frequency, disrupting natural recovery processes, often leading to biodiversity loss (Thrush & Dayton 2002, Olsgard et al. 2008).

There is evidence for the importance of megafauna in Earth system processes through influences on ecosystem structure, biogeochemical cycles, and species interactions (Smith et al. 2016). Despite widespread conservation efforts, the decrease in large bioturbators through climate change, overfishing, bycatch, and habitat loss and modification may be detrimental to ecosystems and their functions (Pimiento et al. 2020). The presence or absence of certain species can trigger cascading effects in ecosystems, impacting food webs and biodiversity. Dugongs and sea turtles adjust their feeding habits in response to the abundance of certain predators (Heithaus et al. 2007, Wirsing et al. 2007). Additionally, bottom trawling can also affect the foraging behaviour of bioturbators such as the yellowed-eye penguin in New Zealand (Mattern et al. 2013). These changes have the potential to influence megafauna-driven bioturbation by altering their foraging behaviours.

The challenge in studying these animals lies either in their high mobility, or difficulty in sampling the pits. However, in the past decade, technological ad-

Table 1. Examples of megafauna known to forage in the sediment. For average disturbance sizes, D: depth; W: width; L: length; –: unknown

Taxonomic class	Species	Conservation Status (IUCN)	Average disturbance size (m)	Estimate sediment turnover	Type of feeding	Reference
Bony fish	Green sturgeon *Acipenser medirostris*	Endangered	> 1000 pits ha^{-1}	–	Pit creator	Moser et al. (2017)
	Common bluestripe snapper *Lutjanus kasmira*	Least Concern	–	–	Pit creator	DeFelice & Parrish (2003)
	Goatfish *Parupeneus* sp.	Least Concern	–	–	Pit creator, bulldozer	McCormick (1995)
	Yellowtail flounder *Myzopsetta ferruginea*	Vulnerable	–	–	Bulldozer	Link et al. (2002)
Cartilaginous fish	NZ Eagle ray *Myliobatis tenuicaudatus*	Least Concern	0.8 × 0.12 (W × D)	700 m^2 in 70 d	Pit creator	Thrush et al. (1991)
	Spotted eagle ray *Aetobatus narinari*	Endangered	–	–	Pit creator	Ajemian et al. (2012)
	Broad cowtail ray *Pastinachus atrus*	Vulnerable	–	1.08 m^3 in 21 d (for *P. atrus, Himantura* spp., *T. lymma* and *U. asperrimus* combined)	Pit creator	O'Shea et al. (2012)
	Himantura spp.	Variable between species				
	Bluespotted lagoon ray *Taeniura lymma*	Least Concern				
	Porcupine ray *Urogymnus asperrimus*	Vulnerable				
	Cownose ray *Rhinoptera bonasus*	Vulnerable	–	–	Pit creator	Ajemian & Powers (2012)
	Nurse shark *Ginglymostoma cirratum*	Vulnerable	–	–	Bulldozer	Tanaka (1973), White et al. (2022)
	Australian whipray *Himantura australis*	Stable	–	~200 t yr^{-1} by a single ray	Pit creator	Crook et al. (2022)
	Hammerhead shark *Sphyrna lewini*	Critically Endangered	–	–	Bulldozer	Holland et al. (1993)
	Bonnethead *Sphyrna tiburo*	Endangered	–	–	Bulldozer	Cortés et al. (1996), Plumlee & Wells (2016)
Reptiles	Loggerhead turtle *Caretta caretta*	Vulnerable	1.5 × 0.45 (W × D)	3 m^3 per feeding	Pit creator	Preen (1996)

Table continues on next page

Table 1 (continued)

Taxonomic class	Species	Conservation Status (IUCN)	Average disturbance size (m)	Estimate sediment turnover	Type of feeding	Reference
Birds	Yellowed-eyed penguin *Megadyptes antipodes*	Endangered	–	–	Bulldozer	Mattern et al. (2007, 2018)
Mammals	Grey whale *Eschrichtius robustus*	Least Concern	8 × 2 × 0.4 (L × W × D)	1.2×10^9 m^3 yr^{-1}	Bulldozer	Johnson & Nelson (1984)
	Humpback whale *Megaptera novaeangliae*	Least Concern	–	–	Bulldozer	Friedlaender et al. (2009), Ware et al. (2014)
	Orca *Orcinus orca*	Data deficient	–	–	Bulldozer	Visser (1999)
	Common bottlenose dolphin *Tursiops truncatus*	Data deficient	0.5 × 0.15 (W × D)	–	Pit creator	Rossbach & Herzing (1997), Quigley et al. (2022)
	Sea otter *Enhydra lutris*	Endangered	0.5 (D)	–	Pit creator	Traiger et al. (2016
	Dugong *Dugong dugon*	Vulnerable	0.21 (W) × 0.4–several metres (L)	–	Trench digger	Cossa et al. (2023)
	Walrus *Odobenus rosmarus*	Vulnerable	47 × 0.4 × 0.3 (L × W × D)	7.5×10^7 m^3 yr^{-1}	Trench digger	Nelson et al. (1987), Gebruk et al. (2021)

vances in imaging and acoustic technology have significantly improved our ability to characterise the seafloor (Misiuk & Brown 2024). Drone imagery and machine learning have also been used to account for bioturbation patterns from megafauna (Crook et al. 2022, Cossa et al. 2023), and to analyse ecosystem functions from invertebrate macrofauna communities (Schenone et al. 2022). Incubation chambers and lander experiments conducted in intertidal and subtidal seafloor environments also offer a range of applications, such as measuring benthic fluxes of oxygen and nutrients (Schenone & Thrush 2020, Kononets et al. 2021). These chambers have been used to assess the impact of invertebrate macrofauna on sediment biogeochemistry (Norkko et al. 2013, Schenone & Thrush 2020), and may also be used to characterise the larger disturbances of megafauna. These tools hold the potential to investigate the effects of megafauna on biogeochemical cycles, offering new venues for exploration in the field.

The term 'ecosystem engineers' encompasses animals capable of changing the distribution of resources (Jones et al. 1994, Kristensen et al. 2012). As such, we believe that larger bioturbators should fall within the same category. As we move forward, it becomes imperative to consider the ecological implications of megafauna bioturbation in the context of a changing climate and anthropogenic pressures. While it is evident that these animals alter sediment structure, thus affecting biogeochemistry, it is unclear to what extent that effect supports ecosystem functioning. Vertebrate megafauna are among the most threatened taxa in the ocean. Table 1 highlights several potential significant bioturbator species at risk, and our approach to conservation should address threats at the individual species level whilst also encompassing the broader context of habitats and ecosystems that includes the functional role of these species. Thus, adopting a process-based approach is crucial to guide effective management actions. Future research should prioritize the investigation of the impact of megafauna on sediment biogeochemistry and the links to ecosystem function. This involves considering not only their physical impact on the seafloor, but also their influence on nutrient cycling, and their overall role on ecosystem functioning. By establishing connections between their behaviours and functional roles, we can enhance conservation efforts though sustainable management of seafloor habitats, ensuring the preservation of their ecological functions.

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