BIOGENIC SEDIMENT MIXING: BRIDGING THE GAP BETWEEN THE MODERN AND THE ANCIENT

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ABSTRACT

Biogenic sediment mixing is a key process in modern environments, which has played a major role in triggering macroevolutionary breakthroughs, including those that took place during the Ediacaran-Cambrian transition. In the modern, several procedures are used to quantify key metrics such as the thickness of the mixed layer, the maximum depth of sediment mixing, and the intensity of biogenic sediment reworking. Although assessing the extent and role of biogenic sediment mixing in the fossil record has been informed by our knowledge of bioturbation in modern oceans, extrapolating concepts and quantifying proxies is problematic.

Complications arise from a series of conceptual barriers, which are sociological, epistemological, and ontological in nature. Sociological barriers reside in the fact that separate scientific communities deal with bioturbation in the modern and fossil record. These obstacles can be effectively removed through increased collaboration among marine benthic ecologists and ichnologists, which will result in enhanced cross-fertilization between fields. Epistemological barriers involve inconsistencies in terminology and conceptual frameworks, such as divergent interpretations of the term "mixed layer." These can be mitigated through the standardization of definitions, clarification of misconceptions, and adoption of unified methodological protocols. Ontological barriers, however, are the most difficult to overcome stemming from the fundamental differences between the nature of the modern and the fossil record, which impact on their corresponding datasets. This is illustrated by the need of adjusting functional modes employed for modern bioturbators for the analysis of the fossil record and integration with paleobiology, and by the difficulties in quantifying biogenic sediment reworking in the fossil record. There are also notable differences in the availability of environmental and ecological correlates most closely associated with bioturbation, which

lead to differences in the ability to determine and compare the relative importance of influential parameters reflected in the fossil record versus the modern. Hence, ancient bioturbated intervals do not fully represent a snapshot of the modern, precluding quantification of some parameters, most notably the thickness of the mixed layer. These limitations underscore the importance of contextualizing bioturbation within its sedimentological framework to better understand the unique nature/characteristics of trace fossil assemblages. Ultimately, a nuanced evaluation of the interplay of bioturbation and sedimentation is essential for advancing interpretations of paleoenvironmental and evolutionary dynamics and increase awareness of the idiosyncratic aspects of the trace-fossil record.

INTRODUCTION

Biogenic sediment mixing consists of the biological reworking of sediment particles, a process commonly referred to as bioturbation (Bromley 1996; Meysman et al. 2006). However, the latter term may be also understood as including biogenically induced pore fluid movement as well (Kristensen et al. 2012), also known as bioirrigation. Bioturbation is a fundamental process in modern environments (Schink and Guinasso 1977; Krantzberg 1985; Aller 1994; Canfield and Farquhar 2009; van de Velde and Meysman 2016; Bianchi et al. 2021; Zhang et al. 2024; Hovikoski et al. 2025; Löwemark 2025). Over the past few decades, significant progress has been made in understanding the mechanisms, extent, and implications of bioturbation (Fig. 1). Furthermore, biogenic sediment mixing strongly impacts isotope signals, introducing age errors up to tens of thousands of years in marine settings, therefore affecting high-resolution time series that form the basis for paleoclimatic and geochemical studies (Löwemark 2025). In parallel with these developments in the study of modern bioturbation, there has been growing recognition of its pivotal role in geobiology, particularly as a driver of macroevolutionary innovation. Bioturbation (together with bioirrigation) is now regarded as a key factor in the Cambrian explosion, the most important evolutionary radiation in marine ecosystems which took place at the dawn of the Phanerozoic (Seilacher 1999; Butterfield 2011; Laflamme et al. 2013; Mángano and Buatois 2014, 2017; Darroch et al. 2018; Gougeon et al. 2018, 2025; Buatois et al. 2020; Mángano et al. 2024).

Assessing biogenic sediment mixing in the fossil record has been informed by our knowledge of bioturbation in modern oceans. However, extrapolating concepts and quantifying proxies based on the modern to the rock record is not without problems (Laing et al. 2022). Some of the challenges stem from sociological (such as the division between scientific communities focused on modern versus ancient systems) and epistemological (such

as different terminologies and conceptual frameworks) barriers. Others are more profound and deeply rooted in ontological difficulties, reflecting the fundamentally distinct nature of the objects under investigation (modern biogenic structures vs. trace fossils) and the proxies employed to address significant research questions. In this paper, we identify barriers that may have led to misconceptions that are firmly entrenched in the literature, illustrate some of these issues with examples, and propose next steps that may help to bridge the gap between the modern and the ancient.

CONCEPTUAL AND TERMINOLOGICAL ISSUES

In general, well-bioturbated modern sediments in fully marine environments are vertically zoned comprising three stacked layers that reflect distinct biological, geological, and geobiological processes (Berger et al. 1979; Ekdale et al. 1984; Savrda 2007; Canfield and Thamdrup 2009; Löwemark 2025) (Fig. 2). These layers are characterized not only by differences in sedimentary fabric and biogenic structures but also by a vertical geochemical profile that corresponds to successive metabolic zones. The uppermost layer known as the mixed zone (or mixed layer) is saturated in water (up to 90%), has low shear strength, is typically well oxygenated, and is fully homogenized by bioturbation of macro and meiofauna (Savrda and Ozalas 1993; Löwemark 2025). This uppermost sediment cap regulates solute exchange between the sediment and the water column influencing nutrient cycling (Laverock et al. 2011; Gautreau et al. 2020). Biodeformational structures are dominant, and discrete traces are typically absent (with the exception of some mucus-lined burrows with limited preservation potential), resulting in bioturbation mottling. Beneath the mixed layer lies the transition zone (or transition layer), a heterogeneous zone due to the activity of burrowing animals that produce discrete traces emplaced in more compacted and stiffer sediments. This

zone is characterized by a vertical environmental gradient (defined by oxygen content of interstitial water, substrate firmness, food supply, and biogeochemical processes) that influences the depth distribution of trace making animals. This results in a vertical partitioning of the endobenthic marine habitat or tiering (Bromley 1990, 1996; Savrda and Ozalas 1993). The deepest sediment zone is known as the historical zone (or historical layer) and is located below the reach of active burrowers. The actual depth of this zone is context dependent and varies across different environmental settings and through geological time (e.g. Teal et al. 2010; Buatois et al. 2016).

In modern settings, the term “mixing depth” is commonly used to refer to the zone of most intense bioturbation (Boudreau 1994; Teal et al. 2008) (Fig. 2). This term is in practice used as a synonym of mixed layer in many studies (Teal et al. 2008; Song et al. 2022). However, this is a broader sense of mixed layer (i.e. not restricted to the uppermost homogenized layer), as it also includes most shallow discrete burrows formed in the transition layer, especially when determining the maximum penetration depth (MPD) of particulate tracers (Gilbert et al. 2021), ventilatory activity (Delefosse et al. 2015), the maximum gallery depth in the frame of resin casts (Davey 1994; Koo et al. 2005; Rosenberg et al. 2008), or in microcomputed tomography-based work (Hale et al. 2014; Pennafirme et al. 2019, Howman et al. 2024). This situation is compounded by the fact that the boundary between the mixed layer *sensu strictum* and the transition layer may include a gradational zone (Berger et al. 1979). Furthermore, modern detailed studies show that deeper sediment layers are biogeochemically active, and burrows and associated microbial consortia extend the functional depth of nutrient cycling (Marinelli et al. 2002; Kristensen and Kotska 2005). The traditional focus on the mixed layer may underestimate the ecological role of this deeper bioturbation.

The two senses of the term mixed layer (i.e. strict and broad senses) have value in themselves, and their use is commonly apparent based on the provided context (including the specific tracers used). However, problems arise when implications of the mixed layer in one sense are extrapolated to the other as both uses of the term have contrasting significance in many regards (e.g., sediment rheology, degree of heterogeneity, modes of penetration in the substrate). For example, the mixed layer in a strict sense is homogenous and has a relatively high saturation in water (>90%), but the mixed layer in the broad sense is more heterogeneous, comprising discrete biogenic structures and displaying a wider array of geochemical parameters and rheology (Teal et al. 2010).

FROM MODERN TO ANCIENT: PITFALLS IN BIOTURBATION METRICS

In the modern, efforts to quantify various aspects of aquatic bioturbation took off during the 60's (e.g., Rhoads 1963; Fager 1964; Berger and Heath 1968), exploded during the 80's–2000's (Fig. 1), and continue today (e.g., Solan et al. 2019; Hull et al. 2020; Hohmann 2022; Song et al. 2022; Hale et al. 2024). Attempts to evaluate the role of bioturbation in the fossil record, including the analysis of different proxies, have also a relatively long history (e.g., Thayer 1979, 1983; Droser and Bottjer 1989; Savrda and Ozalas 1993), but have experienced a renewed interest in recent years (e.g., Mángano and Buatois 2014; Tarhan et al. 2015; Gougeon et al. 2018, 2025; Cribb et al. 2019, 2023; Buatois et al. 2020, 2025; Cribb and Bottjer 2020; Mángano et al. 2024). There is a series of procedures to measure the thickness of the mixed layer in a strict sense, the maximum depth of sediment mixing, and the intensity of biogenic sediment reworking. Quantifying the different aspects of bioturbation in the rock record has proved to be challenging, but doing so remains important because they are not substitutable metrics. For example, greater levels of mixing intensity do not

necessarily lead to greater mixed depths, and the environmental correlates associated with faunal activity contrast to those associated with the mixed depth (Jumars and Wheatcroft 1989; Smith 1992; Boudreau 1998; Buatois and Mángano 2011; Zhang et al. 2024; Zhu et al. 2024). We discuss here the quantification of the thickness of the mixed layer, the maximum depth of sediment mixing, and the intensity of biogenic sediment reworking.

Estimating the thickness of the mixed layer

In the modern, estimations of the thickness of the mixed layer involve either 1D (i.e. the complete 3D information is summed up in a simple profile), 2D (i.e. only access to a partial lateral 2D information), or 3D (i.e. the complete 3D information is accessible) visualization/quantification methods, but also different tracers (from radionuclides, reactive components, to inert or labelled tracers; e.g., Wheatcroft et al. 1994; Gerino et al. 1998; Michaud et al. 2003; D'Andrea et al. 2004; Solan et al. 2004; Maire et al. 2008; Madsen et al. 2011) (Fig. 3). When pooled together, the worldwide mean mixed depth of marine sediments based on a large panel of particulate tracers has been estimated to be ~5-9 cm, (9.8 ± 4.5 cm, Boudreau 1994; 8.37± 6.19 cm, Teal et al. 2008; 5.10 ± 7.51 cm, Zhang et al. 2024), although these values mask considerable variability (25^{th}-75^{th} percentile, 3.8-9.0 cm; Zhang et al. 2024) across different environmental settings. Indeed, previous work has indicated that the thickness of the mixed layer is controlled by the flux of organic carbon, with higher fluxes resulting in a thicker mixed layer, and *vice versa* (Trauth et al. 1997; Smith and Rabouille 2002; Löwemark 2025). Recent analyses confirm these ideas but reveal that the mixed layer is largely associated with differences in sediment organic carbon, primary productivity, salinity, depth, distance to shore, and temperature (Miguez-Salas et al. 2024; Zhang et al. 2024).

The picture from the fossil record is even more complex as the three-tier vertical zonation (while a snapshot of the modern ocean sediment) is not possible to be recovered as vertically stacked layers (Fig. 4). For undisrupted continuous vertical accretion of the seafloor sediment, the mixed and transitional layers at a given time are buried and overprinted by overlying bioturbation becoming the historical layer. Therefore, sedimentary rocks (in contrast to modern sediments) typically show an undifferentiated, background bioturbated fabric overprinted by well-defined discrete traces formed in the transitional layer (Savrda 1992, 2007). In other words, the mixed and transitional layers are recorded and visualized as a palimpsest of mottled sediment crossed-cut by discrete structures (Fig. 4).

The concomitant upward migration of burrows due to vertical accretion of the seafloor has important consequences since it precludes measuring the thickness of the mixed layer in stratigraphic successions (Gougeon et al. 2018). Since discrete bioturbated intervals do not represent snapshots, measuring their thickness does not provide any estimate of the thickness of the original mixed layer. The only situation in which the actual thickness of the mixed layer can be measured is in the case of a total cessation of the bioturbation process in the absence of erosion. This is the case of the so-called frozen tiering profiles formed because of a sudden deoxygenation event (Savrda and Ozalas 1993; Orr 1994) (Fig. 4C). The suppression of bioturbation led to the preservation of an “intact mixed layer” (providing it survived the strong effect of compaction, aided by early diagenetic processes) below an interval of unbioturbated, anoxic, black laminated shale. Even in this case, the measured thickness needs to be corrected, and compaction may be highly variable depending on the original water content and subsequent burial history, among other parameters, with values typically ranging between 50 and 70%. Regardless, the presence of the mixed layer in the rock record can be identified through the recognition of bioturbation mottling overprinted by discrete trace fossils emplaced in the transitional layer (Wetzel 1981; Werner and Wetzel

1982; Savrda 1992; Savrda and Ozalas 1993; Gougeon et al. 2018). This crosscutting pattern has been recognized in fully marine deposits as old as Cambrian Age 2 (Gougeon et al. 2018, 2025).

Measuring maximum depth of bioturbation

In the modern, measuring maximum penetration depth is more straightforward than in the fossil record. In subaqueous environments, this has been done mostly using cores, although investigators have also derived maximum penetration depths using sediment profile imaging in offshore shelf settings (e.g. Germano et al. 2011). However, this is not without problems as some deep-tier structures (e.g., those made by decapod crustaceans) may penetrate deeper than the recovered core (e.g. Pemberton et al. 1976) or camera field of view (e.g. Germano et al. 2011), therefore resulting in the underestimation of the actual maximum depth of bioturbation. A variety of alternate means to quantify maximum burrowing depths are now being used, including burrow casting with resin or plaster, which is providing information not only on penetration depth but on the architecture and co-positioning of biogenic structures (Seike 2023).

Measuring maximum penetration depth is also done on a relatively regular basis in studies dealing with the fossil record. This can be attained with some confidence in the case of well-defined colonization surfaces. A classic example is illustrated by burrows penetrating from the top of an event bed (e.g., tempestite, turbidite). However, even in these cases, care should be taken to detect the influence of possible erosion that may have truncated the upper part of the burrow. Regardless, in the fossil record, this is typically done only for certain ichnotaxa (e.g., some vertical burrows), as in many instances (e.g., regularly meandering, spiraling, and meshed burrows referred to as graphoglyptids), the actual penetration depth

cannot be established. Accounting for compaction should be considered as well to avoid underestimating maximum depth of bioturbation.

In most cases, relative depths of penetration among different trace fossils can be established to reconstruct the tiering structure. This can be done through detailed analysis of crosscutting relationships, burrow boundaries, and burrow fill, and by comparisons with modern examples (Bromley and Ekdale 1986; Bromley 1990, 1996; Taylor et al. 2003). Deeper traces crosscut shallow traces as a response to vertical accretion of the seafloor. The deeper the burrow is emplaced, the better the definition of the burrow morphology and the sharper the burrow boundary are because of increased substrate stiffness with depth. Also, deeply emplaced burrows tend to show higher contrast with the host rock because of particle sorting by the bioturbator or because of passive fill of material coming from the surface (Bromley 1990, 1996; Taylor and Goldring 1993). Burrow-fill in deep-tier trace fossils typically comprises chemically dynamic material encased in reducing sediment, which results in promoting a diagenetic microenvironment that prompts mineralization, which ultimately leads to burrow enhancement (Aller and Yingst 1978; Aller 1988; Bromley 1990, 1996).

Quantifying biogenic sediment mixing

Intensity of bioturbation in the modern is, in practice, typically assessed using D_b, which is defined as the rate at which the variance of particle location changes over time (Wheatcroft et al. 1990; Smith and Rabouille 2002; Teal et al. 2008). As with the thickness of the mixed layer, estimations of D_b can be achieved using the distribution of tracers through the sediment profile (Meysman et al. 2003, 2008). Estimating the degree of bioturbation activity is also central to studies in the fossil record. Following initial attempts in the 50's (Moore and Scrutton 1957), the subsequent proposal by Reineck (1963, 1967) of seven

grades of bioturbation (from 0 for unbioturbated sediments to 6 for full bioturbation) has been met with overall acceptance (e.g., Howard and Frey 1975; Frey and Wheatcroft 1989; Taylor and Goldring 1993; Taylor et al. 2003). These categories were further used to define a bioturbation index (BI) based on burrow density, amount of burrow overlap (two morphological parameters like the ones determined in the modern 2D/3D studies of bioturbation) (e.g. Davey 1994; Mazik et al. 2008; Pennafirme et al. 2019), and the quality of preservation of the primary sedimentary fabric (Taylor and Goldring 1993).

Although time consuming, the use of ichnofabric constituent diagrams allows characterizing type and size of trace fossils, the percentage of bioturbated area per ichnotaxon, and the depth and order of emplacement of each ichnotaxon (Taylor and Goldring 1993). This approach is particularly relevant for the integration with data from the modern as it may allow allocation of a degree of bioturbation to each type of tracemaker. The ichnofabric index, based on a semiquantitative field classification of ichnofabrics as displayed by a series of flashcards, has also been extremely popular (Droser and Bottjer 1986, 1989; Bottjer and Droser 1991; Twitchett and Wignall 1996; Boyer and Droser 2011).

However, assessment of intensity of bioturbation in the fossil record is more nuanced than typically assumed. For example, it is not possible to quantify bioturbation as a measure of unit volume per unit time (as it is in the modern) directly in the fossil record. Also, the use of ichnofabric or bioturbation indexes, although practical in terms of a fast evaluation of degree of bioturbation in stratigraphic successions, may become misleading if this procedure is done in an acritical and automatic fashion. Indexes are easier to use in the cases of discrete trace fossils overprinting an undisrupted sedimentary fabric (e.g. the crustacean burrow *Ophiomorpha* cross-cutting a cross-bedded sandstone), but less so when distinct burrows overprint a mottled fabric. In this latter case, failure to recognize the presence of a bioturbated background would result in significant underestimation of the total degree of

bioturbation and an inappropriate measure of the intensity of biogenic reworking. Also, most ichnofabrics are composite (i.e., produced by the work of successive communities or by the upward migration of a tiered community), particularly under fully marine conditions (Bromley and Ekdale 1986; Savrda 2016). In this context, estimations of the degree of bioturbation may not be relevant to characterize the burrowing potential of individual taxa or of a community as the product is a result of time averaging. Ekdale and Bromley (1991, p. 234) highlighted the limited relevance of quantifying intensity of bioturbation under these conditions in an ironic fashion by stating that "it actually may indicate the degree of enthusiasm of the author rather than any intrinsic quality of the rock!".

In the same vein, estimations may be meaningless if the colonization surface is not located as the true composite nature of the ichnofabric may remain undetected (Savrda 2016; Mángano and Buatois 2020). The only way of overcoming these issues is by avoiding measuring the degree of bioturbation in isolation of the other tools that are an integral part of the ichnofabric analysis (Bromley and Ekdale 1986; Bromley 1996; Buatois and Mángano, 2011).

PERSPECTIVES

We have identified three types of barriers, sociological, epistemological, and ontological, that promote a gap between the modern and the ancient realms of bioturbation. Sociological barriers exist within scientific communities but can be effectively overcome by promoting increased collaboration between marine benthic ecologists and ichnologists, thereby fostering enhanced cross-disciplinary exchange. Attempts in this direction have been produced but they remain relatively uncommon (e.g., Meysman et al. 2006; Plotnick 2012). The same can be said of scientific conferences, which remain quite compartmentalized,

although gatherings like *Ichnia* and *Nereis Park* represent significant advances in the right direction (see Mángano 2021) as they help to improve understanding, break down inter-disciplinary compartmentalization and foster the cross-fertilization of ideas (Raffaelli et al. 2005).

Epistemological barriers can be minimized working on the clarification of conceptual and terminological issues and by the adoption of shared methodological approaches wherever possible. Adoption by ichnologists of the three-partite division of ocean floor sediments used by modern marine benthic ecologists and oceanographers was originally done within the framework of the deep-sea drilling project (Ekdale et al. 1984) and subsequently applied to the analysis of bioturbation in deep time (Gougeon et al. 2018). The functional modes employed for modern bioturbators (François et al. 2002; Solan and Wigham 2005) have also been adopted by ichnologists working with the fossil record, but this displacement from one field to another has needed some degree of adjustment to be fully applicable and to allow for integration with paleobiology (Minter et al. 2016, 2017). Currently, the modern classification of species into certain functional groups of bioturbators is linked to their known or inferred behaviour (e.g., tube construction, crawling) and/or to the observed pattern of particle distribution they produce (Queirós et al. 2013). This example shows that attaining a full common set of concepts and methods may remain impossible as some of the discrepancies reflect differences at a deeper (i.e., ontological) level.

Ontological difficulties are the most complicated challenges to overcome as they are rooted in the disparate nature of bioturbation in the modern and the fossil record, and their corresponding datasets. Some of these problems may seem intractable, but the first step in the direction to mitigate them is to identify some of the corresponding difficulties like, for example, those surrounding the different expressions of the mixed layer in the modern and in the ancient. Ongoing improvements in mapping the spatial variation of the mixed layer in

modern environments represent a significant step forward in evaluating the complexities in sediment mixing across a broad spectrum of latitudinal and depositional gradients today (e.g., Solan et al. 2019; Hohmann 2022; Song et al. 2022; Zhang et al. 2024). In particular, the use of marine cabled observatories and autonomous vehicles, where real-time or near real-time high-frequency seafloor video and sonar images can combine experimental manipulation with direct observations, is valuable to inform on the extent, role, and timing of specific bioturbators in sediment mixing (Robert and Juniper 2012; Ciarolo et al. 2023; Fig. 5). Furthermore, observations of species movement tracks coupled with body size measurements can be used to estimate both horizontal sediment-reworking (Miguez-Salas et al. 2024) as well as vertical mixing rates (D_b) (Robert and Juniper 2012). In addition, defining the zone of the sediment actively involved in geochemical cycling may be more challenging than previously anticipated, as there is significant heterogeneity in this zone. Modern studies have shown that deeper communities involving burrow and bacterial associations can be actively involved in nutrient recycling (Marinelli et al. 2002; Kristensen and Kotska 2005).

Present work in understanding functional groups of important bioturbators is fundamental and will undoubtedly contribute to an enhanced evaluation of the ecology of bioturbation in the fossil record. This is particularly true of post-Paleozoic marine communities, which are characterized by the dominance of the Modern Evolutionary Fauna that makes up the bulk of the modern biosphere (Sepkoski 1981, 1990). Elements of this fauna are the ones that allow for the better extrapolation from the modern to the past because of the commonality of tracemakers. Problems became more acute in the search for modern analogues further back in geological time, and it may be argued that the application of actualism may become quite problematic for the analysis of many Ediacaran-early Paleozoic bioturbators, not only due to uncertainties in the producers but also with respect to marked differences in ecological context.

Beyond the search for qualitative relationships between ancient and modern bioturbation, a much more challenging quantitative approach could be also envisaged. Quantification of modern bioturbation is mainly based on the way the species behave and transport particles (i.e. using the specific accurate models defined for each functional group applied to tracer distribution profile). By experimentally studying burrow structures and sediment reworking (e.g. Turk et al. 2024), one could attempt to find quantitative relationships between some burrow structural parameters and sediment reworking coefficients (R_M; Fig. 3). Although not straightforward (i.e. requiring important experimental and mathematical/statistical efforts), this approach deserves to be explored. There are various model species for bioturbation, such as the surficial modifier urchin *Brissopsis lyrifera* (Hollertz and Duchêne 2001), the gallery-forming biodiffuser polychaete *Hediste diversicolor* (Gilbert et al. 2021), the upward conveyor holothurian *Molpadia oolitica* (Rhoads and Young 1971), and the regenerator decapod *Uca pugnax* (McCraith et al. 2003) that, collectively, represent the typical contrasting modes of bioturbation found within a full benthic community providing that they work as modern analogues of ancient sediment mixers. If such relationships exist, ancient sediment reworking intensity may be estimated by assuming a certain functional proximity of modern species to marine trace fossils.

Studies attempting to apply results from the modern to the fossil record should be aware of the idiosyncratic aspects of bioturbated sedimentary rocks that do not represent a snapshot of the modern but rather the interplay of bioturbation, erosion, and sedimentation, as well as of the limitations of actualism. Integration of the ichnofabric approach within the framework of recent developments in paleoenvironmental reconstruction represents a promising line of research to improve our understanding of the evolutionary history of bioturbation (Gougeon et al. 2025). Scaling from the local to the global is a concern for those dealing with modern as well as ancient bioturbation. In the fossil record, we need to be aware

of Doug Erwin's paleobiological version of Heisenberg Principle (Erwin 2006). On one hand, detailed studies at one site cannot necessarily be extrapolated globally as it is unclear if the local study is representative of global conditions. On the other, global studies necessarily miss the local variances of specific case studies with their inherent detailed information. Balancing these two end members of the scale will be needed to produce an accurate picture of bioturbation in deep time.

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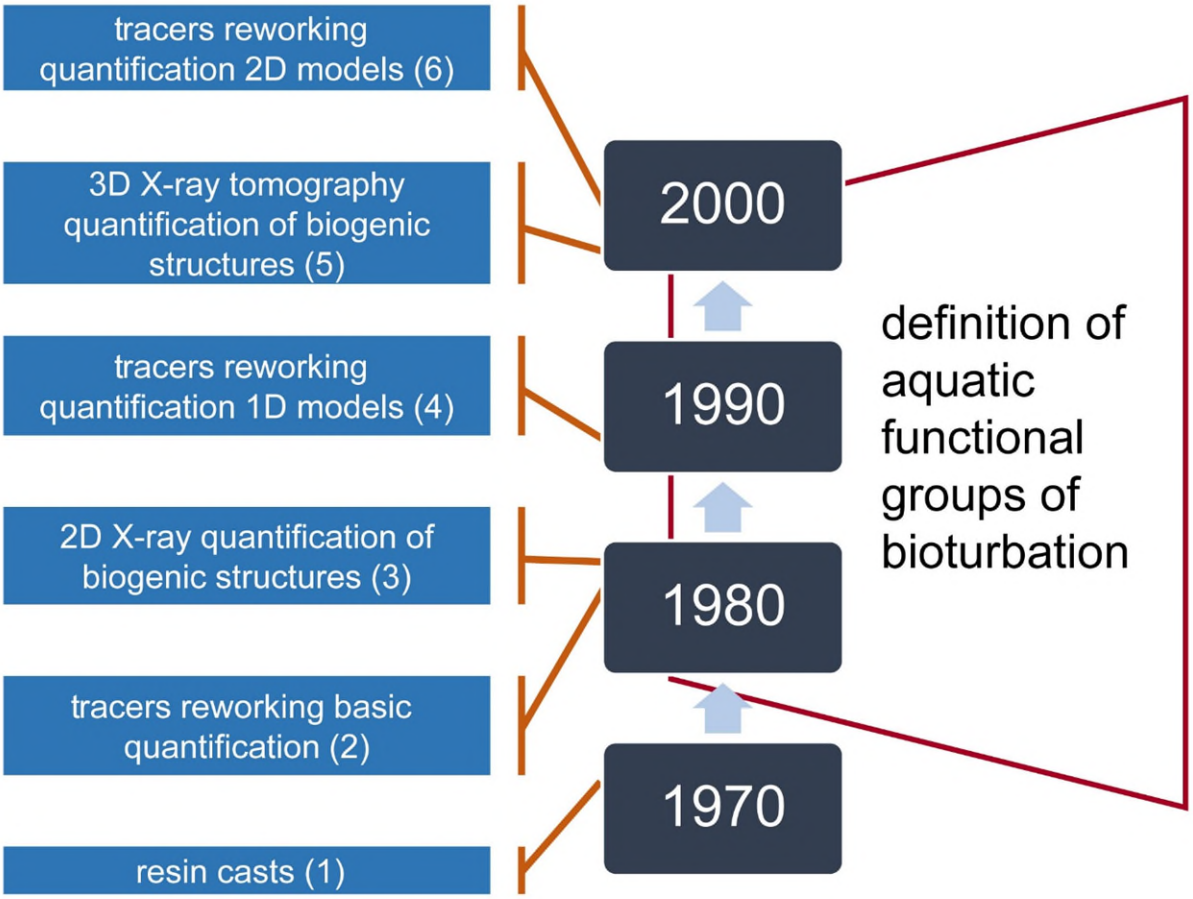

FIG. 1—Timeline presenting the initial publications of major methodological developments in the study and quantification of modern biogenic structures and particle mixing bioturbation (using particulate fluorescent tracers, in particular) in aquatic ecosystems. The 1980–2000 period also led to the definition of aquatic functional groups of bioturbators (Kristensen et al. 2012). Numbers refer to the following sources: (1) Risk et al. (1978), (2) Mahaut and Graf (1987), (3) Aller (1989), (4) Gerino (1990), (5) de Montety et al. (2000), and (6) Gilbert et al. (2003).

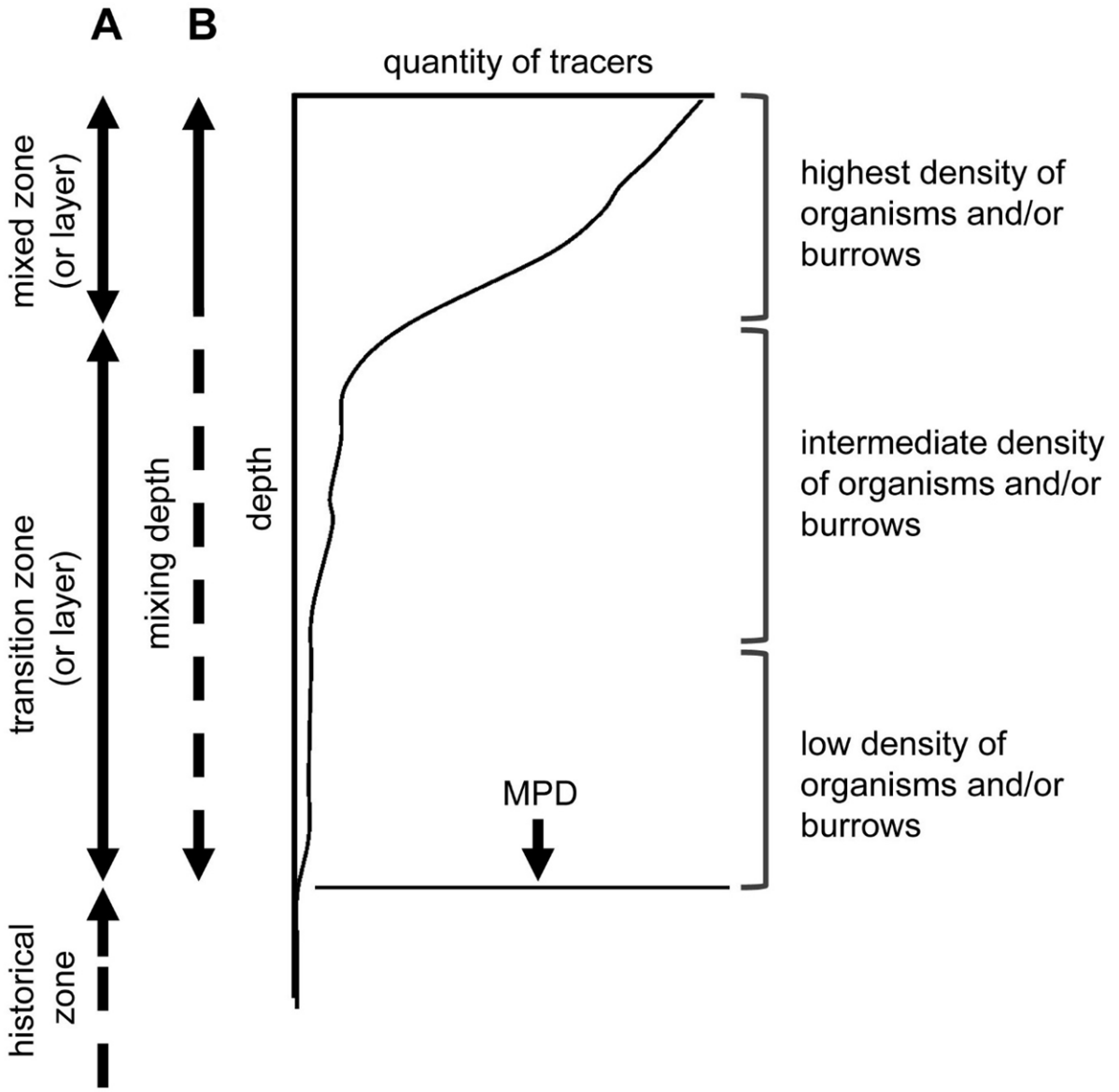

FIG. 2—Hypothetical vertical zonation of tracers (initially placed on the sediment surface) due to a combination of biodiffusive-like and non-local mixing processes. The different denominations of the bio-mixing zonation, either based on the currently accepted tripartite division (A) or on the use of particulate tracers (B), are indicated. MPD refers to the Maximum Penetration Depth of tracers, a proxy used within the framework of modern bioturbation studies involving particulate tracers. This could also refer to the maximum depth of burrows when the biogenic structures are directly visualized using methods such as 3D-tomography.

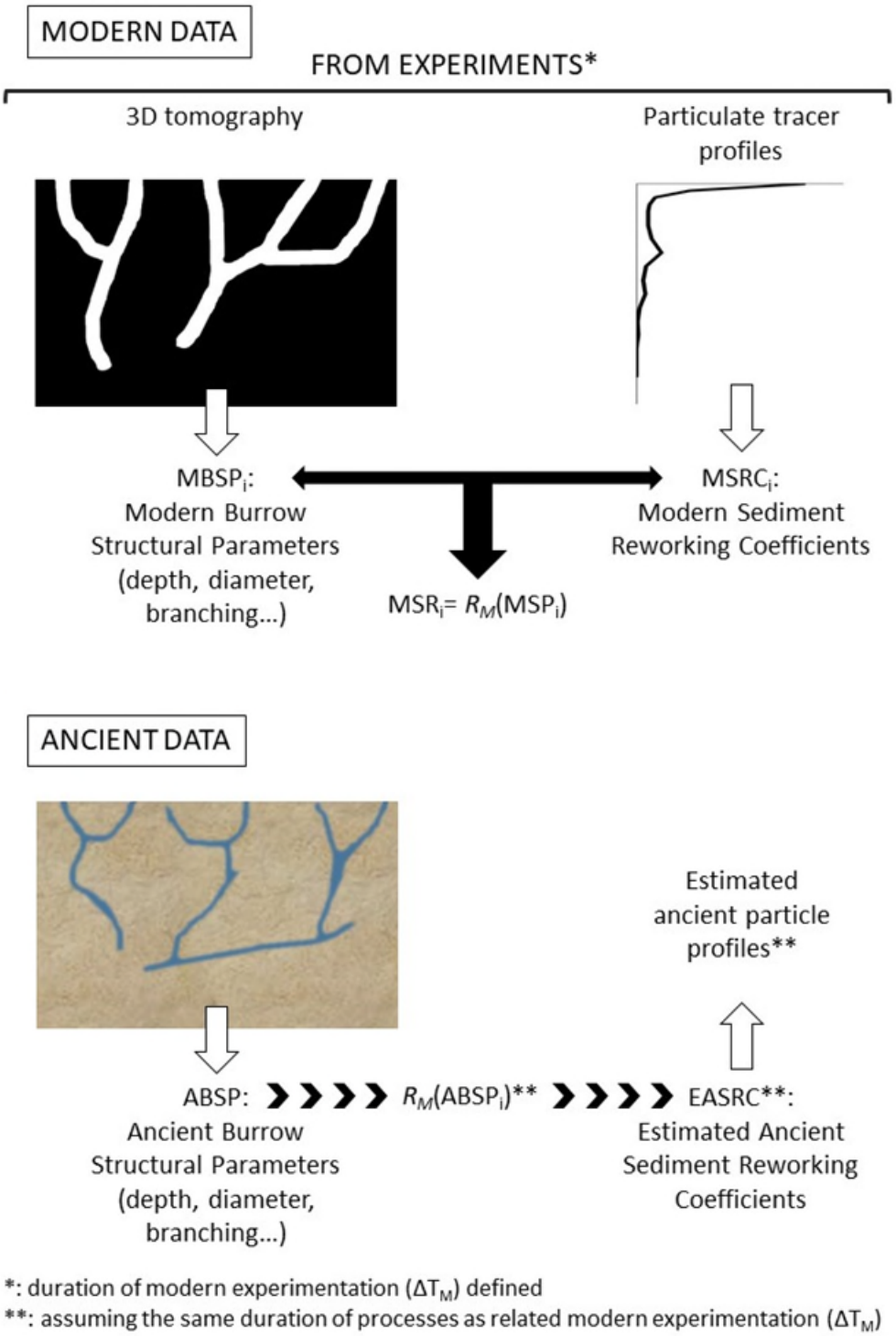

FIG. 3—A possible way of attempting to quantitatively link certain modern burrow structural parameters (MBSP) and modern sediment reworking coefficients (MSRC), and to use these potential relationships (R_M) to produce estimated ancients reworking coefficients (EASR) from ancient burrow structural parameters (ABSP).

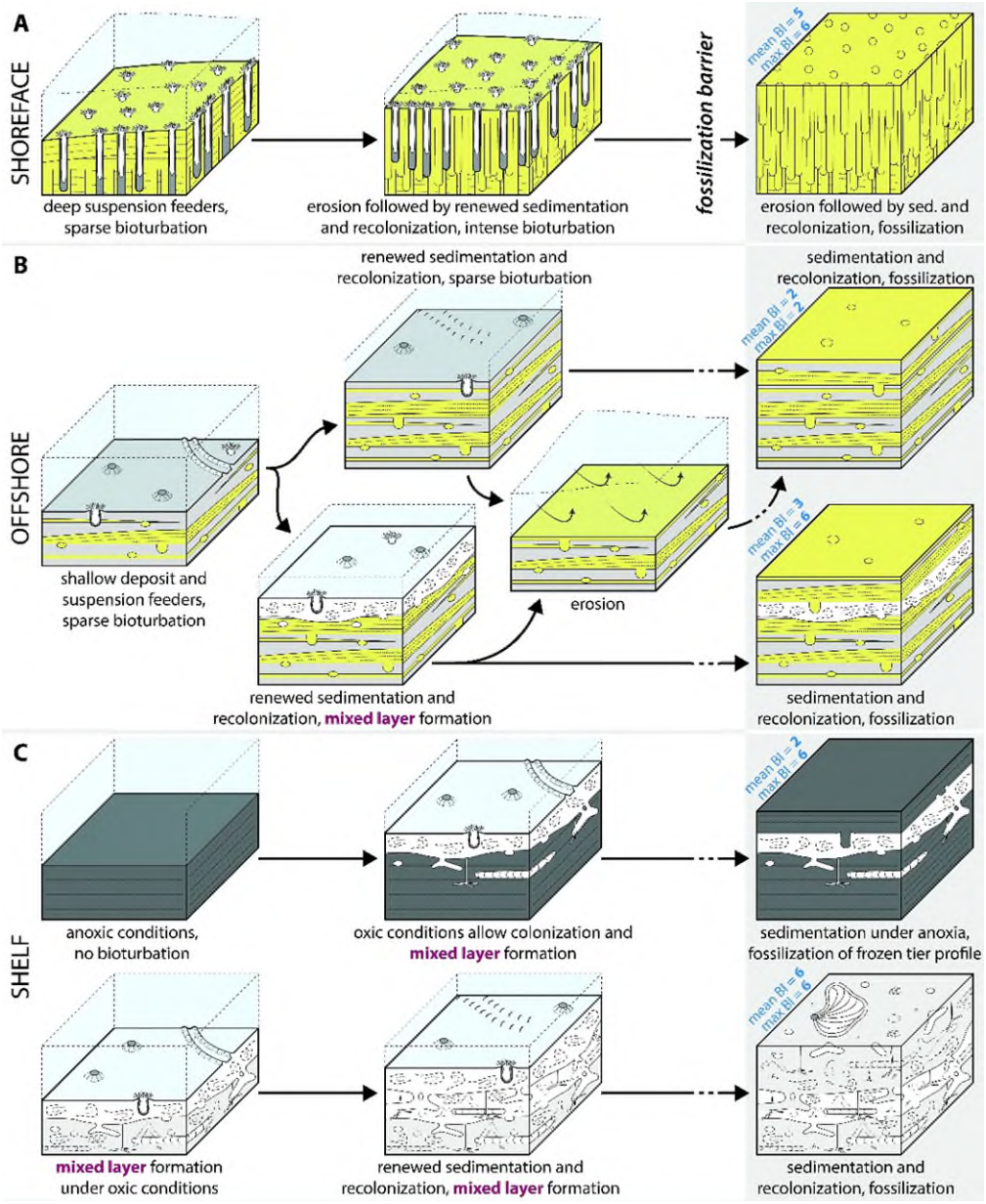

FIG. 4—Taphonomic pathways illustrating the preservation potential of a sediment mixed layer in the fossil record. Note the discrepancies between mean and maximum bioturbation index (BI) (right column), showing that (1) only maximum BI can account for the development of a mixed layer in the fossil record, and that (2) maximum BI = 6 does not necessarily imply the development of a mixed layer (compare pathways A and B/C). **A)** Continuous colonization by suspension feeders in shoreface leading to the formation of "pipe rocks" made of palimpsestic, monospecific assemblages of *Skolithos*. Although the substrate is fully bioturbated, a mixed layer never formed. **B)** The offshore, located between fair-weather and storm wave bases, may provide optimal conditions for deposit and detritus feeders (i.e., surface deposit feeders) to churn the sediment and allow the formation and preservation of a mixed layer. **C)** In the shelf, oxygenation plays a major role in the settlement of deposit and detritus feeders, which can either allow (1) the formation of a mixed layer and preservation of a frozen tier profile (under anoxic-oxic-anoxic conditions), or (2) the continuous formation of mixed and transition layers (under oxic conditions) and preservation of light-on-dark and dark-on-light fabrics (see Savrda 2007, fig. 9.1).

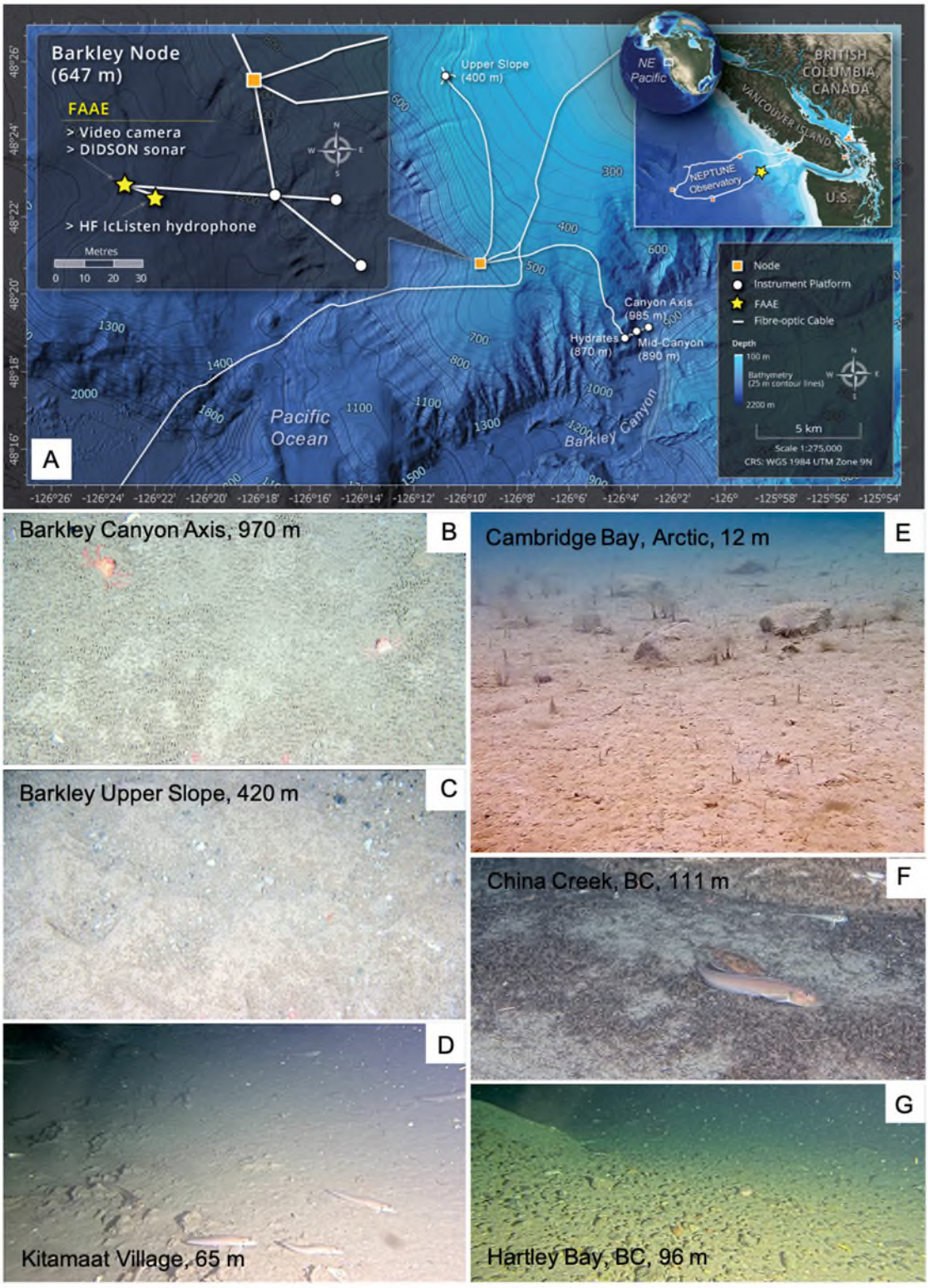

Figure 5—Real-time and high-resolution imagery examples from Ocean Networks Canada aid in the study of modern bioturbation. **A)** Map showing Ocean Networks Canada's Barkley Canyon node of the NEPTUNE cabled observatory in the NE Pacific. FAAE accounts for Fish Acoustics and Attraction Experiment. **B-G)** Seafloor-installed video cameras connected to the cabled infrastructure record hourly video from a range of coastal and deep-sea habitats.