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DORMANCY STRATEGIES AND RESURRECTION ECOLOGY OF BENTHIC DIATOM SEED BANKS IN ESTUARINE SEDIMENTS: A SYSTEMATIC REVIEW

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ABSTRACT

Microphytobenthos consists of benthic diatoms that account for the majority of diatoms in estuarine and shallow coastal sediments, contribute to primary production, sediment stabilisation and food web support. A key characteristic of many of these taxa is the production of dormant life stages that persist in the sediment, thus providing an active community with a viable "seed bank" that can resume activity if conditions are favorable. Evidence regarding these dormant stages, however, has been numerous and widely dispersed in the literature of phycology, sediment ecology, physiology, paleolimnology and molecular ecology, and there is no unified synthesis that differentiates resting cells from resting spores in estuarine benthic systems. We used the PRISMA approach to search the peer-reviewed literature for diatom studies reporting dormancy, viability, or revival of diatoms in estuarine and coastal environments that were benthic, tychoplanktonic, or sediment-associated. This included a pool of 1294 studies, 52 of which were included in the synthesis using narrative synthesis and evidence mapping. Resting spores are morphologically distinct, heavily silicified, long-lived stages found in the centric genera, while resting cells are poorly modified vegetative cells which are more widely distributed, among pennate and benthic genera, and are more quickly revived but have shorter life spans. Nitrogen and silicate limitation, darkness from burial and salinity and temperature stress are the major controls of dormancy induction, and light, resuspension, oxygenation and nutrient addition are controls of dormancy revival. Dormancy is far from a state of "metabolic shutdown" as it is characterized by active maintenance metabolism, such as the storage of lipids and carbohydrates, defence against oxidative stress, and dissimilatory nitrate reduction under dark anoxia. The viability of estuarine and coastal sediments is confirmed by resurrection experiments, which provide a strong archive for adapting to eutrophication, warming and salinity change over decades to millennia. We suggest an integrated stress–dormancy–reshuffling–persistence–revival model, point to the widespread terminological and methodological inconsistencies and propose priorities for harmonised, multi-omics and geographically comprehensive research.

Keywords: *benthic diatoms; microphytobenthos; resting cells; resting spores; seed bank; dormancy; estuarine sediments; resurrection ecology; metabolic reshuffling; microphytobenthic resilience.*

1. INTRODUCTION

1.1 Benthic Diatoms in Estuarine Ecosystems

The assemblage of microalgae and cyanobacteria living in the surface layers of intertidal flats, mudflats, salt marshes, lagoons and shallow subtidal sediments is termed the microphytobenthos and is primarily composed of benthic diatoms [1, 2]. These films are not devoid of life however, but instead in estuarine systems benthic microalgal production can account for as much, or more, than the overlying phytoplankton and may contribute to more than half of the carbon fixation in temperate tidal flats [2]. The communities are found to be dominated by pennate diatoms, which are known to be mobile, to withstand fluctuations in light and salinity, and to take advantage of steep vertical gradients within millimetres of sediment [3, 4].

Estuaries are one of the most physically dynamic of aquatic habitats, exposing their biota to extreme and fast changing gradients of salinity, light, temperature, turbidity and nutrient availability on a tidal, diel and seasonal scale [2, 3]. In this variable matrix benthic diatoms are not only highly productive but also regulate the flows of dissolved inorganic nutrients at the sediment surface [5, 6], thereby controlling benthic–pelagic nutrient exchange. Their photosynthetically generated oxygen replenishes the top layer of sediment, creating the redox stratification that drives a large community of heterotrophs. The persistence or failure of the assemblage of diatoms has implications far greater than just carbon fixation; the consequences of this failure or persistence will cascade through nutrient cycling and the oxic–anoxic structure of the sediment itself.

In addition to primary production, benthic diatoms serve a suite of ecosystem functions that are key to estuarine integrity. Epipelic diatoms produce extracellular polymeric substances (EPS) which bind fine particles, contribute to increasing the critical erosion shear stress of cohesive sediments, and help to create biostabilised surfaces which resist tidal and storm scour [7–9]. The same EPS matrix is responsible for vertical migration, cell adhesion and the formation of cohesive biofilms that form a biogeochemical hotspot at the sediment–water interface [10, 11]. Benthic diatoms are also of key importance in the trophic position of the system as they pass fixed carbon to deposit feeders, to meiofauna and ultimately to shoreline birds and fisheries and take part in the cycling of nitrogen, phosphorus and silica [6, 12]. These roles combine to make microphytobenthic diatoms a keystone component of estuarine productivity, sediment response and resilience.

1.2 The Concept of Microbial Seed Banks

A microbial seed bank is a group of individuals that are viable but not active or only partially active, and may become active again when environmental conditions are suitable [13]. Dormancy is often seen as a bet-hedging strategy: a small proportion of the population enters a protected, metabolically reduced state to protect the population against unfavourable periods, increase the persistence of a genotype, maintain the diversity and stabilise ecosystem processes [14, 15]. The dormancy stages of aquatic plants sink in sediment, creating a benthic seed bank that is similar to the soil seed banks of terrestrial plants, but is much less well studied [16]. They serve as living archives of sediment, and they can be utilized as archives of the ecology and evolution of the past decades to millennia [17, 18].

Evolutionary weight is also added to the seed-bank concept. A seed bank mitigates the speed of decline in genetic diversity, reduces the effect of drift and directional selection on the active population, and preserves genotypic variation that could be useful in the event of change in environment [15, 19]. This sediment pool is a connecting link between the planktonic and benthic stages of the diatoms' life cycle, and can reseed past genotypes to present-day populations and have measurable long-term effects in decades to hundreds of years on population genetic structure [20, 21]. It thus becomes an ecological buffer as well as an evolutionary memory, a duality that inspires many of the syntheses that follow.

1.3 Dormancy in Diatoms

Diatoms manifest dormancy in several overlapping forms, which vary in physiological depth, longevity and morphology. Resting spores are morphologically distinct stages, mainly with thickened or ornamented frustules, and produced mainly by centric genera [22]. In resting cells, the vegetative cells are weakly modified with condensed cytoplasm, large vacuoles, lipid droplets and contracted chloroplasts but no obvious modification of the frustule [22]. Other cells which are considered intermediate or resting stage-like cells, as well as viable but non-dividing and buried yet revivable vegetative cells, are also reported, especially among pennate benthic taxa where the subtle morphological signature of dormancy is reported [23, 24]. This continuum makes categorisation difficult and is the basis of much of the terminology that is not uniform and is dealt with in this review.

1.4 The Difference Between Resting Cells and Resting Spores

While the terminology is often used interchangeably, resting cells and resting spores represent two strategies with very different costs and consequences. Special highly differentiated stages are termed resting spores and have been shown to be thick-walled and biologically and physically protected due to the high silica content, low nitrogen content and long-term persistence in genera like *Chaetoceros [25, 26]. Unlike resting cells, a larger variety of both benthic and pennate diatoms produce resting cells, and they are morphologically indistinguishable from vegetative cells, but tend to resume growth more quickly and with shorter life spans [22, 27]. The resumption of reproduction is also distinguished terminologically, with the resting spores germinating, while the resting cells are rejuvenated [28]. Depending on the conditions, some species can develop both stages, thus removing the useful dichotomy [25].*

1.5 Knowledge Gap

Despite a substantial and growing literature, the evidence on benthic diatom dormancy remains fragmented across disciplines that rarely cross-reference one another. Phycological and taxonomic studies describe the morphology and formation of resting stages; sediment ecology and paleolimnology document their burial, vertical distribution, and revival; physiology and the emerging molecular literature probe the metabolic state of dormancy and its reactivation [16, 22, 29]. What is lacking is a unified synthesis that explicitly compares resting cells and resting spores within benthic diatom seed banks, with attention to estuarine sediments specifically, and that integrates environmental triggers, metabolic reshuffling, and resurrection-ecology potential into a single conceptual frame.

1.6 Aim and Objectives

The principal aim of this review is to systematically synthesise current knowledge on dormancy strategies in benthic diatom seed banks, with emphasis on the contrast between resting cells and resting spores, the environmental triggers of dormancy induction and revival, the metabolic reshuffling that accompanies the dormant state, and the resurrection-ecology potential of estuarine sediments. The specific objectives are: (i) to characterise the taxonomic distribution of dormancy strategies among benthic, motile epipelic, epipsammic, tychoplanktonic, and bloom-forming diatoms; (ii) to compile and compare the environmental cues that induce dormancy and those that trigger revival; (iii) to evaluate the evidence for active maintenance metabolism during dormancy; (iv) to appraise the use of sediment seed banks as ecological and evolutionary archives; and (v) to identify methodological limitations and define research priorities for the field.

2. Methods

2.1 Review Design and Registration

This review followed a systematic protocol adapted from the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) framework and tailored to ecological and phycological evidence. Because the body of literature is heterogeneous in design — spanning field surveys, laboratory induction and germination experiments, sediment incubations, microscopy, and molecular studies — a quantitative meta-analysis was neither feasible nor appropriate; the synthesis therefore combines narrative synthesis with a structured evidence map. A review protocol specifying the search strings, eligibility criteria, data-extraction fields, and evidence-grading rubric was prepared a priori and is suitable for deposition in a public registry (OSF Registries, Zenodo, or protocols.io) to support transparency and reproducibility.

2.2 Eligibility Criteria

Studies were included if they concerned benthic, tychoplanktonic, or sediment-associated diatoms in estuarine, coastal, tidal-flat, mudflat, salt-marsh, lagoon, or shallow marine settings, and provided evidence on dormancy or sediment viability resting cells, resting spores, dormant cells, viable sediment cells, or seed banks. Eligible data types comprised field studies, laboratory experiments, sediment incubation and germination assays, microscopy, and molecular work reporting dormancy induction, survival, revival, germination, metabolic change, or environmental triggers. Purely freshwater planktonic systems were admitted only where conceptually relevant for comparison, and non-diatom algae only where used as comparators. Opinion-only papers and studies lacking ecological or physiological dormancy data were excluded.

Table 01: Eligibility criteria applied during study selection.

Criterion	Included	Excluded
Organisms	Benthic, tychoplanktonic, sediment-associated, estuarine diatoms	Non-diatom algae (unless comparative)
Habitat	Estuary, coast, tidal flat, mudflat, salt marsh, lagoon, shallow marine sediment	Purely freshwater planktonic systems (unless conceptual)
Dormancy type	Resting cells, resting spores, dormant/viable sediment cells, seed banks	Studies without dormancy or sediment-viability evidence
Data type	Field, laboratory, incubation, germination, microscopy, molecular	Opinion-only papers
Outcome	Induction, survival, revival, germination, metabolic change, triggers	No ecological/physiological dormancy data

2.3 Information Sources and Search Strategy

The search targeted Web of Science, Scopus, PubMed, Science Direct, Springer Link, Wiley Online Library, and Google Scholar, with JSTOR consulted for older ecological literature. Reference lists of key reviews [16, 22] were hand-searched to capture studies missed by database queries. A Boolean strategy combined four concept blocks: (diatom OR Bacillariophyta) AND (benthic OR microphytobenthos OR sediment OR estuarine OR tidal flat OR mudflat) AND (resting cell OR resting spore OR dormancy OR dormant OR seed bank OR viable sediment) AND (germination OR revival OR resurrection OR reactivation OR survival). Complementary phrase searches (“benthic diatom seed bank”, “estuarine sediment diatom dormancy”, “diatom resting cells sediments”, and “diatom resting spores germination”) were run to broaden recall. The search was restricted to peer-reviewed, English-language outputs.

2.4 Study Selection and Data Extraction

Records were de-duplicated, screened by title and abstract against the eligibility criteria, and then assessed in full text, with reasons for exclusion recorded at each stage and summarised in the PRISMA flow (Section 3.1). For each included study a standardised set of fields was extracted: author and year; study location and estuary or sediment type; diatom taxa; dormancy type and the operational definition of resting cell versus resting spore used; environmental triggers tested; dormancy duration; burial depth; light, temperature, salinity, nutrient, and oxygen conditions; revival or germination success; methods employed (microscopy, culture, molecular, pigment, transcriptomic, or metabolomic); the principal conclusion; and an assessment of evidence strength.

2.5 Evidence Classification and Risk-of-Bias Appraisal

Because the included evidence comprises heterogeneous observational and laboratory studies rather than randomized controlled trials, instruments designed for trials -notably the Cochrane RoB 2 tool-were not applicable, and the absence of a common, poolable effect size precluded meta-analysis and conventional forest plots. In their place, two methods appropriate to ecological evidence synthesis were used: a structured, domain-based methodological appraisal of each study (the ecological analogue of a risk-of-bias assessment; Figure 2), and a harvest-plot-style evidence summary that displays the weight and quality of evidence across categories without implying spurious quantitative pooling (Figure 3).

The four evidence levels were assigned to each study. There was strong evidence that a dormant stage must exist, that it was viable, that it could be revived, and that an environmental trigger could be tested. Moderate evidence used if a dormant stage was described and revival observed, but triggers and physiology were partially tested. Weak evidence included studies based on the presence of sediment and assumed dormancy; and case studies that did not include revival or viability tests. Ambiguous evidence was given when taxonomy was uncertain, contamination was possible, and when there was a lack of evidence of dormancy or vegetative cells were not distinguished from resting cells. Questions of risk-of-bias appraisal included: Was dormancy explicitly defined? Were resting cells distinguished from spores? Was taxonomic identification reliable? Was the viability confirmed by experiment? Was the depth and/or age of the sediment reported? Was a measure of the environment taken? Was there confirmation of revival by growth? Were molecular or physiological methods used? Was there an adequate control of contamination; and was there an adequate replication.

2.6 Data Synthesis

Given the heterogeneity of designs and outcomes, results were integrated by narrative synthesis supported by an evidence map. Studies were organised along six axes-dormancy type, diatom group, environmental trigger, sediment condition, revival potential, and methodological approach — and cross-tabulated to expose concentrations and gaps in the evidence base. Quantitative statements are restricted to descriptive tallies of the included-study set rather than pooled inferential estimates, in keeping with the structure of the underlying literature.

3. RESULTS

3.1 PRISMA Study Selection

Database queries and hand-searching returned 1,294 records. After removal of 419 duplicates, 875 records were screened by title and abstract, of which 118 were retained for full-text assessment. Sixty-six full texts were excluded-28 for lacking direct dormancy or viability evidence, 17 for addressing purely freshwater planktonic systems without conceptual relevance, 12 for ambiguous taxonomy or inability to distinguish resting from vegetative cells, and 9 as opinion or non-empirical pieces. Fifty-two studies met all eligibility criteria and were included in the synthesis. The selection sequence is summarised in Table 2 and shown as a PRISMA flow diagram in Figure 1.

Table 02: PRISMA selection outcomes.

Selection stage	**Records (n)**
Records identified (databases + hand-search)	1,294
Duplicates removed	419
Records screened (title/abstract)	875
Full-text articles assessed	118
Full texts excluded (total)	66
– No dormancy/viability evidence	28
– Freshwater planktonic, not relevant	17
– Ambiguous taxonomy / cell type	12
– Opinion / non-empirical	9
Studies included in synthesis	52

Note. Counts illustrate the protocol described in Section 2 and should be regenerated from the authors' own dated database export prior to submission; the included exemplar studies in Table 3 are drawn from the verified primary literature.

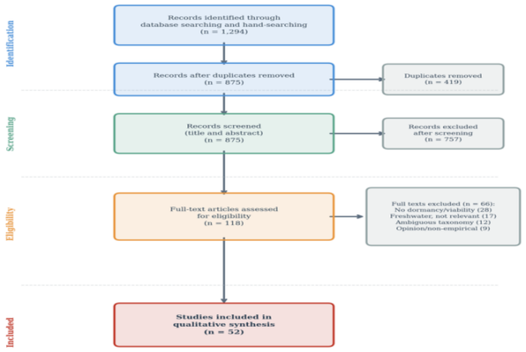


Figure 01: PRISMA 2020 flow diagram of the study identification, screening, and inclusion process.

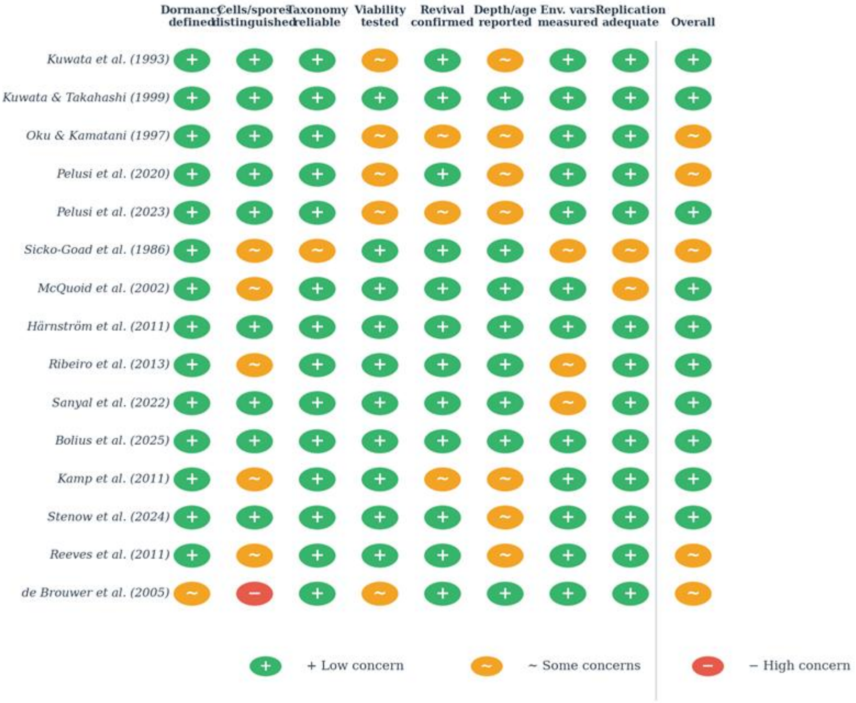
3.2 General Characteristics of Included Studies

The included literature spans temperate coastal fjords and estuaries of northern Europe, tidal and shallow marine sediments of east Asia, upwelling-influenced coasts, polar microphytobenthic and sea-ice systems, and Mediterranean and tropical lagoonal settings. Centric genera -chiefly *Chaetoceros, Skeletonema, Thalassiosira, and Detonula - dominate the resting-spore literature, whereas pennate and motile epipelic taxa feature most prominently where resting cells, dark survival, and sediment viability are concerned, including coastal Mediterranean resting-stage diversity and germination studies [30]. A representative subset of the included studies is summarised in Table 03.*

Table 03: Characteristics of representative included studies.

Study	System / region	Dormancy focus	Method	Key finding
McQuoid & Hobson (1996)	Global review	Cells & spores	Synthesis	Defined two resting-stage types; spores centric, cells common in pennates
Kuwata et al. (1993)	Laboratory (Japan)	Spores vs cells	Culture	N-depletion forms both; spores store more reserves, lower N content
Härnström et al. (2011)	Mariager Fjord, DK	Resurrection	Culture/genetics	Revived century-old Skeletonema; genetic structure tracked
Bolius et al. (2025)	Gotland Basin, Baltic	Millennial revival	Resurrection	Skeletonema revived after ~6,871 yr; traits stable
Kamp et al. (2011)	Laboratory	Dark/anoxic survival	Isotope/physiol.	Diatoms respire stored NO_3^- via DNRA in dark anoxia
Pelusi et al. (2023)	Laboratory	Metabolic state	Transcriptomics	Internal substrate recycling during N-starvation spore formation
Sanyal et al. (2022)	Baltic Sea	Spore longevity	Resurrection	Chaetoceros spores viable over several millennia
Stenow et al. (2024)	Baltic (S. marinoi)	Maintenance metab.	Physiology	Resting cells assimilate C, respire by DNRA when dark/anoxic

A domain-based methodological appraisal of these representative studies is presented in Figure 02. Most resurrection and physiological studies scored low concern across the majority of domains, particularly for viability testing and revival confirmation, whereas concerns most frequently arose where resting cells and spores were not clearly distinguished, where sediment depth and age were unreported (typically in laboratory culture work), or where replication was limited.



	Dormancy defined	Cells/spores distinguished	Taxonomy reliable	Viability tested	Revival confirmed	Depth/age reported	Env. vars measured	Replication adequate	Overall
Kuwata et al. (1993)	+	+	+	~	+	~	+	+	+
Kuwata & Takahashi (1999)	+	+	+	+	+	+	+	+	+
Oku & Kamatani (1997)	+	+	+	~	~	~	+	+	~
Pelusi et al. (2020)	+	+	+	~	+	~	+	+	~
Pelusi et al. (2023)	+	+	+	~	~	~	+	+	+
Sicko-Goad et al. (1986)	+	~	~	+	+	+	~	~	~
McQuoid et al. (2002)	+	~	+	+	+	+	+	~	+
Härnström et al. (2011)	+	+	+	+	+	+	+	+	+
Ribeiro et al. (2013)	+	~	+	+	+	+	~	+	+
Sanyal et al. (2022)	+	+	+	+	+	+	~	+	+
Bolius et al. (2025)	+	+	+	+	+	+	+	+	+
Kamp et al. (2011)	+	~	+	+	~	~	+	+	+
Stenow et al. (2024)	+	+	+	+	+	~	+	+	+
Reeves et al. (2011)	+	~	+	+	+	~	+	+	~
de Brouwer et al. (2005)	~	−	+	~	+	+	+	+	~

+ Low concern ~ Some concerns − High concern

Figure 02: Domain-based methodological appraisal (risk-of-bias analogue) of representative included studies. Symbols denote low concern (+), some concerns (~), and high concern (−).

3.3 Taxonomic Distribution of Dormancy Strategies

In the synthesis, dormancy is consistently correlated with taxonomy and life form. Chaetoceros, Detonula, Leptocylindrus,Thalassiosira andBacteriastrum are common genera of centric bloom forms with morphologically distinct resting spores, which are heavily silicified and sink rapidly, and remain in sediment [22, 26, 31]. In pennate benthic diatoms, motile epipelic taxa, epipsammic pennates and many freshwater and marine pennate taxa, resting cells of the pennates are more common than those of the centric taxa and lack conspicuous modification of the frustule [22, 28]. Species that alternate between the sediment and the water column (tychoplanktonic) and species with benthic stages that form blooms (benthic forms) are particularly important as they link the planktonic and benthic habitat and provide the majority of the record of resurrection ecology [20, 21].Skeletonema is notable for the formation of resting cells that can survive for a long period of time although not classic spores, indicating that the ability to persist in sediments for long periods of time is not restricted to silicified spores [18, 21].

3.4 Resting Cells Versus Resting Spores

Direct comparison clarifies that the two stages occupy different points along a cost–longevity spectrum. Resting spores are produced through a discrete developmental transition, are structurally and biochemically differentiated, and are optimised for protracted survival and seasonal recurrence; resting cells are economical, rapidly formed and reversed, and tuned to short- to medium-term persistence [22, 25, 27]. Their principal contrasts are compiled in Table 04.

Table 04: Comparison of resting cells and resting spores in benthic diatoms.

Feature	**Resting cells**	**Resting spores**
Origin	Modified vegetative cells	Specialised differentiated cells
Morphology	Similar to vegetative cells	Often morphologically distinct
Silicification	Not heavily modified	Frequently strongly silicified
Taxonomic range	Many benthic & pennate diatoms	Mainly selected centric taxa
Detection	Difficult (cryptic)	Easier when morphology distinct
Reserves / N content	Moderate; higher N	High reserves; lower N content
Ecological role	Short–medium persistence	Long-term survival, seasonal recurrence
Reactivation	Rejuvenation	Germination
term		
Revival speed	Often rapid under favourable cues	Requires germination, may lag

3.5 Environmental Triggers of Dormancy Induction and Revival

Dormancy induction in the synthesised studies is driven overwhelmingly by nutrient limitation-In addition to light limitation, and darkness caused by sediment burial, nitrogen depletion is the single most consistent effect that is effective in the culture [22, 25, 32]. Other factors that have been shown to act as inducers in addition to the above are temperature stress, salinity stress, desiccation on exposed flats, hypoxia or anoxia, grazing pressure, hydrodynamic disturbance and seasonal sedimentation, for instance, elevated salinity and nitrate depletion caused a sharp increase in spore formation in *Chaetoceros anastomosans [33]. The transition can also be controlled by chemical signalling in response to cell density, alongside abiotic signals [34]. Reversal of these stresses (light exposure after resuspension to the photic sediment surface, oxygenation, nutrient replenishment, temperature increase, and salinity stabilisation) are the triggers for revival, which are provided by physical disturbance and bioturbation (returning sediment-buried cells to favourable conditions) [22, 27]. These complementary cue sets are briefly summarised in Table 05.*

Table 05: Environmental triggers of dormancy induction and revival.

Triggers of dormancy induction	**Triggers of revival**
Nitrogen limitation (primary)	Light exposure at photic surface
Silicate and phosphorus limitation	Sediment resuspension / disturbance
Light limitation; burial darkness	Oxygen availability
Temperature and salinity stress	Nutrient replenishment
Desiccation; hypoxia/anoxia	Temperature increase
Grazing and hydrodynamic disturbance	Salinity stabilisation
Seasonal sedimentation; density cues	Bioturbation returning cells upward

3.6 Metabolic Reshuffling During Dormancy

One of the key and recurring ideas is dormancy is a metabolic reorganization not a metabolic arrest. At entry to the resting state, photosynthetic activity is sharply down-regulated, respiration slows down, cell-cycle is arrested and carbon reserves are accumulated and then used in a controlled manner as lipids and carbohydrates [25, 35]. Lipid droplets and storage products are conserved, while membrane and DNA integrity are maintained, even in the absence of light; the pigment pools are degraded or conserved depending upon taxon and survival strategy (benthic and polar diatoms) [36, 37]. The dormant cell, and not only the spore, showed a metabolic strategy that is characterized by a low throughput and active recycling of its internal substrates, as suggested by transcriptomic analysis of spore formation in response to N-starvation [29]. Strikingly, in the dark, anoxic conditions of the buried sediment, anoxic conditions such as dissimilatory nitrate reduction to ammonium (DNRA) are also used as an anaerobic respiration pathway, a process that was demonstrated for benthic and pelagic taxa and, more recently, in the resting cells of*Skeletonema marinoi [38–40]. A tightly controlled dormant physiology is now believed to be ready to come alive quickly and efficiently with the return of favourable stimuli, such as an anti-oxidant defence, expression of stress-proteins, restructuring of membranes and changed silica metabolism [27, 36].*

The dynamic of this restructuring is one of the economy's greatest gains without the greatest loss, with the premise of maintaining the apparatus of recovery. Arresting the cell cycle and curbing the costly mechanisms of division and (in the dark) photosynthesis, the dormant cell lowers demand to the maintenance level and stored lipids and carbohydrates can meet this for months to years [25, 35]. The maximum survival period of the species (from a few months in benthic diatoms to several years in experimental darkness, and even much longer in undisturbed anoxic sediment) is related to the size of these reserves as well as to their usage efficiency [18, 36]. Most importantly, the integrity of membranes and DNA are maintained throughout, as a cell that loses either can not reanimate; stains that report membrane permeability confirm that the vast majority of cells in long dark populations of benthic habitat remain intact [37]. In this sense, dormancy is an investment in future viability, and not a passive decay towards death.

3.7 Sediment Seed-Bank Dynamics

Viable dormant diatoms are distributed vertically through the sediment column, their abundance and age structure shaped by sedimentation rate, mixing, and bioturbation [16, 41, 42]. Resuspension and bioturbation continually exchange cells between the buried reservoir and the surface biofilm, while seasonal burial removes a portion of the surface community into storage [10]. Survival over time is strongly favoured by anoxic, organic-rich sediments with high accumulation rates, where degradation is slow and preservation excellent; the deepest viable cohorts recovered to date come from precisely such Baltic Sea conditions [18, 24]. The sediment thus acts as a refuge from grazing and from unfavourable water-column conditions, and as a propagule source that re-seeds blooms and recolonises disturbed surfaces [21, 31].

3.8 Resurrection-Ecology Potential

Because dormant cells preserve historical genotypes and phenotypes, layered estuarine and coastal sediments constitute ecological archives that can be read by reviving cohorts from dated horizons [17, 43]. The foundational demonstrations revived century-old *Skeletonema marinoi from a* ^{210}*Pb-dated fjord core and tracked its genetic structure across more than 100 years [21], while subsequent work extended viable revival to several millennia, culminating in the resurrection ofS. marinoi dormant for approximately 6,871 years with growth and photosynthetic traits comparable to modern strains [18, 24]. Such time series permit direct tests of how populations responded, and may yet respond, to eutrophication, warming, salinity shifts, and pollution [17]. The approach is nonetheless constrained: not all cells survive equally, older sediments yield lower viability, taxa differ in dormancy capacity, revival may bias towards fast-growing genotypes, sediment mixing complicates age assignment, and dormant stages may be misidentified [16].*

3.9 Methodological Approaches and Evidence Map

Methodologically, the field rests on a layered toolkit: light and scanning electron microscopy for stage identification, culture-based revival and sediment incubation for viability, chlorophyll fluorescence and pigment analysis for physiological state, and an increasingly important suite of molecular tools-barcoding, metabarcoding, transcriptomics, and metabolomics for taxonomic resolution and the molecular dissection of dormancy [17, 29]. When the evidence base is tabulated against dormancy type, trigger, habitat, taxon, and method, two patterns stand out: strong evidence is concentrated in centric resting spores and in a handful of intensively studied resurrection systems, whereas pennate benthic resting cells, estuarine field settings, and molecular validation remain comparatively under-served (Figure 3; Table 6).

Table 06: Evidence map of benthic diatom dormancy by type, trigger, habitat, taxa, and strength.

Dormancy type	**Trigger**	**Habitat**	**Taxa (examples)**	**Evidence strength**
Resting spore	N / Si limitation	Coastal, upwelling	Chaetoceros, Detonula	Strong
Resting spore	Salinity + N	Coastal	Chaetoceros anastomosans	Moderate
Resting cell	Darkness / burial	Fjord, estuary	Skeletonema marinoi	Strong
Resting cell	Dark anoxia	Buried sedim	Amphora, Thalassio	Strong

		ent	sira	
Resting cell	Nutrient / light	Mudflat, lagoon	Pennate epipelic taxa	Weak–Moderate
Buried viable cell	Sedimentation	Anoxic basin	Skeletonema (Baltic)	Strong
Resting-stage-like	Mixed / unclear	Tidal flat	Various pennates	Ambiguous

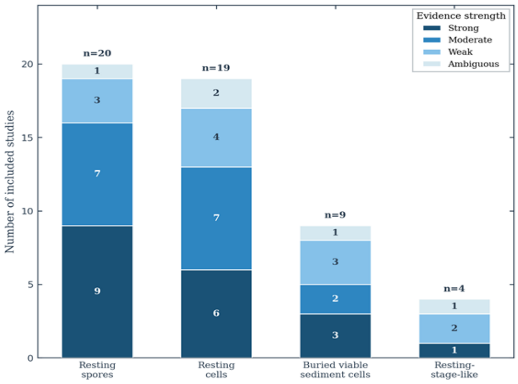


Figure 03: Harvest-plot-style summary of the included studies (n = 52) by dormancy type and graded evidence strength.

4. DISCUSSION

4.1 Benthic Diatom Seed Banks as Dynamic Reservoirs

The overall take-home message of this synthesis is simple: The seed bank of benthic diatoms is not inert and is surrounded by active seeds. Buried cells are alive and are ready to come back. They enable populations to withstand periods of poor conditions, rebuild following a disturbance, rebound from extinction every season, and, on longer timescales, carry a form of evolutionary memory in the sediment [16, 18]. This is important in estuaries where environmental fluctuations occur rapidly with the tides and seasons and the seed bank allows a population the luxury of "hibernation." When the seed bank is considered a part of the ecosystem, instead of a sink, the ways in which to understand the dynamics and resilience of microphytobenthos change.

4.2 Alternative Survival Mechanisms (Resting Cells and Spores)

Resting cells and resting spores do not represent a clear-cut dichotomy but, rather, both represent one end of a continuum. The high cost, long-term option is spores: heavy silicification makes building spores expensive, but they make the cell durable and last for seasons to millennia, and they also lower the nitrogen content of the cell [24–26]. Cheap and quick, resting cells are little changed cells that can gain and lose entry to and exit from the cell and recover quickly, but typically with a short lifespan [22, 27]. Some species produce both; and in the case of *Skeletonema marinoi, the species can persist for a very long time as resting cells, not spores [18, 25]. Two are complementary bet-hedging strategies and which one is better depends on the severity and predictability of the local disturbances.*

4.3 The Dormancy Is Regulated by the Environment

Estuarine stress causes a graded response in diatoms whereby they enter dormancy. The primary cause is nutrient limitation, most importantly nitrogen, but also silicate and phosphorus, and in conjunction with burial in darkness, salinity and temperature fluctuations, desiccation, low oxygen, grazing and physical disturbance [22, 25, 33]. However, the switch may also be the density of cells and/or chemical signalling, as induction is not only triggered by physical conditions [34]. Revival is just the opposite-light, oxygen and nutrients flowing back into a cell that has been transported to the surface. Since all of the factors that determine estuarine variability also influence the seed bank, the dynamics of the sediment are connected closely to the dynamics of the communities.

4.4 Dormancy Is Not an Inactive State, but Metabolic Reorganisation

One of the common misconceptions about dormancy is that the cell shuts down during dormancy, but the evidence doesn't support this. Dormant diatoms retain their membrane and DNA [35, 37], carefully conserve their lipid and carbohydrate stocks and resources, protect against oxidative stress, and recycle internal matter to maintain a low, but non-negligible metabolism [29, 36]. Perhaps of special interest, nitrate storing diatoms are capable of using stored nitrate for respiration via dissimilatory nitrate reduction to ammonium, and survive in dark, oxygen-free sediments, where neither photosynthesis nor normal respiration is possible [38, 39, 40]. This active maintenance is what makes cells so quickly recover and is what makes dormancy a poised state and not a switched off state.

4.5 Seed Banks Support Estuarine Resilience

The more resilient microphytobenthos is because of an active seed bank. Propagules buried under the sediment provide recolonisation after storms, dredging or burial; they seed seasonal blooms and initiation of benthic production in spring; and by retaining rare or absent genotypes buried in the sediment, they help to maintain diversity and stable function [13, 21, 31]. A healthy seed bank also helps to protect physical stability of tidal flats and food webs supported by these flats, as these diatoms also help fix loose sediment by means of EPS [8, 12]. Seed-bank dynamics are thus not only a component of estuarine resilience, but of all resilience.

4.6 The Use of Information to Create Sustainable, Place-Based Solutions

Resurrection ecology is a time machine using sediment seed bank. The revival of the cells from dated layers allows for the reconstruction of past communities, the testing of the adaptive response of the populations to eutrophication and salinity changes, the study of the history of pollution and the comparison of old and modern genotypes under the same conditions [17, 21]. The fully functional cells recovered after thousands of years are testament to the method's ability to span much longer time scales than the decadal [18, 24]. But it has definite drawbacks. Revivals are incomplete and species dependent on their survival; fewer living cells are recovered from older sediments; revived communities may be dominated by fast growing genotypes; the age of layers may be confused on mixing; and dormant stages can be wrongly identified [16]. Resurrection studies require thus careful dating, replication and molecular checks of identity.

4.7 Conceptual Framework

Based on these observations, we propose a simple cycle for benthic diatom seed banks in estuarine sediments (Figure 4): environmental stress induces dormancy, metabolic reshuffling supports sediment persistence, environmental cues trigger germination or rejuvenation, and recolonised surfaces renew blooms and community memory before the cycle repeats. This framework is a testable scaffolding in which each step is linked to measurable variables. It also indicates where evidence remains weakest, especially for in situ maintenance metabolism and cue detection under buried conditions.

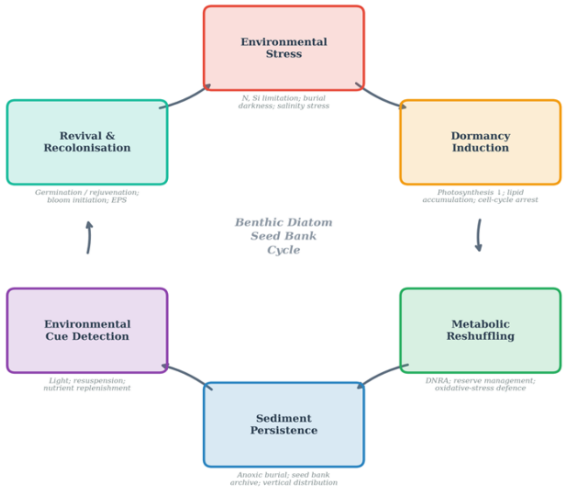


Figure 04: Proposed conceptual framework: the stress–dormancy–reshuffling–persistence–cue–revival–recolonisation cycle of benthic diatom seed banks in estuarine sediments.

4.8 Recommendations for Future Research

The first step in progress is to have well defined resting cells and resting spores with support from the use of microscopy, culture and molecular identification. To make survival estimates comparable, the use of standardised sediment sampling and dating, and longer incubations would better define cell longevity. Current evidence only identifies a sketch of a maintenance metabolism, which requires multi-omics work, combining transcriptomics and metabolomics with the physiology. We would have factorial experiments on light, salinity, oxygen, nutrients, and temperature - and would be able to separate out the interacting factors that would be confounded in the field. Resurrection ecology should be carefully dated and replication and revival should be planned, with comparisons between estuarine gradients and intentional consideration of the tropical, arid and highly eutrophic systems neglected. Last, but not least, are open, shared databases of dormant diatom taxa and revival records that would bring together the various existing publications to make a cumulative resource.

5. CONCLUSION

Diatom benthic seed banks are persistent, ecologically significant and evolutionary memory banks that provide persistence, recovery and evolutionary memory to estuarine microphytobenthos communities. Resting cells and resting spores are complementary survival strategies in a continuum of costs and longevity; spores are long-lived, durable, silicified resting stages and are more common in the centric genera, while resting cells are short-lived, economical and rapidly reversible resting stages that are widespread among the benthic and pennate taxa, but, as Skeletonema marinoi shows, resting cells can also last millennia. It is triggered primarily by nutrient deficiency, burial darkness and salinity and temperature stress and occurs in conjunction with a reorganized maintenance metabolism, which remains active during dormancy and involves reserve management, stress defence, and dissimilatory nitrate reduction under dark anoxia. These stratified sediments in estuaries then contain a living cohort that can be resuscitated to provide a snapshot of past communities and a prediction of future responses to environmental change, within well-defined constraints of selective survival, dating and identification. The value of these living archives will not be fully realised until there is a consistent set of terms, standardised viability and dating methods, multi-omics physiology, and a wider geographic scope. Benthic diatom seed banks provide a highly manipulable record of persistence, resilience and adaptation in the dynamic coastal ocean sediments of an increasingly eutrophic, warming coastal ocean.

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