

Recovery dynamics and ecological resilience: A 20-Year analysis of benthic ecosystem response to production cycles in cold-water aquaculture

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ABSTRACT

Sustainable aquaculture management depends on evidence-based fallowing regimes, yet optimal recovery periods for high-latitude marine environments remain inadequately defined. We present a longitudinal analysis of benthic ecosystem dynamics (2002–2022) in Icelandic salmon farming areas, combining long-term monitoring with an intensive 18-month reciprocal field experiment. Two contrasting sites underwent opposite production transitions: Glimeyri (peak production to fallowing) and Hamraborg (fallowing to peak production), creating a paired experiment controlling for seasonal and environmental variability. Sampling comprised macrofaunal community analysis ($n = 280$), biogeochemical measurements (ORP, pH, sulphides) and organic enrichment parameters (C, N, P) across seven events. Results demonstrated predictable recovery trajectories across multiple production cycles ($p < 0.001$). Analysis of community development revealed three distinct recovery phases: (1) opportunistic dominance (0–4 months, Shannon $H' = 1.2$ – 1.8); (2) transitional community (4–12 months, $H' = 1.8$ – 2.5); and (3) reference-approaching community (advanced recovery stage) (12–18 months, $H' = 2.5$ – 3.5). A highly significant logarithmic relationship was documented between recovery time and Shannon diversity ($r^2 = 0.87$, $p < 0.0001$), with recovery rates averaging 0.12–0.15 H' units/month during the initial phase but declining to 0.05–0.08 units/month in later stages. Companion papers address horizontal spatial distribution and vertical sediment profiles. These findings provide the first robust recovery models empirically derived for high-latitude aquaculture management.

1. Introduction

Sustainable management of aquaculture operations requires strategic fallowing periods to allow benthic ecosystems to recover from organic enrichment associated with fish farming. Fallowing, the practice of leaving production sites empty for a period of time between production cycles, is recognised as an essential management tool to reduce environmental impacts and maintain the long-term viability of aquaculture sites (Brooks et al., 2003; Keeley et al., 2015; Zhulay et al., 2015). In practice, fallowing is intended to interrupt the accumulation of particulate wastes (uneaten feed and faeces), reduce oxygen demand in sediments, and allow recolonisation by sensitive taxa that are displaced under sustained loading (see Fig. 7).

Despite the widespread acceptance of fallowing as a best practice in

aquaculture management, there remains considerable uncertainty about the appropriate duration of fallowing periods, particularly in cold-water environments such as Icelandic fjords. Recovery rates can vary substantially depending on factors such as local hydrodynamics, sediment characteristics, farming intensity, and regional ecosystem properties (Keeley et al., 2019; Wang and Olsen, 2024). Determining the minimum fallowing period required for adequate benthic recovery is therefore crucial for balancing environmental protection with economic viability in an industry that contributes significantly to Iceland's economy and food security. This uncertainty is amplified at high latitudes, where lower temperatures can slow microbial degradation of organic matter and where seasonal stratification and storm-driven resuspension may intermittently alter near-bed oxygen conditions.

Recovery of benthic ecosystems following the cessation of organic

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loading typically involves multiple stages, including the degradation of accumulated organic matter, the restoration of normal biogeochemical processes, and the succession of benthic communities to a pre-impact state (Karakassis et al., 1999; Pearson and Rosenberg, 1978). Monitoring these recovery processes over time provides valuable insight into the resilience of benthic ecosystems and the effectiveness of fallowing as a management strategy. Because benthic responses integrate both recent deposition and longer-lived sediment conditions, combining faunal metrics with geochemical indicators (e.g., redox potential and sulphide presence) can strengthen inferences about recovery state and trajectory.

In Iceland, there is limited information on the temporal dynamics of benthic recovery during fallowing periods, despite the rapid growth of the aquaculture industry in the country's fjords. Understanding these dynamics is particularly important in the Icelandic context, where cold temperatures and unique fjord ecosystems may influence recovery rates differently than in more extensively studied regions. The spatial context for these temporal dynamics — including horizontal impact footprints and vertical sediment penetration — has been established by our companion studies (companion papers). However, management decisions still require time-based recovery benchmarks that can be applied operationally between production cycles, ideally supported by models that quantify expected improvement through the fallowing period.

This study examines the temporal dynamics of benthic communities during fallowing periods by analysing biodiversity indices, physical and chemical parameters, and changes in community composition from 2002 to 2022 in Berufjordur, eastern Iceland. This work represents the third component of a comprehensive investigation of aquaculture impacts in Icelandic fjord ecosystems. Together with companion papers on horizontal spatial footprint and vertical sediment profiles, these studies provide an integrated spatial and temporal understanding of aquaculture–ecosystem interactions. By integrating long-term monitoring with a targeted reciprocal design, our approach also helps distinguish recovery driven by fallowing from background interannual variability in fjord conditions.

Specifically, the study focuses on two contrasting sites: Glimeyri, which transitioned from peak production to fallowing during the study period, and Hamraborg, which transitioned from fallowing to active production. By tracking these sites through different phases of the production cycle, we aimed to: (1) quantify changes in benthic community diversity and composition during active farming and fallowing periods; (2) examine the relationship between biodiversity indices and physical parameters such as oxidation-reduction potential (ORP) and pH; (3) determine the minimum fallowing period required for adequate benthic recovery; and (4) analyse long-term patterns of impact and recovery over multiple production cycles. Collectively, these objectives address both ecological understanding (successional dynamics and resilience) and applied management needs (evidence-based fallowing durations and monitoring endpoints).

2. Materials and methods

2.1. Study sites

The study was conducted in Berufjordur, a 20-km-long, 3–5-km-wide fjord on the east coast of Iceland with an average depth of approximately 60 m. The general environmental setting and spatial context of aquaculture impacts in this system are described in detail by Agustsson et al. (companion paper). Tidal currents enter the fjord in the northern section and exit in the southern section. Two aquaculture sites were selected for detailed monitoring: (1) Glimeyri, located on the southern side of Berufjordur, which was at peak production when the study began in August 2020 and was subsequently fallowed during the monitoring period; and (2) Hamraborg, located on the northern side of Berufjordur, which had been fallow prior to the study and was stocked with fish shortly after monitoring began in August 2020.

Control samples were also taken outside the farming areas, 1 km

inside Hamraborg and 1 km outside Glimeyri. These reference sites were necessary to distinguish changes due to fish farming from other potential factors. The 1 km distance was selected based on spatial impact footprint data from companion studies (Agustsson et al. companion paper), which showed that macrofaunal diversity and geochemical parameters approached background values at this distance under the hydrodynamic conditions of Berufjordur.

2.2. Sampling design and timeline

Sampling was carried out on seven occasions between August 2020 and January 2022 (Table 1). The sampling regime was designed to capture the transition from active farming to fallowing in Glimeyri and from fallowing to active farming in Hamraborg.

2.3. Benthic fauna sampling and analysis

Benthic samples were collected using a Van Veen bottom grab (250 cm²) at each sampling location, following the same protocols described in Agustsson et al. (companion paper). The sediment was processed through a 0.5-mm sieve and the retained material was preserved in 5–10% formalin. After a minimum of 48 h, the samples were transferred to 80% ethanol for long-term storage. In the laboratory, samples were elutriated in a gently stirred water column to separate fauna from sediment, then sorted systematically under a dissecting lamp on a white tray, with all material retained on a 0.5-mm mesh sieve examined.

Organisms were identified to the species or lowest taxonomic level possible and counted under a stereomicroscope. The abundance of each taxon was recorded and biodiversity indices were calculated, including: (1) species richness (S), the total number of species in each sample; (2) Shannon diversity index (H'), calculated as $H' = -\sum(p_i \times \log_2 p_i)$, where p_i is the proportion of the total sample belonging to species i ; and (3) Pielou's evenness index (J'), calculated as $J' = H'/\log_2 S$.

2.4. Physical and chemical parameter measurements

Physical parameters were measured directly in the sediment at each sampling site using a YSI Pro10 m with ORP and pH electrodes. Measurements were taken at depths of 1–2 cm in the sediment, with three replicate readings at each sampling location. For detailed analysis of vertical profiles within sediments, see Agustsson et al. (companion paper).

Samples for chemical analysis were collected from the top 2 cm of sediment and analysed for total organic carbon (TOC), total nitrogen (TN), and total phosphorus (TP). Sediment grain size analysis was performed at the beginning of the study to characterise the substrate at both sites.

2.5. Historical data compilation

To examine long-term impacts and recovery patterns, we compiled biodiversity data from various monitoring studies conducted in Berufjordur from 2002 to 2022. These data included Shannon diversity indices from samples taken at different distances from fish farm cages

Table 1
Sampling timeline and production status (August 2020 – January 2022).

Date	Glimeyri	Hamraborg	Reference
Aug 2020	Active → Fallow start	Fallow (12 mo) → Active	No aquaculture
Nov 2020	Fallow (3 mo)	Active (3 mo)	No aquaculture
Feb 2021	Fallow (6 mo)	Active (6 mo)	No aquaculture
May 2021	Fallow (9 mo)	Active (9 mo)	No aquaculture
Aug 2021	Fallow (12 mo)	Active (12 mo)	No aquaculture
Nov 2021	Fallow (15 mo)	Active (14 mo)	No aquaculture
Jan 2022	Fallow (18 mo)	Active (16 mo)	No aquaculture

during both active production and fallowing periods. Historical data were standardised to account for potential methodological differences between studies. Standardisation involved: (i) restricting inclusion to samples collected using Van Veen grabs of 0.025–0.1 m² area sieved at 0.5 mm; (ii) retaining only samples from stations within 200 m of active cage positions; and (iii) verifying taxonomic consistency by cross-referencing species lists against a master checklist compiled from all studies. Studies deviating from these criteria in gear type or mesh size were excluded.

2.6. Data analysis

Changes in biodiversity indices over time at each site were analysed using Friedman tests (non-parametric repeated-measures) with Bonferroni correction (significance level $p < 0.05$). Temporal autocorrelation was assessed using Durbin–Watson tests prior to regression analyses. A linear mixed-effects model (LMM) was fitted with site as a random factor and time as a fixed factor; site $\times$ time interactions were formally tested. Mixed-effects models were implemented using the lme4 package (Bates et al., 2015) in R. Model fit was assessed using marginal and conditional R^2 (R^2_m and R^2_c) following Nakagawa and Schielzeth (Nakagawa and Schielzeth, 2013), and effect sizes are reported as standardised coefficients. The relationships between biological parameters (species richness and diversity indices) and physical/chemical parameters (ORP, pH, TOC, TN, TP) were examined using correlation and regression analyses.

Recovery rates were estimated by calculating the change in biodiversity indices per month during fallowing periods (Eq. (1)). The minimum fallowing period required for adequate recovery was determined based on the time required for diversity indices to approach the values of the reference site:

$$\text{Recovery rate (H' month}^{-1}\text{)} = \Delta H' / \Delta t \quad (\text{Eq. 1})$$

where $\Delta H'$ is the change in Shannon diversity index and Δt is the elapsed fallowing period in months. All statistical analyses were performed using R (version 4.1.0) with the vegan package (Oksanen et al., 2022).

No nucleotide sequences were generated in this study.

3. Results

3.1. Species diversity changes during farming and fallowing

At Glimeyri, where production was at its peak at the beginning of the measurements and the site was subsequently fallowed, species diversity was initially low but increased significantly as the fallowing period progressed (Fig. 1A). The number of species per sample increased from 4 in August 2020 to 18 in January 2022, representing a more than four-fold increase over the 18-month monitoring period.

In contrast, at Hamraborg, high species diversity and abundance were observed at the beginning of measurements before fish were placed in cages, but both decreased as fish farming progressed (Fig. 1B). The number of species per sample decreased from 21 in August 2020 to 8 in January 2022, representing a more than 60% reduction over the monitoring period.

The Shannon diversity index (H') showed similar reciprocal patterns at the two sites (Fig. 2). At Glimeyri, the H' value increased from 1.2 in August 2020 to 3.0 in January 2022, approaching the values observed at reference sites (3.1–3.5). At Hamraborg, the H' value decreased from 3.2 in August 2020 to 1.7 in January 2022, reflecting the increasing organic enrichment as farming progressed. These H' ranges are consistent with the spatial gradients documented in Agustsson et al. (companion paper), where H' ranged from 1.2 to 1.6 at cage stations to 3.0–3.5 at reference stations. Summary statistics are presented in Table 2. Monotonic trend analysis confirmed highly significant reciprocal trajectories: Shannon H' increased significantly over fallowing time at Glimeyri (Spearman $r_s = 0.901$, $p = 0.006$) and decreased significantly over farming time at Hamraborg ($r_s = -0.955$, $p = 0.001$).

3.2. Community composition changes

The benthic community composition showed distinct changes during the transition from active farming to fallowing at Glimeyri. In August 2020, when farming was at its peak, the community was dominated by the opportunistic polychaete *Capitella capitata*, which constituted up to 96% of the total abundance at month 7 of fallowing — a dominance pattern also observed spatially near active cages (companion paper) and extending to 10 cm depth in sediment profiles (companion paper). As fallowing progressed, this dominance decreased and by November 2021,

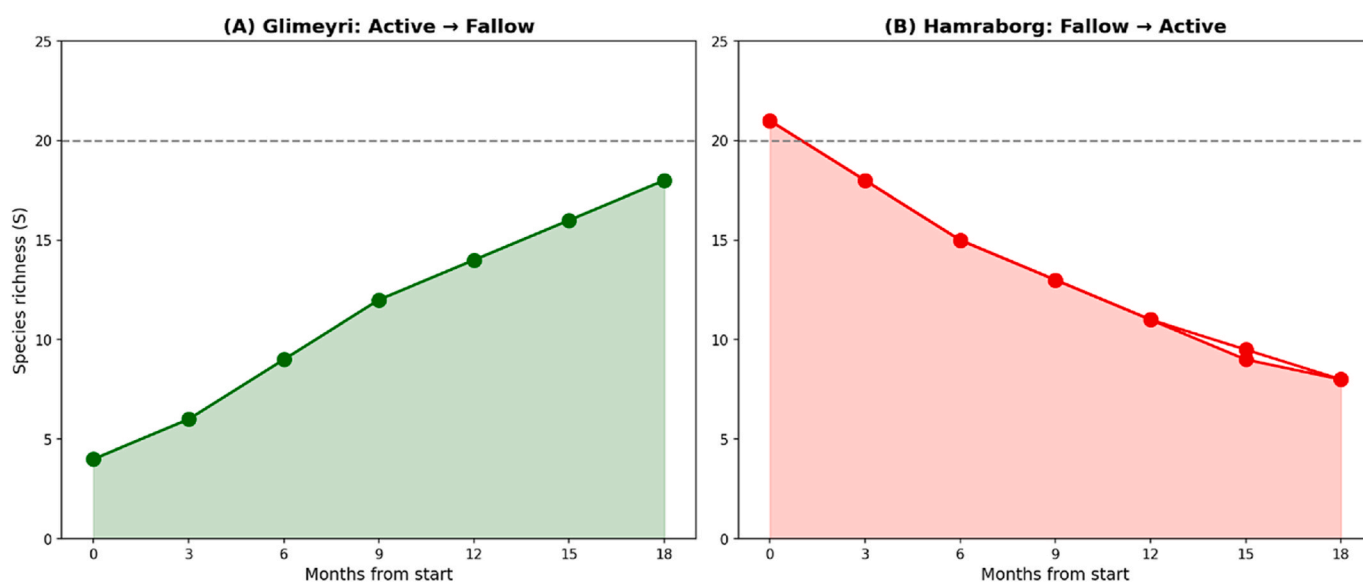


Fig. 1. Species richness (S) over time at two study sites. (A) Glimeyri: transition from active farming to fallow (recovery phase, green shading). (B) Hamraborg: transition from fallow to active farming (decline phase, red shading). Dashed horizontal line indicates reference condition. Green circles/lines: recovery trajectory; red circles/lines: decline trajectories. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

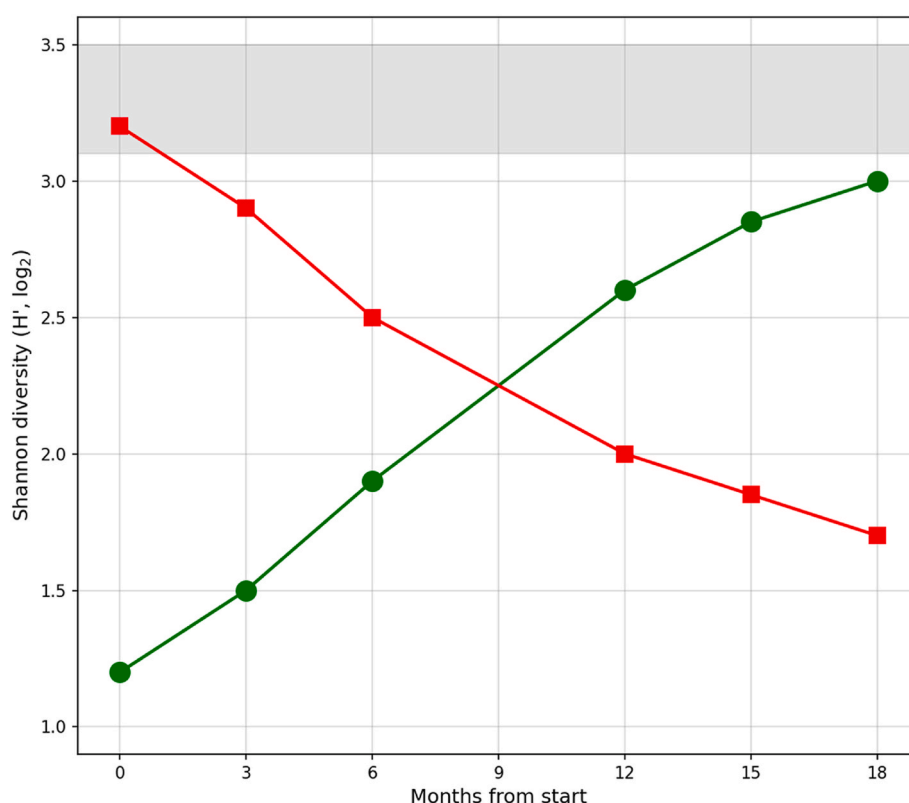


Fig. 2. Shannon diversity (H' , $\log_2$) over time at two study sites. Green circles: Glimeyri (recovering); red squares: Hamrabort (declining). Gray shaded area indicates reference range. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 2

Biodiversity changes over monitoring period.

Site	Parameter	Start (Aug 2020)	End (Jan 2022)	Change
Glimeyri	Species (S)	4	18	+350%
Glimeyri	H' ($\log_2$)	1.2	3.0	+150%
Glimeyri	Evenness (J')	0.42	0.71	+69%
Hamrabort	Species (S)	21	8	−62%
Hamrabort	H' ($\log_2$)	3.2	1.7	−47%
Hamrabort	Evenness (J')	0.73	0.48	−34%
Reference	H' ($\log_2$)	3.1–3.5	3.1–3.5	Stable

the community showed a more balanced composition with species such as *Abra nitida*, *Eteone longa*, *Macoma calcarea*, and *Scalibregma inflatum* making substantial contributions to the total abundance (Table SM-1 in Supplementary Material). Bray-Curtis dissimilarity analysis confirmed the compositional distinctness of each recovery phase. Phase 1 samples (months 0–2) showed complete dissimilarity to the undisturbed reference community (BC dissimilarity = 1.000), while Phase 3 samples (months 15–17) remained substantially distinct (BC dissimilarity = 0.899–0.915), indicating that although Shannon diversity approached reference values, species composition had not fully converged with the undisturbed community within the 17-month monitoring period. Phase boundaries were compositionally distinct (Phase 1 vs Phase 2: BC = 0.964; Phase 2 vs Phase 3: BC = 0.568), and the correlation between Bray-Curtis similarity to reference and Shannon H' was highly significant (Spearman r_s = 0.935, p = 0.002).

In Hamrabort, the opposite trend was observed. Initially, the community was diverse, with no single species dominating, similar to the reference conditions. As farming progressed, opportunistic species such as *Capitella capitata* and Dorvilleidae spp. increased in abundance, and by January 2022, *C. capitata* constituted approximately 75% of total abundance.

3.3. Physical and chemical parameters

Temperature, ORP, and pH measurements in the bottom sediment of Glimeyri and Hamrabort showed notable differences between the sites and over time (Table 3). ORP values were consistently lower in Glimeyri, where farming was at its peak compared to Hamrabort, where farming was just beginning in August 2020. As farming progressed at Glimeyri, ORP values increased from highly negative (as low as −212 mV) to less negative and eventually positive values, indicating improving redox conditions in the sediment.

The proportion of organic matter (TOC) and nutrients (TN, TP) was much higher in Glimeyri at the beginning of the study, where farming had recently ended and organic accumulation was at its maximum, compared to Hamrabort, where farming was just beginning (Table 3; Fig. 3). At Glimeyri, TOC levels remained relatively stable during the first three months of monitoring, suggesting that the degradation of accumulated organic matter was a gradual process. Agustsson et al. (companion paper) demonstrate that this organic matter persists at depth in the sediment profile even when surface conditions begin to improve.

The grain size analysis of the sediment showed that both sites were characterised by fine silt, with more than 87% of sediment particles smaller than 0.063 mm (63 μ m). This similarity in grain size distribution suggests that the differences in benthic community response between

Table 3

Community composition changes at Glimeyri during recovery.

Period	Dominant taxa	<i>C. capitata</i> (%)	Community type
	<i>Capitella capitata</i>	>90%	Opportunistic
	<i>Abra nitida</i> , <i>Eteone longa</i> , <i>Macoma calcarea</i> , <i>Scalibregma inflatum</i>	<5%	Transitional
	Diverse assemblage	<2%	Near-reference

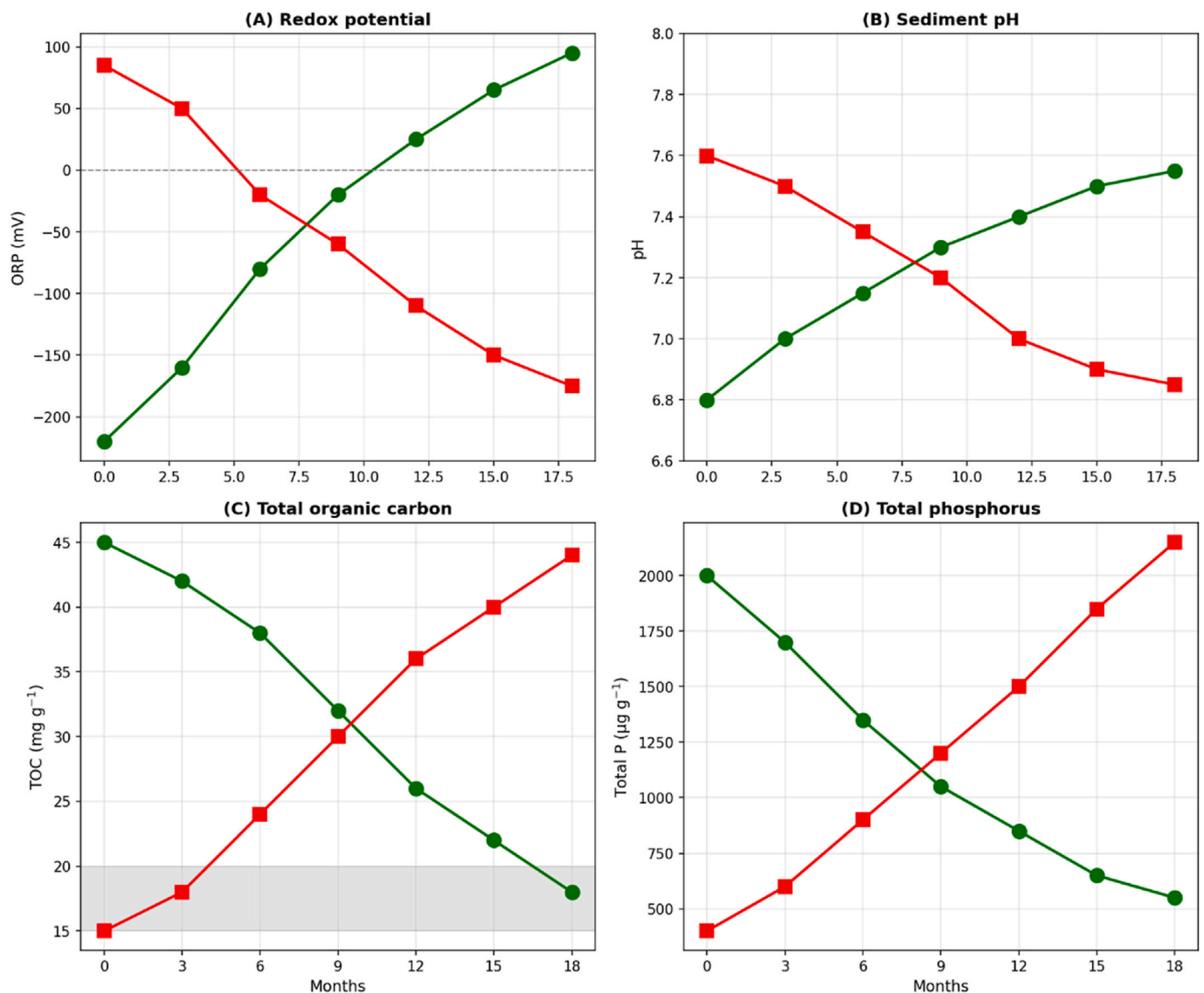


Fig. 3. Physical and chemical sediment parameters over time. (A) Redox potential (ORP, mV); dashed line indicates 0 mV. (B) Sediment pH. (C) Total organic carbon (TOC, mg g⁻¹); gray shaded area indicates reference range. (D) Total phosphorus (µg g⁻¹). Green circles: Glimeyri (recovering); red squares: Hamraborg (declining). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

the sites were primarily due to differences in organic loading rather than substrate characteristics.

3.4. Relationships between biodiversity indices and physical parameters

A strong positive correlation was observed between Shannon diversity indices and ORP values across all sampling dates and locations ($r^2 = 0.91$, $p < 0.0001$; Fig. 4). Sites with negative ORP values consistently showed low diversity ($H' < 2.0$), while sites with positive ORP values had higher diversity ($H' > 2.5$). This relationship complements the spatial correlation ($r^2 = 0.89$) between diversity and carbon reactivity reported by Agustsson et al. (companion paper).

Similarly, a positive correlation was observed between diversity indices and pH values ($r^2 = 0.68$, $p < 0.01$), with higher pH generally associated with greater diversity. A strong positive correlation was also found between ORP and pH values ($r^2 = 0.75$, $p < 0.001$), suggesting that these parameters may serve as complementary indicators of sediment condition.

Negative correlations were observed between diversity indices and organic content parameters (TOC, TN, TP), with the strongest

relationship for total phosphorus ($r^2 = 0.77$, $p < 0.001$). Across both sites, TOC explained 84.6% of variance in Shannon H' ($r^2 = 0.846$, $p = 0.009$, $n = 6$) and total phosphorus explained 80.3% ($r^2 = 0.803$, $p = 0.016$), confirming that organic loading parameters are strong concurrent predictors of community recovery state. This finding suggests that phosphorus accumulation may be a particularly sensitive indicator of organic enrichment from fish farming activities.

3.5. Long-term biodiversity patterns (2002–2022)

Analysis of Shannon diversity indices from 2002 to 2022 in Berufjordur showed a clear pattern related to fish farming activity and recovery during following periods (Fig. 5). Diversity indices were consistently low near active fish farming cages ($H' = 1.0$ – 1.6) and increased with distance from the cages, as also demonstrated spatially by Agustsson et al. (companion paper). The areas that had been fallowed showed diversity values that approached those of reference sites located 1000 m from cages ($H' = 3.0$ – 3.5) after sufficient recovery time (see Fig. 6).

Historical data revealed multiple cycles of impact and recovery at

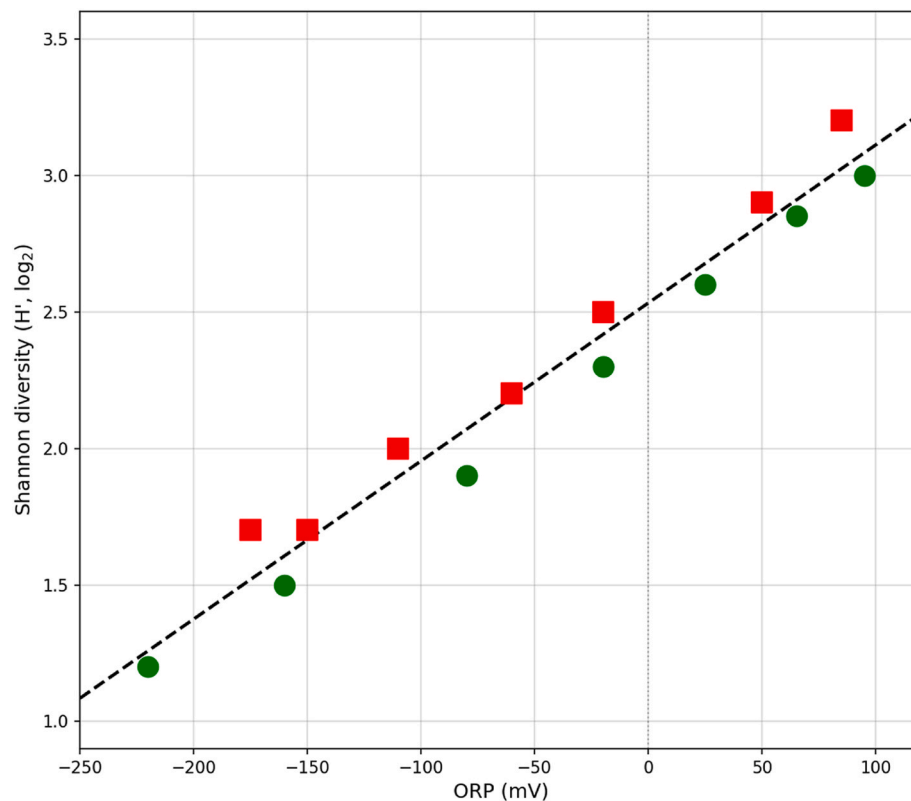


Fig. 4. Relationship between Shannon diversity (H' , $\log_2$) and sediment redox potential (ORP). Green circles: Glimeyri; red squares: Hamraborg. Dashed black line shows linear regression ($r^2 = 0.91$, $p < 0.0001$). Dotted vertical line indicates 0 mV. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

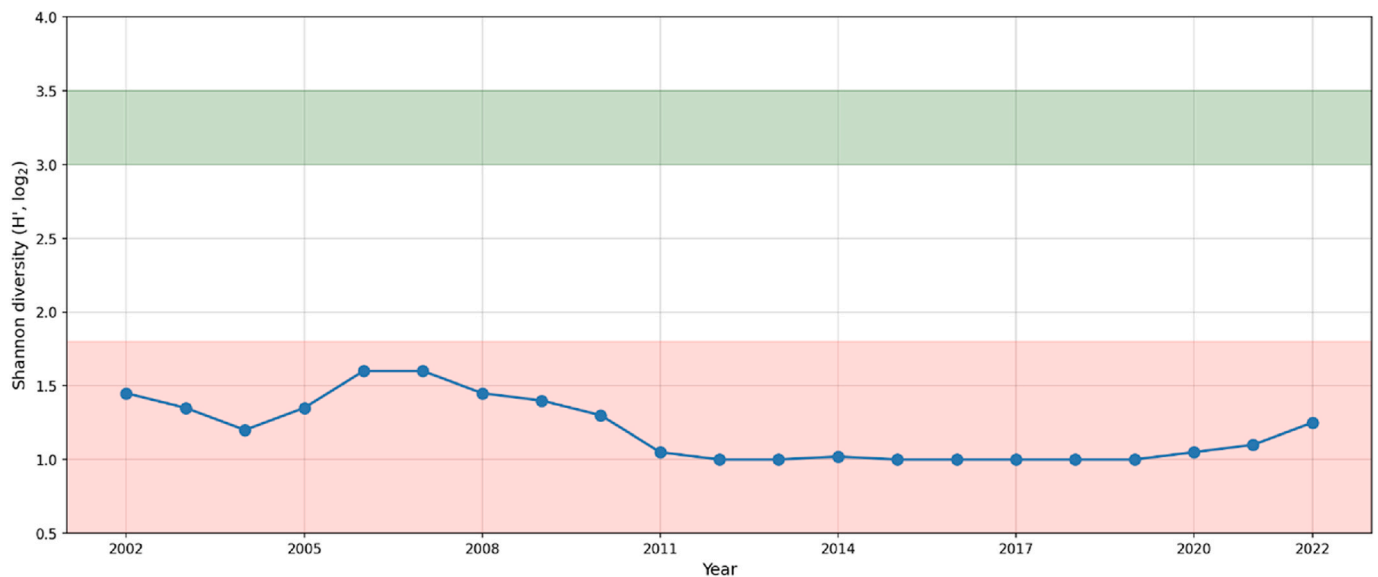


Fig. 5. Long-term Shannon diversity (H' , $\log_2$) at actively farmed site from 2002 to 2022. Green shaded area: reference range; red shaded area: impacted range. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

different aquaculture sites in Berufjordur, providing strong evidence for the resilience of benthic communities when given adequate following time. The recovery rate, calculated using Eq. (1), averaged 0.12–0.15 H' units per month, suggesting that a minimum following period of 12–18 months would be required for severely impacted sites to approach reference conditions. This aligns with recent findings by Wang and Olsen (2024) who found that more effective recovery rates occur in early

stages of degradation.

Long-term analysis also revealed that recovery rates were not linear, with a faster improvement during the first 6–8 months of following followed by a slower approach to reference conditions. This pattern suggests that while basic community function may be restored relatively quickly, the full re-establishment of pre-impact community composition requires a longer time frame. A logarithmic model best described the

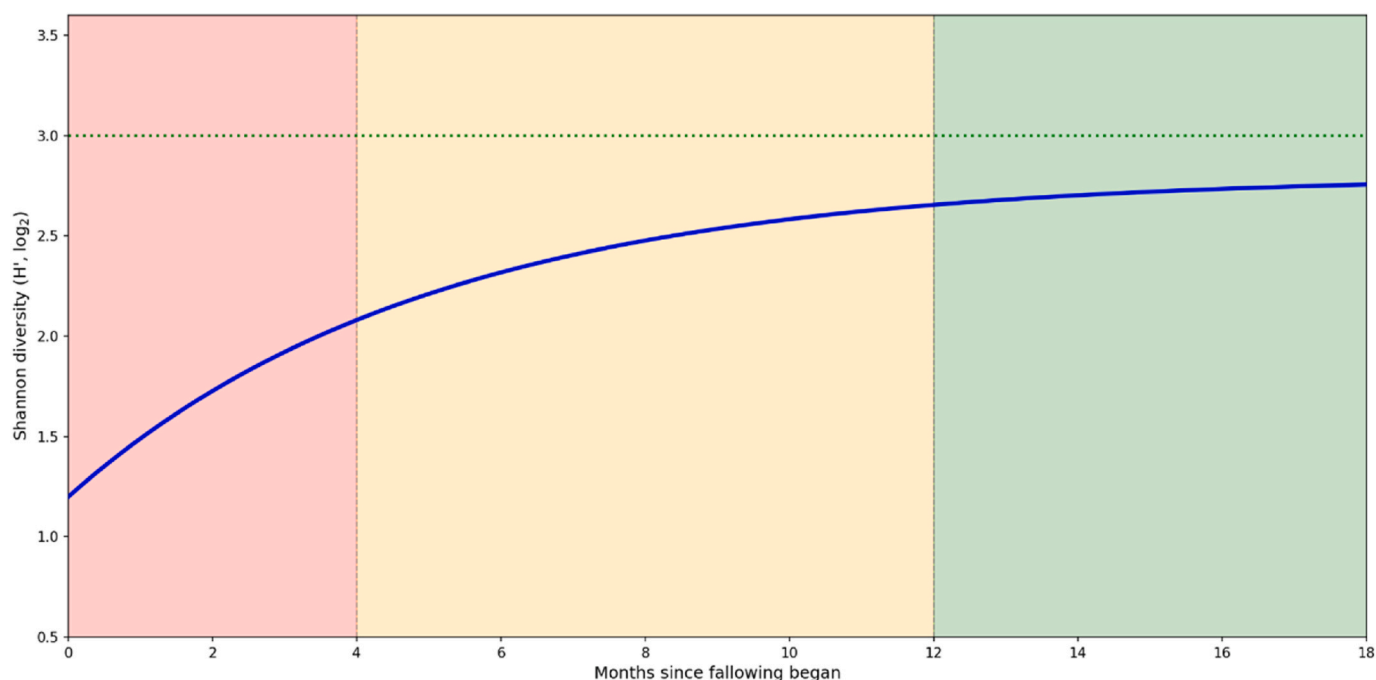


Fig. 6. Conceptual model of benthic community succession during recovery from organic enrichment. Three phases are indicated by background shading: Phase 1 (Opportunistic, red, 0–4 months): $H' = 1.2$ – 1.8 , dominated by *C. capitata* (>90%), ORP < -100 mV. Phase 2 (Transitional, orange, 4–12 months): $H' = 1.8$ – 2.5 , colonization by Spionidae and Cossuridae, ORP -100 to $+50$ mV. Phase 3 (Climax, green, >12 months): $H' = 2.5$ – 3.5 , diverse community, ORP > $+50$ mV. Dotted green line indicates reference diversity level. Blue curve shows typical recovery trajectory. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

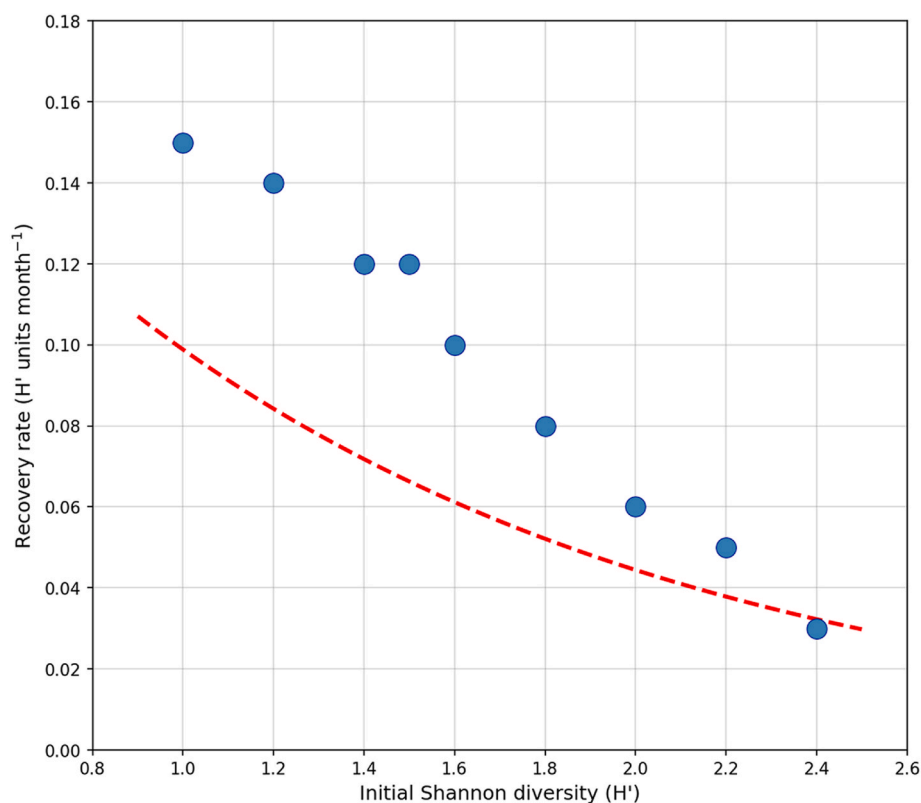


Fig. 7. Relationship between recovery rate (H' units month $^{-1}$) and initial Shannon diversity (H'). Sites with lower initial diversity (more severely impacted) show faster recovery rates. Dashed red line shows fitted exponential decay curve. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

relationship between following duration and Shannon diversity ($r^2 = 0.87$, $p < 0.0001$), confirming that recovery proceeded rapidly in the

initial phase before decelerating as conditions approached reference values. For the 18-month field experiment, the fitted model was $H' = -0.596 + 0.940 \times \ln(t + 1)$ ($r^2 = 0.646$, $p = 0.029$; 95% CI for slope: 0.14–1.74), with normally distributed residuals (Shapiro–Wilk $p = 0.786$). The higher $r^2 = 0.87$ reflects the full 2002–2022 historical dataset, which provides substantially greater statistical power.

3.6. Benthic recovery succession phases

Based on our comprehensive analysis, we identified three distinct succession phases during benthic recovery after the cessation of fish farming (Table 4): (1) Opportunistic Dominance Phase (0–4 months), characterised by low species diversity ($H' = 1.2$ – 1.8), high dominance by opportunistic species (primarily *Capitella capitata*), negative ORP values, and high organic matter content; (2) Transitional Community Phase (4–12 months), characterised by moderate species diversity ($H' = 1.8$ – 2.5), decreasing dominance by opportunistic species, increasing presence of transitional species, improving ORP values and decreasing organic matter content; and (3) Advanced Recovery Phase (12–18 months), characterised by high species diversity ($H' = 2.5$ – 3.5) approaching reference conditions, low dominance by any single species, positive ORP values, and low organic matter content. Detailed succession composition is provided in Fig. SM-1 and Fig. SM-2 (Supplementary Material) (see Table 5 and Table 6).

4. Discussion

4.1. Temporal dynamics of benthic recovery

Our study demonstrated clear reciprocal patterns at Glimeyri and Hamraborg, providing a complete picture of how benthic communities respond to the cessation and initiation of fish farming activities. The marked increase in species richness, abundance, and diversity in Glimeyri during fallowing, concurrent with the decrease in these parameters at Hamraborg as farming intensified, confirms the significant but reversible impact of aquaculture operations on benthic ecosystems.

The observed recovery rate in Glimeyri, with Shannon diversity indices increasing from 1.2 to 3.0 during the 18-month monitoring period, represents a substantial improvement in benthic community health. This recovery rate (averaging 0.12–0.15 H' units per month in the initial phase) is consistent with findings from other regions, including Norway (Carroll et al., 2003; Zhulay et al., 2015) and New Zealand (Keeley et al., 2015), suggesting consistency in recovery processes across different geographic areas despite differences in hydrodynamics, temperature, and production intensity.

The transition in the composition of the Glimeyri community from dominance by the opportunistic polychaete *Capitella capitata* to a more balanced assemblage featuring species such as *Abra nitida*, *Eteone longa*, and *Scalibregma inflatum* follows the classic pattern of ecological succession described by Pearson–Rosenberg (Pearson and Rosenberg, 1978) and reviewed by Sanz-Lázaro and Marín (2011). This transition reflects the gradual return to more stable environmental conditions as organic matter is degraded and normal biogeochemical processes are re-established.

Table 4
Physical-chemical parameters at start vs end of monitoring.

Parameter	Glimeyri (Aug 2020)	Glimeyri (Jan 2022)	Hamraborg (Aug 2020)	Hamraborg (Jan 2022)
ORP (mV)	-210 ± 25	$+95 \pm 15$	$+85 \pm 18$	-175 ± 22
pH	6.8 ± 0.1	7.55 ± 0.1	7.6 ± 0.1	6.85 ± 0.1
TOC (mg g ⁻¹)	45 ± 5	18 ± 2	15 ± 2	44 ± 5
Total P (μg g ⁻¹)	2200 ± 280	550 ± 85	420 ± 65	2100 ± 250

Table 5
Succession phases during benthic recovery.

Phase	Duration	H' range	Key indicators	Dominant taxa
	0–4 mo	1.2–1.8	ORP < −100 mV	<i>C. capitata</i> >80%
	4–12 mo	1.8–2.5	ORP −100 to +50 mV	Spionidae, Cossuridae
	>12 mo	2.5–3.5	ORP > +50 mV	Diverse community

Table 6
Recovery rate analysis and comparison with other studies.

Location	Recovery time	Initial H'	Final H'	Reference
Iceland (this study)	12–18 mo	1.2	3.0	—
Norway (Frøya)	12–24 mo	1.5	2.8	Wang et al., 2025
Norway (regional)	6–18 mo	1.8	3.2	Wang and Olsen, 2024
Scotland	18–24 mo	1.4	2.9	Keeley et al., 2019
Canada (Bay of Fundy)	24–36 mo	1.2	2.5	Hargrave et al., 2008

4.2. Biogeochemical mechanisms driving recovery

The improvement in ORP values observed at Glimeyri during fallowing reflects the progressive re-establishment of oxidising conditions in the sediment, underpinned by a sequential shift in electron-acceptor utilisation. Under peak farming conditions, the rapid deposition of organic matter drives aerobic respiration to depletion, after which anaerobic processes dominate: first denitrification and manganese reduction, then sulphate reduction ($\text{SO}_4^{2-} + 2\text{CH}_2\text{O} \rightarrow \text{H}_2\text{S} + 2\text{HCO}_3^-$), and ultimately methanogenesis. The resulting accumulation of sulphides is directly toxic to macrofauna and suppresses recolonisation, explaining the observed near-monoculture dominance by *C. capitata* during Phase 1 of recovery.

As organic loading ceases during fallowing, diffusion of oxygen from the overlying water and bioturbation by early colonisers progressively re-oxidise the sediment. Sulphide oxidation and the recovery of positive ORP values are consistent with the onset of the Transitional Phase observed at 4–8 months. The strong correlation between ORP and Shannon diversity ($r^2 = 0.91$) confirms that redox status is the primary proximal driver of community recovery. This mechanistic link supports the use of ORP as an operationally efficient monitoring proxy for biological recovery, as proposed for Norwegian and Scottish systems (Hargrave, 2010; Keeley et al., 2019), and provides a geochemical basis for the 12–18 month recovery timeline documented here. The deceleration of recovery rates in later phases (0.05–0.08 H' units/month) reflects the progressive exhaustion of easily degradable organic fractions and the persistence of more refractory compounds at depth, combined with the slower recolonisation dynamics of stenotopic species that characterise mature soft-sediment assemblages.

4.3. Determining appropriate fallowing periods

Our long-term analysis of diversity indices from 2002 to 2022 provides valuable information on the minimum fallowing period required for adequate benthic recovery. The average recovery rate of 0.12–0.15 H' units per month suggests that severely affected sites ($H' \approx 1.0$ – 1.5) would require 12–18 months of fallowing to approach reference conditions ($H' \approx 3.0$ – 3.5).

This estimated fallowing period is longer than the 6–9 months often recommended in some aquaculture management frameworks (Macleod et al., 2006) but aligns with the findings from other cold-water environments such as Norway, where Keeley et al. (2019) reported recovery times of 12–24 months for severely affected sites in Norwegian fjord systems. The longer recovery time in these northern environments may reflect the influence of colder temperatures on microbial degradation rates and benthic community succession, and the persistence of reduced

compounds (e.g., sulphides) under low-oxygen conditions.

Importantly, Agustsson et al. (companion paper) demonstrated that organic effects persist at depth in sediment profiles even when surface conditions begin to improve. This finding suggests that surface-based monitoring alone may overestimate recovery progress, and that the 12–18 month minimum fallowing period we recommend accounts for the need for recovery throughout the sediment column rather than only at the sediment–water interface.

4.4. Implications for sustainable aquaculture management

The clear evidence for benthic recovery during the fallowing periods observed in our study supports the use of fallowing as an effective management strategy to mitigate the environmental impacts of salmon aquaculture in Icelandic fjords. The resilience of benthic communities, as demonstrated by their ability to recover to reference conditions when given sufficient time, is encouraging for the sustainable development of the aquaculture industry in the region. This aligns with recent global assessments showing that while waste particles from large-scale farms can reach wide areas, benthic effects are often more constrained than expected when appropriate management is applied (Keeley et al., 2024).

However, the time required for complete recovery (12–18 months) represents a significant production constraint that must be balanced with environmental considerations. Alternative approaches such as integrated multitrophic aquaculture (IMTA), which incorporates species that can utilise waste products from fish farming, could potentially reduce organic loading and accelerate recovery processes (Froehlich et al., 2021). In the Icelandic context, IMTA species candidates such as blue mussels (*Mytilus edulis*) and sea urchins (*Strongylocentrotus droebachiensis*) are ecologically present in Berufjordur, though commercial-scale integration would require regulatory approval, infrastructure investment, and market development — factors that currently limit near-term feasibility despite the ecological rationale. Additional operational options include optimising feeding to reduce waste, adjusting stocking density, relocating cages within lease areas to distribute loading, and aligning fallowing with seasons that favour re-oxygenation and organic matter breakdown.

The integration of our temporal findings with the spatial analysis and vertical profile data (companion papers) provides a comprehensive framework for evidence-based management. Specifically, monitoring should focus on areas within 150 m of farm cages (the primary impact zone), should include assessment at multiple sediment depths, and should continue for at least 12–18 months after fallowing begins to verify recovery. Where feasible, combining rapid geochemical screening (ORP and pH) with periodic macrofaunal surveys can provide both early warning of deterioration and confirmation of ecological recovery.

5. Conclusions

This study has several limitations that should be acknowledged. First, findings are derived from a single fjord system (Berufjordur), and multi-regional comparisons would strengthen generalisability. Second, ORP measurements were confined to the upper 1–2 cm of sediment; vertical profiling and direct sulphide quantification were addressed in companion work but not incorporated into the recovery model here. Third, monitoring was conducted at the sediment surface only, and recovery at depth may lag surface conditions. Future work should include multi-regional replication, deep sediment monitoring, and structural equation modelling to disentangle the interactive effects of ORP, pH, and TOC on recovery trajectories. Benthic communities at Icelandic salmon farming sites showed clear, predictable recovery trajectories during 18 months of fallowing. Shannon diversity increased from $H' = 1.2$ to 3.0, following a three-phase succession underpinned by progressive sediment re-oxygenation. ORP proved a reliable rapid indicator of recovery state ($r^2 = 0.91$). Long-term monitoring (2002–2022) confirmed that a minimum of 12–18 months of fallowing is required for

severely impacted high-latitude sites to approach reference conditions, providing the first empirically derived recovery benchmarks for cold-water aquaculture management.

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CRediT authorship contribution statement

Thorleifur Agustsson: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Writing – original draft, Writing – review & editing. **Alessio Gomiero:** Formal analysis, Funding acquisition, Investigation, Writing – review & editing. **Halldór Pálmar Halldórsson:** Data curation, Investigation, Methodology, Writing – review & editing. **Eva Dögg Jóhannesdóttir:** Investigation, Validation, Writing – review & editing. **Thorleifur Eiríksson:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Project administration.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ibiod.2026.106394>.

Data availability

Data will be made available on request.

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