Effects of Blue mussel dredging on biodiversity and functional diversity in soft-bottom communities in the Lammefjord and Holbæk Fjord, Denmark

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Preface

This master's thesis was conducted at the Department of Ecoscience, Aarhus University, and examined the effects of blue mussel dredging on biodiversity, community composition, biomass, and functional diversity in soft-bottom communities of Lammefjord and Holbæk Fjord, Denmark. This was done by comparing benthic surveys from 1996 with surveys conducted in 2025. The study aimed to contribute to the understanding of how anthropogenic disturbances in the form of mussel dredging, influence ecological structures and functions in soft-bottom coastal marine ecosystems.

The thesis is presented as a monograph, following an introduction to the ecological effects of bottom-contact fisheries and benthic community ecology, the study design, methods, and analytical approaches are described. The subsequent chapters present the results and discuss their ecological implications as for a conclusion with perspectives for management and future research.

Special thanks to Save the Isefjord Association, for making awareness and action on this matter, and to Jesper Philip Christensen, Lasse Tor Nielsen, Mikael Sejr, Nikolaj Reducha Andersen, for collecting biological samples used in this study. Thanks to Cordula Göke for processing the data of trawl activity, as well for Signe Høgslund and Kitte, Line.

Last but not least, a special and sincere thanks to my supervisors, Jørgen L. S. Hansen and Peter Grønkjær, for a great, enjoyable, and educational collaboration. It has been a true pleasure working with you both, and I am very grateful for all your guidance, valuable discussions, and continuous support throughout this project. It was a joyful and very valuable journey, and I would like to thank you both for all the time and energy you have put into this project.

Appreciation is also extended to all contributors involved in sample collection and data preparation, whose efforts formed the foundation of this study.

Tabel of contents

Abstract

Blue mussel dredging is a widespread fishing method which physically disturbs the seabed and affects the diversity and biomass of benthic communities and ecosystem functioning. This study aimed to investigate the effects of intensified mussel dredging on soft-bottom macrozoobenthic communities in Lammefjord, Denmark. Using a Before-After Control-Impact (BACI) design, benthic community assemblages were compared between the heavily dredged Lammefjord and compared with the less dredged Holbæk Fjord, before (1996) and after (2025) the intensified dredging in Lammefjord, 2024. Biodiversity indices, biomass, community composition and functional traits were analyzed using univariate and multivariate approaches. The results showed a significant decline in biodiversity and abundance in Lammefjord over the 29-year period, compared to Holbæk Fjord. No effect of trawling was found on benthic biomass. The functional trait analyses implied a tendency towards a disturbed system of dredging by favoring opportunistic infaunal species with planktonic larvae development. Furthermore, no negative tendency was found regarding food chain interactions. The results implied that long-term mussel dredging can have long-term impacts on biodiversity and functional diversity in soft-bottom habitats and empathizes the importance of incorporating ecological interactions into fisheries management to support the sustainable fishing practices.

Resume

Blåmuslingeskrab er en udbredt fiskerimetode, der fysisk forstyrrer havbunden og har vist at påvirke diversiteten og biomassen af bundlevende organismer samt forstyrre økologiske mekanismer. Formålet med dette studie var at undersøge effekterne af intensiveret blåmuslingeskrab på blødbunds samfundet af bundfauna i Lammefjorden, Danmark. Ved anvendelse et Before-After Control-Impact (BACI) design, blev bentiske prøver sammenlignet mellem den intensivt skrabede Lammefjord og den mindre skrabede Holbæk Fjord, før (1996) og efter (2025) intensiveringen af fiskeriet i Lammefjorden, 2024. Biodiversitetsmål, biomasse, samfundssammensætning og funktionelle træk blev analyseret ved både univariate og multivariate analyser. Resultaterne viste et signifikant fald i biodiversitet og individtæthed i Lammefjorden over den 29-årige periode, sammenlignet med Holbæk Fjord. Der blev ikke fundet nogen effekt af muslingeskrab på biomassen. Analyser af funktionelle træk indikerede en tendens mod et forstyrret system forårsaget af muslingeskrab ved favoriseringen af opportunistiske infauna arter med planktonisk udvikling. Ydermere, blev der ikke observeret nogen negativ effekt på bentiske fødekæde interaktioner. Resultaterne tyder på, at langvarigt blåmuslingeskrab kan have betydelige langsigtede konsekvenser på biodiversitet og funktionel

diversitet i blødbundshabitater. Studiet understreger behovet for at inddrage økologiske interaktioner i fiskeriforvaltningen for at sikre et mere skånsomt fiskeri.

1. Introduction

Anthropogenic pressures are some of the leading drivers of global habitat disruption and biodiversity crisis (Kaiser et al., 1998; Lundquist et al., 2013; McLaverty et al., 2024; Pommer et al., 2016). In marine habitats, coastal areas are of special focus, as they support highly productive habitats and important nursery areas for a large proportion of marine life (McLaverty et al., 2023a, 2024). However, these environments are highly exposed to multiple anthropogenic pressures such as eutrophication, pollution, overfishing and seabed disturbances caused by bottom-contact fisheries (Bromhall et al., 2022; Kaiser et al., 1998; Lundquist et al., 2013; McLaverty et al.,2020a; Sparks-McConkey and Watling, 2001; Riemann and Hoffmann, 1991). In Danish coastal waters, eutrophication, overfishing and bottom trawling have received increasing attention due to their impacts on benthic ecosystems and declining diversity (Hansen and Josefson, 2024; Riemann and Hoffmann, 1991).

1.1 Fishing history of bottom trawling and dredging in Danish waters

Bottom trawling has been widely used on a global scale for centuries and has been practiced in Danish waters since the early 1900s (Jarvis and Brennan, 2024; Pommer et al., 2016). Multiple studies have demonstrated that bottom-contact fishing gears physically disturb the seafloor through direct interaction such as scraping and ploughing, when elements such as nets and chains interact with the seabed, resulting in sediment mixing, resuspension (Dolmer et al., 2001; Hansen and Andersen, 2024; Kaiser et al., 1998; McLaverty et al., 2023a; Pommer et al., 2016; Sparks-McConkey and Watling, 2001; Tillin et al., 2006). Yet, it remains an essential component of global food production (Jarvis and Brennan, 2024). A specific type of bottom-contact fishing gear is the mussel dredge, which is used for harvesting bivalves such as Blue Mussel (*Mytilus edulis*), Common cockles (*Cestoderma edule*) and European flat oysters (*Ostrea edulis*). In Denmark, mussel dredging became increasingly intensive during the 1980's, with landings from 1989-1999 reaching approximately 100.000 tonnes y^{-1} in Limfjorden, 30.000 tonnes y^{-1} in The Belt Sea/Kattegat and 5.000 - 10,000 tonnes y^{-1} in the Danish Wadden Sea (Petersen, Nielsen and Freitas, 2024). Today, dredging activity have been constrained to take place in Limfjorden, Isefjord, The Belt Sea and several fjords along the eastern Jutland coast, Western part of the Baltic Sea (Landbrugs- og Fiskeristyrelsen, n.d).

1.2. Impacts of dredging

The dredge is a 1.5-2m wide and 2-3m long chain net, attached to a line on a fishing vessel weighing 100-250 kg (Petersen, Nielsen and Freitas, 2024). Compared to many other bottom-contact fishing gears, mussel dredges penetrate relatively deep into the sediment of approximately 2-5 cm (Bromhall et al., 2022; Dolmer et al., 2001). An area can be dredged multiple times within the same year, due to the inefficiency of the gear leading to an increase in fishing activity in the area (Petersen, Nielsen and Freitas, 2024). The coastal benthic communities are therefore being exposed to high natural and human impacts (McLaverty et al., 2023a), resulting in a potential strong resilience to disturbance, but less diverse community, compared to offshore communities (Mac Donald et al, 1996; McLaverty et al., 2023a; Josefson and Hansen, 2004). However, a negative impact of dredging on coastal soft-bottom communities compared to deeper offshore areas, has been of doubt, since offshore habitats are considered to be more stable (MacDonald et al., 1996) and that near-shore areas in open seas often are exposed to natural disturbances, such as tides, currents, storms and salinity gradients (MacDonald et al., 1996; McLaverty et al., 2023a).

Disturbance has long been recognised as one of the key drivers for a rich community and high biodiversity (Thrush and Dayton, 2002). This relationship was described by Connell (1978) through the intermediate disturbance hypothesis (IDH), which proposes that maximum species richness occurs at intermediary levels of disturbance and intensity. In less disturbed environments, communities are often dominated by a few highly competitive species with slower growth, lower reproductive rates and limited dispersal capacity, highly disturbed areas tend to favour opportunistic and fast-colonizing species characterized by rapid growth, early reproduction and high dispersal capacity (Bertness, 2007; Kaiser et al., 2011; McLusky and Elliott, 2007). Benthic communities exposed to long-term dredging often undergo several successional stages. Initially, the species abundance increases, followed by an increase in diversity (van der Linden et al., 2016), while over time, opportunistic species become dominant followed by a reduction in species abundance and diversity. Opportunistic species are often the first to respond to a disturbance, due to specific traits (dispersal ability, disturbance tolerance and high reproductive rates (van der Linden et al., 2016). Therefore, disturbance acts as a selective force on life-history strategies (Bertness, 2007; Kaiser et al., 2011; McLusky, and Elliot, 2007). These patterns are also consistent with the ‘Stability-time hypothesis’ by Sanders (1968) in the way that communities exposed to the extreme environment of

continuously disturbance (e.g. trawling), leads to a reduced diversity compared to the less disturbed, non-dredged areas (Dolmer et al., 2001; MacDonald et al., 1996; Sanders, 1968; Tillin et al., 2006)

1.3. Short-term - long-term - direct and indirect impacts

The effects of mussel dredging can be defined as "short-term" and "long-term" effects. Short-term effects are detectable within months to few years by high mortality rates, reduced biomass, diversity and body size (Hansen and Andersen, 2024; Johnson et al., 2025). Long-time effects can be observed over decades and may result in population decline and alterations in the community structure (Dolmer et al., 2001; Hansen and Andersen, 2024). Furthermore, dredging also causes both "direct" and "indirect" impacts across spatial and temporal scales. Direct impacts are the physical interaction between fishing gear and the seabed, resulting in invertebrate mortality and habitat alterations through removal of reefs, seagrass beds, sediment removal and resuspension (Sparks-McConkey and Watling, 2001), while indirect impacts are seen in long alterations in the community structure and loss of biodiversity (Hansen and Andersen, 2024; Tillin et al., 2006).

2. Benthic community ecology

Soft-bottom habitats may initially seem biologically poor, however, these benthic communities can be highly diverse and productive, containing both epifaunal and infaunal species adapted to a wide range of ecological niches and environmental conditions (Bertness, 2007; Kaiser et al., 2011; Lundquist et al., 2013; McLusky and Elliott, 2007). Epifaunal species such as the bivalve *Mytilus edulis*, and gastropods *Littorina* sp. create biogenic habitat structures that provide settlement habitats, refuge from predation and sediment stabilisation. Infaunal organisms such as the burrowing annelids, bivalves and amphipods, influence sediment structure and biochemical processes through feeding activity, sediment mixing (bioturbation), and burrow ventilation (bioirrigation) which regulate the transport and turnover of organic matter, sediment oxygenation and the movement of dissolved and particulates material within the marine sediments (Høgslund et al., 2019; Pommer et al., 2016). Especially taxa such as *Arenicola marina*, *Tubificoides* sp., Capitallideae and several spionids are strongly associated infaunal species (Bertness, 2007; Kaiser et al., 2011; McLusky and Elliott, 2007). Other species such as *Hydrobia* sp. and *Corophium* sp., can inhabit both surface and deeper sediment layers depending on feeding activity and environmental conditions. Furthermore, benthic species can also be categorized by feeding strategies. Suspension feeders filter small organic particles and phytoplankton from the water column, while deposit feeders utilize organic material within or on the sediment surface and can further be categorized as surface or subsurface deposit feeders. Some

species can shift feeding strategy regarding to available food resources. While *M. edulis* are solely suspension feeders, and the sandworm *A. marina* a typical deposit feeder, species such as the burrowing *Macoma balthica* can both be defined as suspension and deposit feeder since it can utilize phytoplankton by filtration and collect detritus from the sediment surface. This flexibility makes the organism adapted to several food resources regarding the environmental conditions. *Peringia ulvae* is a grazer and deposit feeder, which feeds on detritus and microalgae on the sediment surface, on mudflats (Bertness, 2007; Kaiser et al., 2011; McLusky and Elliott, 2007). Other species such as the polychaete *Alitta succinea*, are defined as an omnivore, since it both feeds on sediment detritus, but also hunts smaller invertebrates and prey on damaged individuals. Therefore, the soft-bottom ecosystem is a complex ecosystem, containing many different well adapted species to the specific environmental conditions, making them vulnerable to anthropogenic stressors such as dredging.

2.1. Functional groups

An important component in benthic ecosystems, are their contribution in ecosystem functioning, by different functional traits or functional groups. Physical disturbance from bottom-gears may affect these functional groups differently and thereby alter ecosystem functioning and energy flow within soft-bottom habitats. Suspension-feeding bivalves are important components of soft-sediment ecosystems by filtering phytoplankton and suspended organic matter from the water column, and thereby linking pelagic primary production with benthic secondary production (Bertness, 2007; Kaiser et al., 2011; Lundquist et al., 2013; McLusky and Elliott, 2007). As these organisms depend on stable sediment conditions and water column filtration, they may be sensitive to sediment resuspension and physical disturbance caused by dredging activities. Other groups are deposit-feeding organisms, including annelids, amphipods and gastropods, as they process organics material directly within sediments and contribute to nutrient cycling, sediment oxygenation and bioturbation through feeding and burrowing activities. Surface deposit feeders utilize organic material located at the sediment-water interface, including protozoans, diatoms and fungi and their local effects are therefore restricted to the upper 2-3 cm of the sediment. Because of their habitat position and close interaction with surface sediments, these organisms may be strongly affected by repeated sediment resuspension and disturbance of surface sediments. In contrast, subsurface deposit-feeders both live in and feed on deeper sediments and can have important effects on sediments up to 30 centimetres deep (Bertness, 2007; Kaiser et al., 2011; Lundquist et al., 2013; McLusky and Elliott, 2007). Predators and scavengers, additionally play a crucial role within the ecosystem in regulating populations sizes and trophic interactions (Pommer et al., 2016). These groups consist of gastropods,

annelids, sea stars and crabs, and exhibit different feeding strategies, mobility and sediment interaction (Bertness, 2007; Kaiser et al., 2011; Lundquist et al., 2013; McLusky and Elliott, 2007; Pommer et al., 2016).

2.2. Importance of metapopulations and connectivity

To understand how the populations of benthic invertebrates persist and fluctuate in size and distribution, the metapopulation theory is a useful framework for understanding these processes. The theory explains that populations are structured as networks of spatially separated subpopulations occupying discrete habitat patches, which are connected through dispersal of individuals or propagules (Hanski, 1998). This connectivity strongly influences recolonisation dynamics and recovery potential following disturbances by recruitment success, population growth and survival. These processes depend on the continuous supply of individuals from adjacent populations (Pastor et al., 2018; Thorson 1950). Local populations may occasionally become extinct due to demographic stochasticity or the Allee effect where small population sizes are vulnerable to random population fluctuations (Krebs, 2014). Populations may also become locally extinct, caused by natural environmental disturbances, but anthropogenic impacts are some of the present causes of declining benthic populations, in modern times. Therefore, in marine benthic systems, larval dispersal is typically the primary mechanism that connects these spatially separated populations.

Many marine benthic invertebrates have evolved different larval development strategies in response to varying environmental conditions, for spatial competition and resources, but initially start their life cycle with a planktonic life stage, where the larvae are dispersed by ocean currents and mixing of the water column (Bendtsen and Hansen, 2013). Here, a high proportion of these species produce planktonic larvae (planktotrophy) which feeds on phytoplankton and remain in the water column for several days to multiple months before settling to the seabed (Pastor et al., 2018). Planktotrophic larvae can therefore disperse over long distances through ocean transport and play an important role in maintaining population connectivity and sustaining metapopulations between geographically separated regions (Pastor et al., 2018; Bendtsen and Hansen, 2013). Another type of planktonic larvae is the lecithotrophic larvae, which only feeds on a parental yolk reserve, rather than phytoplankton and spend shorter periods in the water column before settling to the seabed (Bertness, 2007; Kaiser et al., 2011; McLusky and Elliott, 2007). Compared to planktotrophic species, these larvae therefore exhibit lower dispersal potentials and ranges (van Denderen et al., 2022). Other, organisms exhibit direct development and skip the planktonic larval stages by producing offspring which remain closely

associated with local habitats. Such populations rely strongly on local persistence and self-recruitment and are often more well adapted to stable and less disturbed environments, where competitive dominance of the larvae may be favoured large body sizes over dispersal ability. On the contrary, species with direct development, are more vulnerable to repeated disturbance than planktotrophic and lecithotrophic larvae (Bendtsen and Hansen, 2013; van Denderen et al., 2022). Consequently, disturbance can shape a community in the way of promoting certain species due to the interaction between ocean transport, larval dispersal and successful recruitment (Bendtsen and Hansen, 2013).

3. Knowledge gap

The ecological impacts of mussel dredging and bottom contact fisheries on benthic communities have been well documented with several studies demonstrating reductions both abundance, species richness, biomass, and alterations in community structure following physical disturbance (Dolmer et al., 2001; Sparks-McConkey & Watling, 2001; Kaiser et al., 2006; Sköld et al., 2018). However, most studies have focused on short-term experimental disturbances or recovery processes measured over periods of weeks to months following dredging events (Dolmer et al., 2001; Dernie et al., 2003; Bromhall et al., 2022). Other studies have investigated the effects of chronic trawling using spatial gradients in fishing intensity, demonstrating long-term changes in biodiversity, biomass and community composition (Tillin et al., 2006; Pommer et al., 2016; Sköld et al., 2018). However, relatively few studies have been able to assess ecological changes over decadal timescales using historical baseline data from the same ecosystem. Furthermore, previous studies have primarily focused on taxonomic responses such as abundance, biomass and species richness, while comparatively less attention has been given to long-term changes in functional community composition and ecological traits (Tillin et al., 2006; Thrush & Dayton, 2002). Functional changes may occur even when taxonomic responses appear limited and may provide a more sensitive indicator of ecosystem degradation and resilience.

3.1. Research questions

Therefore, the aim of this study was to investigate how decal recurrent mussel dredging affects the biodiversity, functional composition and population dynamics of benthic invertebrate communities, and the potential ecological consequences in a shallow soft-sediment fjord habitat. This study was conducted in Lammefjorden, Zealand, Denmark, since the fjord has been subjected to extensive dredging for blue mussels (*Mytilus edulis*) in 2024, shifting from a three-year dredging cycle to an annual fishing activity. Thus, this project aims to document the baseline of the newly intensified

dredging areas in 2024, and to describe the long-term development of the fjord systems from 1996 to 2024 as well as the recovery processes of the seabed during the first season after dredging in 2025. This will be investigated by following questions: 1. How do species richness and biodiversity of macrozoobenthos differ between dredged and non-dredged areas; 2. What changes are observed in species composition and functional groups of macrozoobenthos as a result of dredging; 3. How does dredging affect population size and biomass of benthic invertebrates; and 4. What implications do the results have for management and sustainable fisheries in the future. It is hypothesized that: 1. The species richness and diversity will decline in dredged areas, compared to non-dredged areas; 2. Dredging will decrease population size and biomass; 3. The species composition will shift towards opportunistic fast-colonizing infaunal species with planktotrophic larvae, including subsurface deposit feeders and scavengers, and finally, that 4. Dredging will affect the benthic trophic interactions with altering food resources for demersal fish

4. Materials and methods

4.1 Study area

The effects of mussel dredging were investigated in Lammefjorden and compared with a less intensified dredged area in Holbæk Fjord. Both fjords are sub-fjords located in the southwest part of Isefjorden, Denmark and covers an area of ~56 km^2 in Lammefjord and ~21 km^2 in Holbæk Fjord with a mean depth of ~5.6 m, ranging from ≤0.8-10m. The Isefjord system is classified as a mesohaline estuarine environment (PSU>18) (Nielsen, Sømod and Christiansen, 2001), influenced by inflow of mesohaline surface water coming from Kattegat typically 18 - 25 PSU (NOVANA data) and local freshwater inputs (Christensen et al., 202; Bendtsen & Hansen, 2013).

4.2 Study design

The design of the study is a Before/After and Control/Impact (BACI) design (figure 1) and is developed to detect if environmental changes have an impact on mean abundance and population dynamics (Underwood, 1992). It assumes that changes due to anthropogenic disturbances in the impacted location will have a different effect on population dynamics compared to a natural change in the control location (Underwood, 1992). In this study, this was assessed by analysing spatial and temporal variation in biodiversity and benthic community by random sampling of benthos, in the impacted area, Lammefjord, and compared with the control area, Holbæk Fjord, in a 29-year period (1996-2025), where 1996 represents before impact, and 2025 represents after the impact, in 2024.

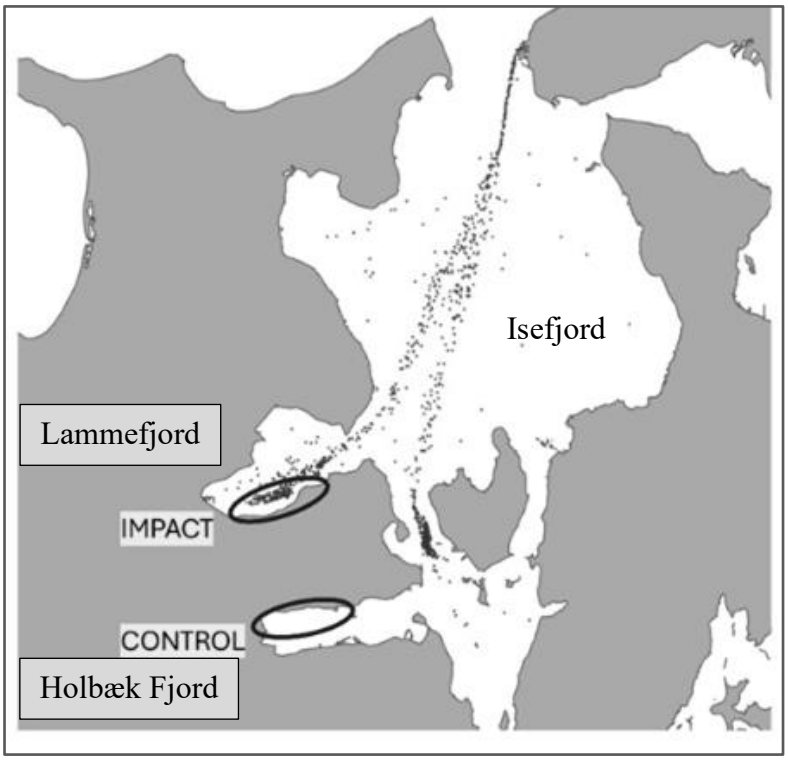


Figure 1. Isefjord with adjacent Lammefjord and Holbæk Fjord. Dots indicate VMS-ping from vessels likely to trawl.

4.2.1. Field methods

Marine sediment samples were collected in late spring (7-9 May 2025) at 10 stations in Lammefjorden and in early summer (3 June 2025) at 8 stations in Holbæk Fjord (figures 2, and 3; table 1.2). At each station, five benthic replicates were taken using a HAPS core sampler (Kanneworff & Nikolaisen, 1973) with a sampling area of 0,0123m^2, except for station T2 (n=3), 10032 (n=6) and 10033 (n=6), following the protocol described in Hansen & Josefson (2020). This results in a total sample size of 47 samples in Lammefjord and 43 in Holbæk Fjord. All samples were sieved the same day as sampled, through a 1 mm quadratic mesh (certified sieve), so that only material >1 mm was retained. The retained materials were then transferred into plastic containers and additionally added 96% ethanol to a final concentration of 70% for conservation (Linden et al., 2016; Hansen & Josefson, 2014). To analyse the potential long-term impact of dredging on the benthic community within the BACI-design framework, the sampling locations in 2025 were identical to those in 1996. In Lammefjord, 11 stations were sampled containing six replicates in each station accounting for 63 samples in total. In Holbæk Fjord 9 stations was sampled with six replicates per station, except 10033 where only one

sample was collected. In total this accounted for 49 samples in total (figure 2.3; table 1.2). The samples collected in 1996 were taken using different sampling methods and sampling areas where most samples were taken with a HAPS sampler (0,015 m^2), and some samples with a Van Veen grab (0,025m^2) and a smørstikke (0,0079 m^2).

Figure 2. Map of sample stations for Lammefjord with ODA-number and location ID from 1996 and new location ID represented with round brackets, for new stations in 2025.

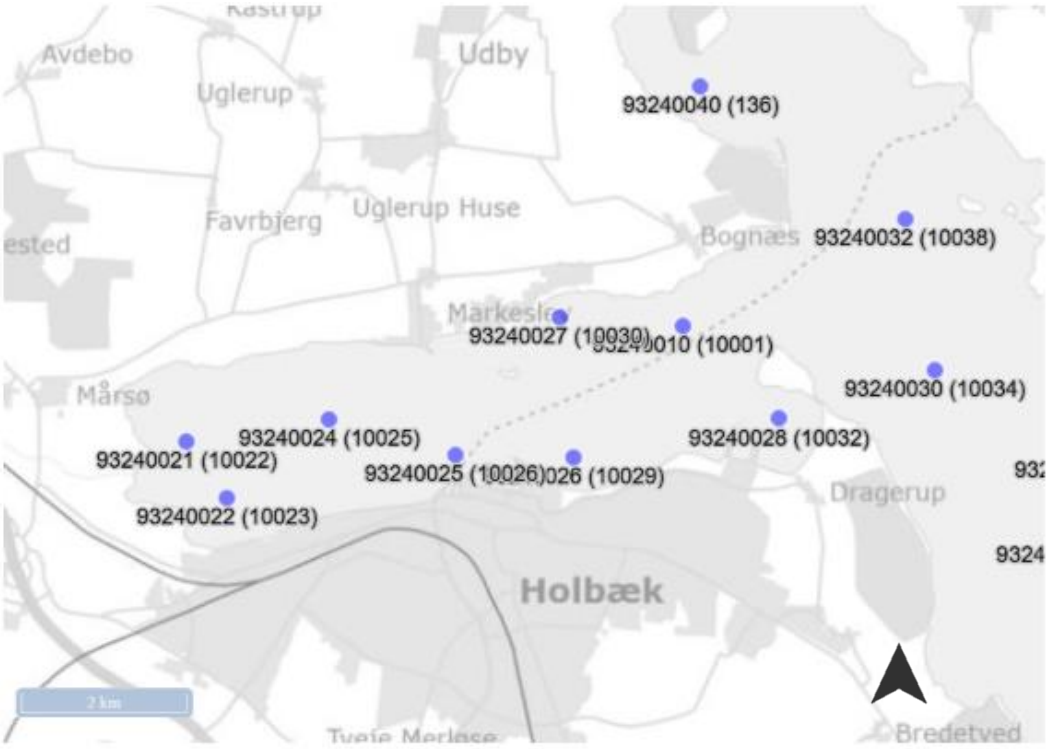


Figure 3. Map of sample stations for Holbæk Fjord with ODA-number and location ID from 1996 and new location ID represented with round brackets, for new stations in 2025.

Tabel 1. Stations n=10 for sampling sites in Lammefjord 2025 and 11 stations in 1996 including coordinates given in decimal degrees (WGS84), sampling methods and depth of sites.

Location	Sampling tool	Year	Latitude	Longitude	Depth(m)
10002	Haps	1996/2025	55,80200003	11,71017	10/9,9
10050	Haps	1996/2025	55,78033003	11,62183	5.2/5.2
10052	Haps	1996/2025	55,77700003	11,65183	4/4
10053	Haps	1996/2025	55,78817003	11,64683	5/5
10055	Haps	1996	55,79117003	11,6835	9.1
10056	Smørstikke/Haps	1996/2025	55,80867003	11,66017	1.8/1.8
10057	Smørstikke/Haps	1996/2025	55,81450003	11,67017	2.3/2.3
10058	Van Veen/Haps	1996/2025	55,80067003	11,6835	3/3
10059	Haps	1996/2025	55,80783003	11,69017	6.3/6.3
10060	Haps	1996/2025	55,79383003	11,71683	3.6/3.6
10061	Haps	1996	55,80483003	11,71933	11,5
T2	Haps	2025	NA	NA	NA

Tabel 2. Stations n=8 for sampling sites in Holbæk Fjord 2025 and n=9 stations in 1996 including coordinates given in decimal degrees (WGS84), sampling methods and depth of sites.

Location	Year	Sampling tool	Latitude	Longitude	Depth(m)
10001	1996/2025	Haps	55,73567	11,75067	9/8.1
10022	1996	Smørstikke	55,72050	11,67017	0,8
10023	1996	Smørstikke	55,72050	11,67017	1,5
10024	2025	Haps	55,73217	11,6735	2/2
10025	1996/2025	Haps	55,72783	11,68850	3.5/3.5
10026	1996/2025	Haps	55,72383	11,71017	3.6/3.6
10029	1996	Haps	55,72150	11,73083	3
10030	1996/2025	Smørstikke/Haps	55,73700	11,72933	2.2/2.2
10032	1996/2025	Smørstikke/Haps	55,72617	11,76683	1.2/1.2
10033	1996/2025	Van Veen/Haps	55,74200	11,76733	3.5/3.5
J	2025	Haps	NA	NA	NA

4.2.2. Laboratory methods

In the laboratory, all samples were sieved through a 500 µm sieve with tap water and rinsed into a tray using a spray bottle with tap water until all material was transferred. Small amounts of sieve residue were transferred from the tray into a petri dish with horizontal markings for fine sorting under a Leica MZ12 stereomicroscope. The benthic invertebrates were fine sorted by transferring into similar individuals to square glass jars 40 x 40 mm and identified to the lowest possible taxonomic level using key literature for marine benthic invertebrates (Table 3). The number of individuals were noted in an excel sheet for subsequent diversity analysis. For biomass measuring, identified animals were measured using a Mettler Toledo AT261 DeltaRange weight, by placing all similar individuals from a jar, on a piece of tissue paper for approximately 20 seconds to remove excess water. The animals were then weighed with a precision of four decimals. Biomass was initially estimated as wet weight (gm^{-2}). This benthic community data was then compiled into a "taxa-biomass-by-sample" - and "taxa-species-by-sample' matrix (Linden et al., 2016). The animals were then transferred to a test tube with 70% ethanol for preservation and labelled with station and sample number and species name and was sealed with a piece of cotton. All glasses were then put into a jar containing 70% ethanol (Hansen & Josefson, 2020).

Table 3. Taxonomic literature list used for species identification.

Phyla	Taxonomic literature
Annelida	Barnich, R. (2011). Identification of scale worms in British and Irish waters. Frankfurt: Senckenberg Research Institute. Kirkegaard, J.B. (1992). Havbørsteorme I: Errantia. København: Dansk Naturhistorisk Forening. Kirkegaard, J.B. (1996). *Havbørsteorme II: Sedentaria*. København: Dansk Naturhistorisk Forening. Køie, M. & Kristiansen, A. (2023). *Havets dyr og planter*. 3. udgave. København: Gyldendal. ISBN 978-87-02-36898-7.
Arthropoda	Dahms, H.-U., Fornshell, J.A. & Fornshell, B.J. (2006). Key for the identification of crustacean nauplii. Organisms, Diversity & Evolution, 6, s. 47–56. Enckell, P. H. 1980. Kräftdjur. Fältfauna. - Signum, Lund. 685 pp. Zettler, M.L. & Zettler, A. (2017). Marine and freshwater Amphipoda from the Baltic Sea and adjacent territories. Harxheim: ConchBooks. Køie, M. & Kristiansen, A. (2023). *Havets dyr og planter*. 3. udgave. København: Gyldendal. ISBN 978-87-02-36898-7. Lincoln, R.J. (1979). British marine Amphipoda: Gammaridea. London: British Museum (Natural History), Cromwell Road, SW7 5BD. (Publication no. 818). ISBN 0565008188.
Bryozoa	Hayward, P.J., 1985. Ctenostome bryozoans. Keys and notes for the identification of the species. Synopses of the British Fauna (New Series), No. 33. Published for the Linnean Society of London and The Estuarine and Brackish-Water Sciences Association by E.J. Brill/ Dr. W. Backhuys, London, Leiden, Köln, København.
Chordata	Køie, M. & Kristiansen, A. (2023). *Havets dyr og planter*. 3. udgave. København: Gyldendal. ISBN 978-87-02-36898-7.
Cnidaria	Køie, M. & Kristiansen, A. (2023). *Havets dyr og planter*. 3. udgave. København: Gyldendal. ISBN 978-87-02-36898-7.
Echinodermata	Køie, M. & Kristiansen, A. (2023). *Havets dyr og planter*. 3. udgave. København: Gyldendal. ISBN 978-87-02-36898-7.

Mollusca	Alf, A, Brenzinger, B, Haszprunar, G, Schrödl, M & Schwabe, E 2020, A Guide to Marine Molluscs of Europe, ConchBooks, ISBN 978-3-948603-00-7 Bondensen, P. 1991. Danske Havmuslinger. Natur og Museum.23. årgang, nr2, 2. udgave. Naturhistorisk Museum Århus. Bondensen, P. 1994. Danske havsnegle. Natur og Museum. 33. årgang, nr.2. 2.udgave. Naturhistorisk Museum Århus. Christensen, J.M., Larsen, S. & Olesen Nyström, B. (1978). Havmuslinger. København: Gyldendalske Boghandel, Nordisk Forlag A/S. (Gyldendals grønne håndbøger). ISBN 87-01-42641-9. Køie, M. & Kristiansen, A. (2023). *Havets dyr og planter*. 3. udgave. København: Gyldendal. ISBN 978-87-02-36898-7.
Nemertini	Køie, M. & Kristiansen, A. (2023). *Havets dyr og planter*. 3. udgave. København: Gyldendal. ISBN 978-87-02-36898-7.
Nematoda	Køie, M. & Kristiansen, A. (2023). *Havets dyr og planter*. 3. udgave. København: Gyldendal. ISBN 978-87-02-36898-7.

4.3. Biodiversity analysis

4.3.1. Community analysis

The distribution and alterations of biodiversity and community compositions among fjords and stations, were analysed by a combination of univariate and multivariate approaches. All statistical and community analysis was proceeded using RStudio-2026.01.0-392 and PRIMER © ver.–7. Taxonomic nomenclature was quality checked through World Register of Marine Species (WorMS) on 12/02-2025 to ensure validity of species names. Spatial visualizations were generated using Rstudio to generate plots for illustrating differences in diversity.

4.3.2. Diversity indices - Alpha, Beta and Gamma diversity

For documenting how bottom dredging has affected Lammefjorden over the 29-year period, changes in biodiversity were assessed at different spatial scales and diversity indices. Alpha diversity was defined diversity indices calculated for a single sample including species richness (S), Margalef's index (D), Shannon-Weiner diversity (H'), Simpson's index (L1), Simpson's inverse index (L2), Standardized species richness (ES10) and evenness (J'), which was calculated for all single Haps samples from each fjord and each year in PRIMER © ver. 7. (Clarke & Warwick, 2001; Hansen & Andersen, 2024). The beta diversity (local scale) then tests the variation in species composition among stations, while gamma diversity (regional scale) then represents the overall diversity at the

fjord scale which compares differences in species composition between Lammefjord with adjunct basins such as Holbæk Fjord and the Isefjord system. On a regional (fjord) scale, mean values ± SE were calculated on aggregated samples within each fjord, and respective year. To test for significant differences around the means a non-parametric Wilcoxon test was used. On a local (station) scale, mean values ± SE were calculated for each subsample, of each station, and compared across stations and years and followed by a calculated change for each station.

4.3.3. Species richness (S)

Species richness (S), the total number of species present after counting all individuals (N) on sample-station-fjord scale.

4.3.4. Expected number of species for 10 individuals (ES10)

Is a finer scale of species richness (S), since it represents the expected number of species within a random subsample of 10 individuals, based on rarefaction. It is less influenced by differences in total abundance or sampling effort compared to traditional species richness measures.

4.3.5. Margalefs index (D)

Is another variant of species' richness, measuring the number of species present for a given number of individuals (Clarke and Warwick, 2001), and was calculated as:

(1)

$$D = (S-1) / \ln(N)$$

4.3.6. Shannon-Wiener Index (H')

The Shannon diversity metric (Shannon & Weaver, 1949) accounts for both species richness and the evenness of individuals among species, between samples (Clarke and Warwick, 2001). This was calculated as:

(2)

$$H' = -\Sigma p_i \log (p_i)$$

Here, S represents the number of species, p_i the proportion of individuals belonging to species *i* (n_i / N), and N as the total number of individuals. This index is traditionally calculated with a logarithm base 2 (Hansen & Andersen, 2024).

A high H' indicates many species and a relatively even distribution of individuals, whereas a low H' indicates few species or strong dominance by one or a few species.

In relation to dredging, this type of disturbance often reduces H' because it favours opportunistic and fast-growing species. As a result, this type of disturbance reduces evenness and may also reduce species richness, leading to lower overall diversity.

4.3.7. Simpsons index (Lambda, L1, L2)

Simpsons index (Lambda) describes the probability that two randomly selected individuals from a sample belong to different species (Clarke and Warwick, 2001). This was calculated in two as:

(3)

$$L1= \Sigma(p_i)^2$$

And the inverse Simpson's index (L2):

(3)

$$L2= 1-\Sigma(p_i)^2$$

Here, p_i represents the proportion of species *i*. This index is less sensitive to sample size and gives more weight to dominant species (Hansen & Andersen, 2024. The index varies between 1 = high, and 0 = low, where a high Lambda indicates a high diversity and low dominance whereas Lambda close to 0, indicates a strong dominance by few species.

4.3.8. Pielou's evenness index (J')

This diversity index measures how even individuals are distributed within the different species (Clarke and Warwick, 2001), since evenness is independent of species richness and specifically reflects balance in abundance distribution. This index is developed to detect if few species dominates even if the species richness is high.

(5)

$$J' = H' / H'_{max} = H'/logS$$

Here, H' accounts for the observed Shannon diversity and logS as the maximum possible Shannon diversity if all species were equally abundant. H'_{max} is the maximum possible value of the Shannon diversity (H') and would be achieved if all species (S) are equally abundant between all samples

(LogS) (Clarke and Warwick, 2001). Values close to 1 indicates a highly even community, and values close to 0 indicates dominance by a few species.

4.3.9. Species -turnover rate

To make a qualitative analysis of a community shift due to dredging disturbance (Cuesta Núñez et al., 2023) on a temporal scale, a species turnover-rate was calculated in Rstudio with packages "readxl, dyplr" and the function "Sorensen_turnover". This measurement was calculated by the temporal development of community composition between beta-diversities:

(6)

$$\beta = \frac{(b + c)}{2a + b + c}$$

Here, a is the number of shared species between the two communities, in this case on a regional scale (between Lammefjord and Holbæk Fjord 2025, and 1996), as for within both fjords on a temporal scale (2025 and 1996), b accounts for the number of species which only occurs in the first year, defined as "lost species" from 1996, and c constitutes the number of species which only occurs in the second year, defined as the "gained species", in 2025. The result is represented as following variables: βsor = total difference between β-communities, βsim = Turnover and βsne = Nestedness

4.3.10. Phyla analyses

Mean ± SE abundance of aggregated values of all phyla was calculated for each fjord and year.

4.4. SAR analysis

For estimating dredge activity effect on biodiversity, a swept area ratio (SAR) was roughly estimated by the calculation of the dredged (swept) area, based on VMS pings recorded from dredging vessels, from Lammefjord 2024. The total number of pings was calculated within a predefined 500 × 500 m grids and assigned to respective stations. The number of pings was multiplied by 14, which represented an assumed mean distance sailed between two "pings" and the values were then multiplied by 4 corresponding to assumed summed withs of the two mussel dredgers to calculate the swept area (SAR). Finally, swept area ratio (SAR) was calculated by dividing swept area with 250.000m^2 (the area of the 500 × 500 m). Diversity patterns in Lammefjord were investigated using the diversity indices species richness (S), Margalef's (D), Shannon diversity (H), ES10, Evenness, and Simpson's index (L1, L2), total abundance and biomass. Dredging intensity was quantified using SAR values (% swept area ratio). As the data were not normally distributed, relationships between

dredging intensity and diversity parameters were tested using Spearman rank correlations test in RStudio version 2025.09.2+418.

4.5. Biomass analysis

4.5.1. Wet weight (WW) biomass data from 19996 from both Lammefjord and Holbæk was calculated and converted from dry wet weight (DWW) biomass data to WW in relation to Gogina et al. (2022) and Ruhmor et al. (1987) (only for nematodes).

Tabel (4). Conversion factors of different taxonomic levels used for the calculation of wet weight biomass, from dry weight biomass.

Taxonomic group	DW to WW (g^{-1}) Conversion factor
Amphipoda	0.145
Anthozoa	0.187
Ascidiacea	0.178
Bivalvia	0.489
Bryozoa	0.161
Echinodermata	0.35
Gastropoda	0.463
Hydrozoa	0.164
Mysida	0.15
Nemertea	0.159
Nematoda	4.35
Platyhelminthes	0.165
Polychaeta	0.168

4.5.2. Fjord-scale biomass

Biomass density (gm^{-2}) was calculated by dividing total weight of individuals per sample with the surface area of the respective sampling method used in 1996 and 2025, corresponding to 0,0123 m^2 for Haps in 2025 and 0,015 m^2 in (1996), Van Veen grab 0,025 m^2 and smørstikke 0,0079 m^2 (1996). Biomass data was transformed on a $\log_{10}$ scale for comparison and visualisation.

4.5.3. Station-scale biomass

Biomass data (gm^{-2}) were analysed per station, fjord, and year. Biomass values were log_{10}-transformed to reduce skewness and heterogeneity in variance among samples. Mean biomass and standard error (SE) were calculated from the transformed data for each station. Values were back transformed to the original biomass scale using 10^x.

4.5.4. Dredging effect on benthic food chain

To investigate the effect of dredging on the benthic trophic food chain biomass, the species contributing the most to the community biomass, were identified by grouping the data by fjord, year and species, followed by a summation of biomass values (gm^{-2}) across all samples within each fjord and year. Samples from Lammefjord were compared with samples from all stations located in Isefjord Yderbredning from year 1996 and 2024, using data extracted from the database: https://odaforalle.au.dk/login.aspx, accessed May 13, 2026.

4.6. Functional trait analysis

4.6.1. AMBI - Classification system

The AZTI Marine Biotic Index (AMBI) is a trait-based analysing tool which can be used for detecting changes in community structure and ecological conditions, based on a classification-system that ranks different species into specific functional traits categories. These categories are ranked as (EG I-V), based on tolerance of disturbance and are mostly coupled with pollution, but can also be used for analysing a mechanical disturbance as bottom dredging. Category I species are defined as the least tolerant species to disturbance and category V as the most tolerant species (Borja et al., 2000). The distribution of the different ecological groups within a community then shapes the basis of the biotic index (BI), and ranges from 0 to 7, reflecting the ecological condition of the given site (Borja et al., 2000).

4.6.2. Community-weighted mean (CWM)

Besides diversity, species richness and AMBI, biological traits were further investigated since they provide more detailed ecological information that richness alone may not detect. Traits categories were defined for each species, as larval type (planktonic, lecithotrophic and direct), feeding mode (deposit, suspension, predator, scavengers, parasite, grazers and omnivore), longevity (very short = <1yr, short= 1-3yr, medium = 3-10yr and long= >10yr), and habitat (epifauna, infauna). The application of trait-based measures can be used to better detection of environmental impacts and disturbances such as dredging (Hansen and Andersen, 2024; Bolam et al., 2017). For analysing shifts

in community composition, a community-weighted means (CWMs) was calculated to quantify fjord-level trait composition based on species abundances, following standard trait-based approaches (Liu et al., 2026). For each fjord and year, all samples were pooled, and species abundances were summed across samples. Traits were given equal weights, such that the sum of trait scores per species equalled 1.

Species abundances were converted to relative abundances within each fjord-year:

(7)

$$p_i = \frac{A_i}{\sum A_i}$$

where A_i is the total abundance of species *i*.

For each trait category, CWM values were calculated as the sum of relative abundances weighted by trait scores:

(8)

$$\text{CWM} = \sum_{i=1}^{n} (p_i \times t_i)$$

where t_i is the proportional trait score of species *i* for the given category. Therefore, CWM values represent the proportion of the total community abundance associated with a given trait category.

4.7. Multivariate analysis

4.7.1. Bray Curtis and nMDS

To assess changes in diversity patterns of the benthic community, multivariate analysis was used for detecting changes in community structure on a spatial and temporal ordination and descriptive biological indices were used to describe the change patterns (Sparks-McConkey and Watling; 2001). This was done in PRIMER 7 based on species abundance data, where an overall transformation was proceeded to reduce dominating species. A Bray-Curtis similarity analysis was proceeded followed by adding a dummy variable with value 1 to compensate for many 0 values. The biological similarity between stations and fjords, was visualized in Non-metric Multidimensional Scaling (nMDS) plots, to detect community differences as for driving environmental factors causing community differentiation. This was done to compare community patterns between Lammefjord and Holbæk

Fjord and compared with data from the ODAforalle database: https://odaforalle.au.dk/login.aspx, for detecting similarity pattern and infer possible connectivity patterns with Isefjord Inderbredning, Isefjord Yderbredning, Hesseløbugten, Southern Kattegat and central Kattegat close to Anholt.

4.7.2. ANOSIM and SIMPER analysis

An analysis of similarities (ANOSIM) was used to assess if dredging affected the community composition of macrozoobenthos between dredged and non-dredged sampling stations. The analysis was proceeded in PRIMER ver. 7, where species abundance data were transformed for reducing dominating species, followed by a Bray-Curtis dissimilarity matrix. The ANOSIM was then based on dissimilarity and used to evaluate community differences between groups. To identify which species contributed most to the differences between groups, a SIMPER-analysis was performed (Clarke and Warwick, 2001)

5. Results

5.1 Univariate analysis of diversity indices

5.1.1. Comparison of diversity between Lammefjord and Holbæk Fjord 2025

The results showed that the benthic community composition between both fjords differed moderately (table 4.5; fig. 4). In 2025, differences in abundance and diversity indices were observed between Lammefjord and Holbæk Fjord. Lammefjord exhibited a higher mean abundance (80.5 ± 15.99), than Holbæk Fjord (42 ± 7.24) but was not significant (p=0.4212) (table 4.5; fig. 4). On the contrary, all diversity indices (D, ES10, J', ES10, H', L1 and L2) were in general significant lower in Lammefjord 2025, compared to Holbæk Fjord (table 4.5; fig. 4) except for S (number of species per sample) with no significance, but a strong tendency, indicating that the community contained more individuals but fewer species and lower overall diversity. Simpson's indices further suggest differences in species dominance structure between the fjords, with Lammefjord showing indications of stronger dominance by fewer species (L1=0.6 ± 0.04) compared to Holbæk Fjord (L2=0.8 ± 0.01).

Table 4. Comparisons of diversity development in the two fjords between the two surveys in 1996 and 2025. Values are calculated from the results of sample-level diversity indices computed in PRIMER and represent mean ± standard error.

Fjord	Year	N	S	D	J'	ES10	H'	L1	L2
Lf	1996	164.9 ± 2.24	10.0 ± 0.62	2.1 ± 0.09	0.8 ± 0.01	4.9 ± 0.13	2.4 ± 0.07	0.3 ± 0.02	0.8 ± 0.02
Lf	2025	80.5 ± 15.99	7.4 ± 0.68	1.9 ± 0.11	0.7 ± 0.04	3.8 ± 0.23	1.7 ± 0.12	0.4 ± 0.04	0.6 ± 0.04
Hf	1996	101.7 ± 5.25	9.8 ± 0.64	2.3 ± 0.12	0.8 ± 0.02	4.9 ± 0.17	2.4 ± 0.09	0.3 ± 0.02	0.8 ± 0.02
Hf	2025	42.0 ± 7.24	9.1 ± 0.90	2.6 ± 0.13	0.8 ± 0.02	4.8 ± 0.27	2.3 ± 0.14	0.3 ± 0.03	0.8 ± 0.01

Tabel 5. Significance levels obtained from spatial and temporal comparisons of diversity indices between the Lammefjord (Lf) and Holbæk Fjord (Hf) with a Wilcoxon-test, from 1996 to 2025. Significance levels: * p <0.05, ** p< 0.01, *** p< 0.001, ns = not significant.

Fjord/year	N	S	D	J'	ES10	H'	L1	L2
Lf - Hf 1996	0.3158 ns	0.9436 ns	0.4907 ns	0.8796 ns	0.9977 ns	0.9043 ns	0.9953 ns	0.9159 ns
Lf - Hf 2025	0.4212 ns	0.2155 ns	0.0003 ***	0.0492 *	0.0014 **	0.0003 ***	0.0002 ***	0.0004 ***
Lf 1996 - 2025	0.0144 *	0.0039 **	0.0727 ns	0.7509 ns	0.0002 ***	0 ***	0 ***	0.0503 ns
Hf 1996 - 2025	0.0065 **	0.3606 ns	0.1005 ns	0.0211 *	0.6027 ns	0.8602 ns	1 ns	0.0029 **

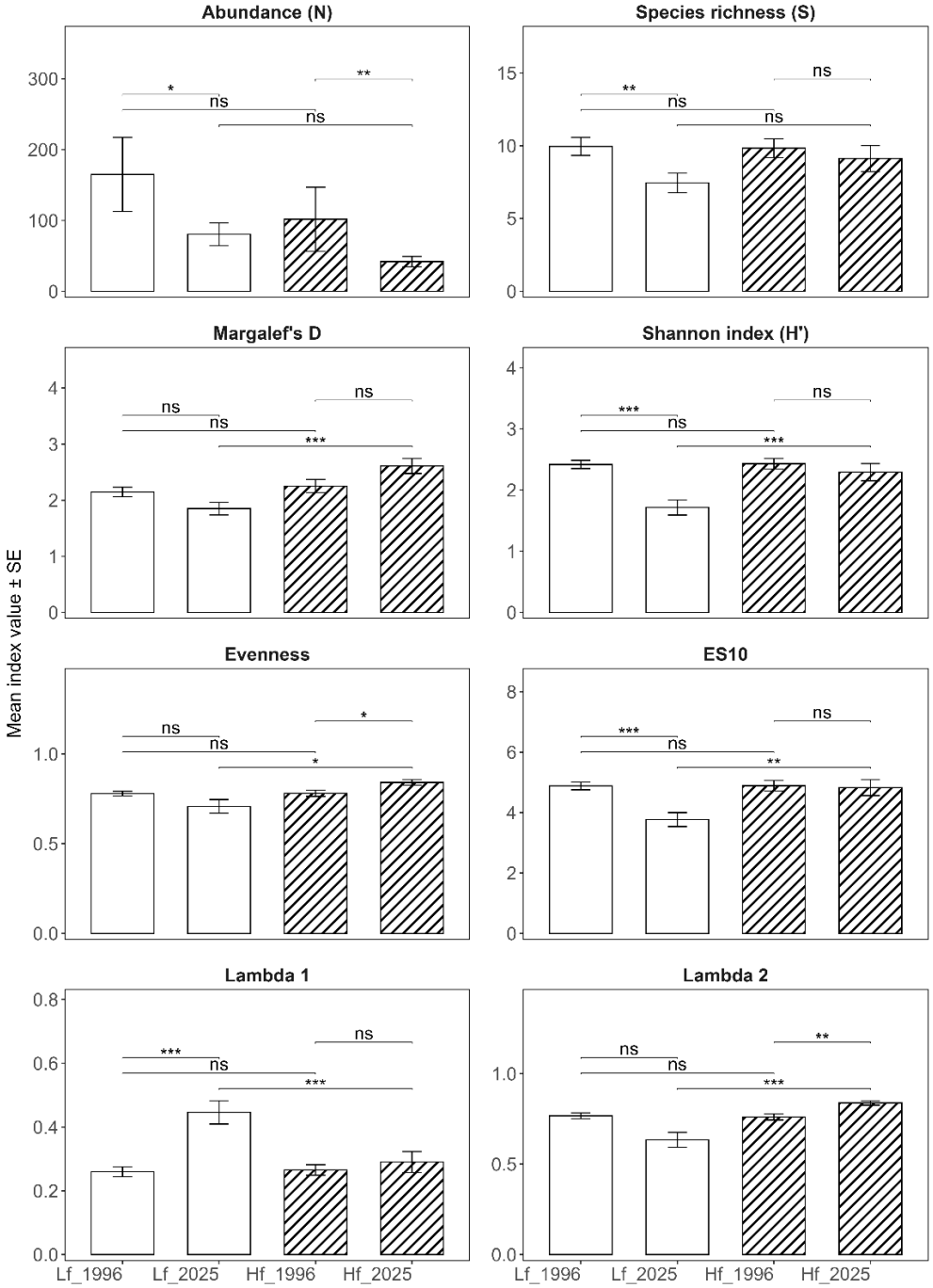


Figure 4. Mean ± SE diversity indices calculated from sample-level data for Lammefjord (Lf) and Holbæk Fjord (Hf) in 1996 and 2025. Indices include species richness (S), Margalef's richness (D), Shannon diversity (H′), evenness (J'), ES10, and Simpson's diversity indices (Lambda 1 and Lambda 2 (inverse Simpson's)). Statistical differences between years within each fjord were tested using Wilcoxon rank-sum tests. Significance levels: * p <0.05, ** p <0.01, *** p <0.001, ns = not significant.

5.1.2. Diversity development in Lammefjord 1996-2025

The univariate analysis showed a clear decline in several diversity metrics in Lammefjord between 1996 and 2025 (table 4.5; fig. 4). The mean abundance (N) showed a significant, major decline by 50% from 164.9 ± 2.24 individuals per sample in 1996 to 80.5 ± 15.99 in 2025 (p=0.0144) (table 4.5; fig. 4). This reduction in abundance was associated with a significant decline in mean species richness (S) 10.0 ± 0.62 in 1996 to 7.4 ± 0.68 in 2025 (p=0.0039). The decline in diversity was supported by a significant decrease in standardized richness (ES10) from 4.9 ± 0.13 to 3.8 ± 0.23 (p=0.001) as for a decrease in Margalef˙s index (D) (2.1 ± 0.09 to 1.9 ± 0.11) but with no significance p=0.0727). The Shannon diversity (H') also revealed a strong significant decline in the Lammefjord from 2.4 ± 0.07 to 1.7 ± 0.12 (p<0.0001). These declines indicate that the reduction in species richness was not only driven by a reduction in abundance, but as a general loss of diversity within the community. The Simpson's dominance indexes (L1 and L2) both showed a significant strong increase in 2025 (L1= 0.4± 0.04, 0.3 ± 0.02; p=0.000), (L2= 0.6 ± 0.04 – 0.8 ± 0.02; p=0.0503). The evenness only exhibited a minor non-significant change from 0.8 ± 0.01 in 1996, to 0.7 ± 0.04 in (p=0.7509). Overall, the results indicate a temporal shift towards a decreased diversity and increased dominance by fewer taxa in Lammefjorden over the 29-year period.

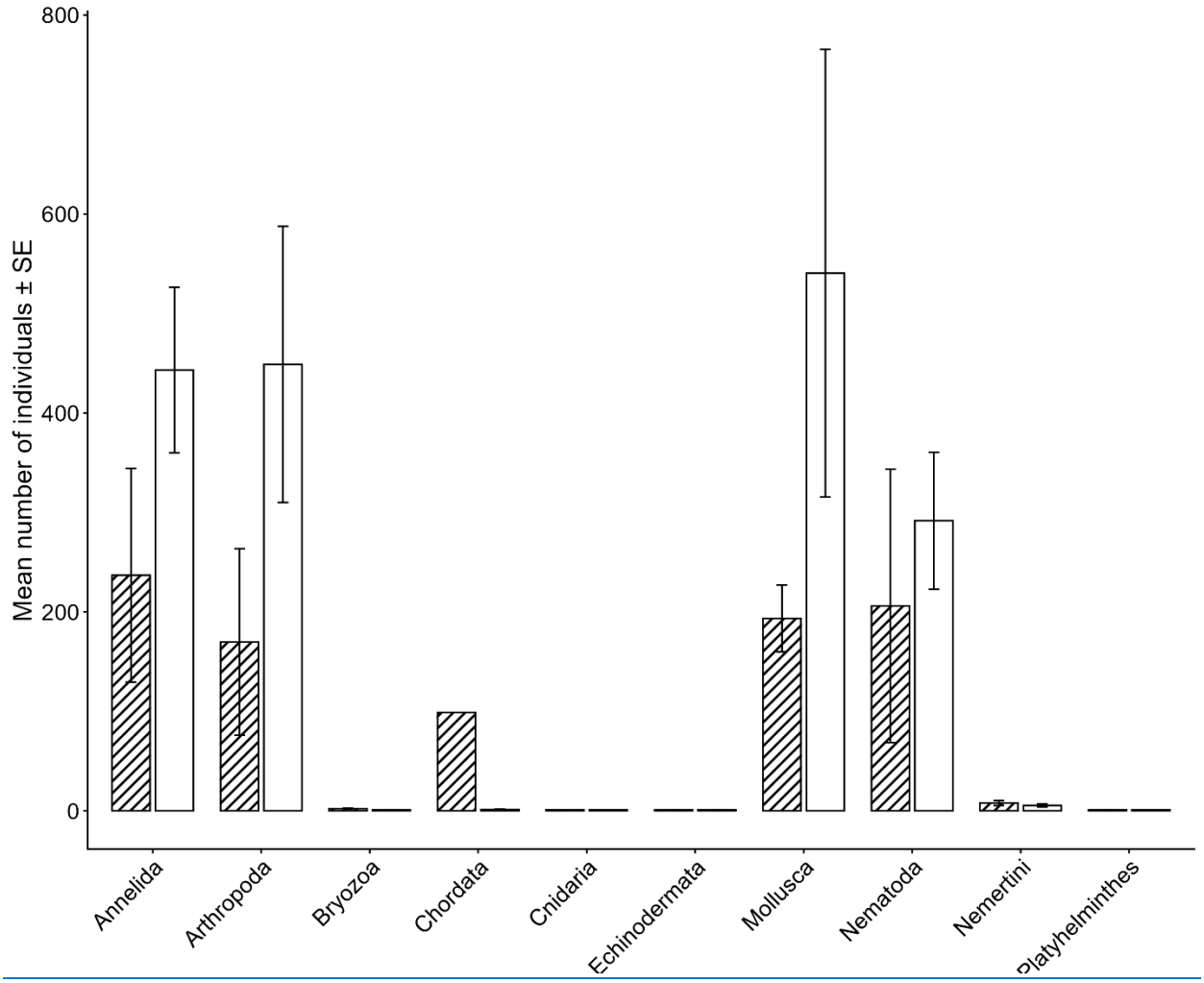
5.1.3. Change in community structure

The observed change in community structure was supported by a shift in both phylum-level abundance and species composition shown in figure 5 and table S1, S2 and 6. In Lammefjord, a major decline in Annelida 443.17 ± 83.23 to 104.60 ± 17.11), Arthropoda (448.83 ± 138.79 to 30.60 ± 6.69) and Nematoda (291.67 ± 68.89 to 20.33 ± 10.09) were observed, as for a minor decrease in Mollusca (540.50 ± 225.05 to 500.17 ± 105.43), and Nemertea (5.50 ± 1.48 to 3.67 ± 1.33). Furthermore, a minor increase was observed in Echinodermata (1.00 ± 0.00 to 1.50 ± 0.50) and Cnidaria (1.00 ± 0.00 to 5.00 ± 0.77). Platyhelminthes and Bryozoa were not observed in 2025.

Species richness declined from 70 species in 1996 to 58 in 2025 resulting in a net loss of 12 species over the 29-year period. 41 species were observed in 1996, but not in 2025, including serval polychaetes and bivalves (e.g. *Notomastus latericeus, Pholoe inornata, Nephtys hombergii, Ophelia rathkei, Macoma balthica*) as well as crustaceans (*Gammarus oceanicus, Idotea balthica*) (Table S2). These species have been replaced by 29 new species in 2025, by taxas such as *Hediste diversicolor*, *Streblospio shrubsolii*, *Mya arenaria*, *Gammarus locusta*, and *Idotea chelipes.* A shift in the

dominance of different groups has shown that polychaetes such as *Capitella capitata* have been replaced by *Pygospio elegans*, *Alitta succinea* and *Polydora cornuta*. The Hydrobiidae family *Ecrobia venstrosa* and *Hydrobia acuta neglecta* has been replaced by a total dominance of *Peringia ulvae*. Another gastropod species such as *Pusillina sarsii* has also been dominated by *Peringia ulvae*, in 2025 (tabel S1). Most abundant species in Lammefjord 1996 was *Pusillina sarsii* (2516 ind/m^2), *Nematoda.* (1750 ind/m^2), *Monocorophium insidiosum* (1459 ind/m^2), *Chironomus salinarius* (955 ind/m^2), *Polydora cornuta* (871 ind/m^2) and *Capitella capitata* (846 ind/m^2). Other dominating species was *Tubificoides benedii* (433 ind/m^2), *Mytilus edulis* (320 ind/m^2), *Peringia ulvae* (210 ind/m^2) and *Microdeutopus gryllotalpa* (200 ind/m^2). In 2025 most dominant species were *Peringia ulvae* (2462 ind/m^2), *Pygospio elegans* (218 ind/m^2), *Mya arenaria* (162 ind/m^2), *Mytilus edulis* (134 ind/m^2) and *Microdeutopus gryllotalpa* (128 ind/m^2).

a)



b)

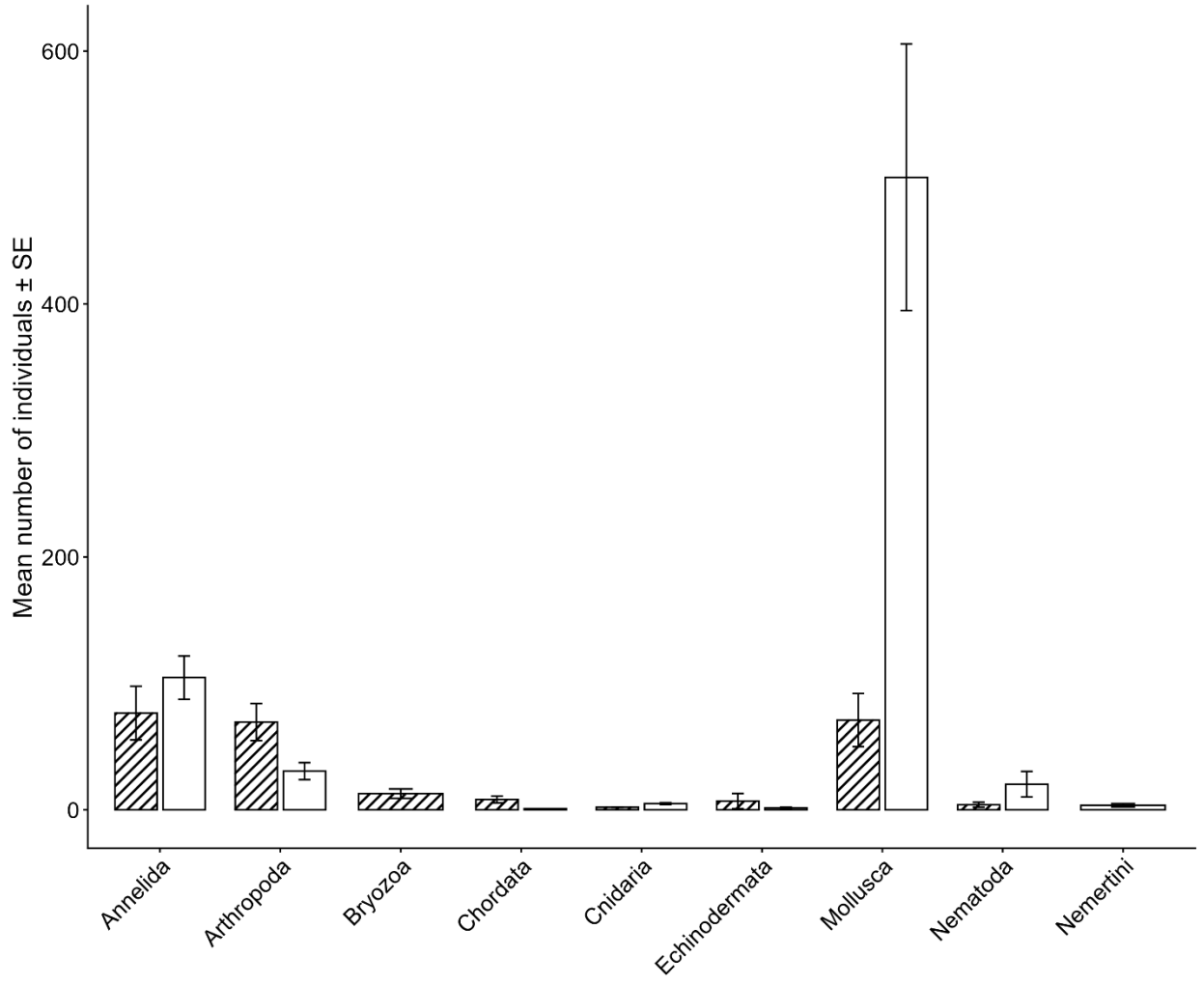


Figure 5a.b. Mean ± SE number of individuals at phylum level in Lammefjord (white) and Holbæk Fjord (dashed), 1996 (a) and 2025 (b).

Table 6. Mean abundance ± SE values of represented phyla in Lammefjord and Holbæk fjord 1996-2025. NA indicates that the phylum was not recorded in the given year.

Phyla	Lf 1996	Lf 2025	Hf 1996	Hf 2025
Annelida	443.17 ± 83.23	104.60 ± 17.11	236.83 ± 107.33	76.50 ± 21.23
Arthropoda	448.83 ± 138.79	30.60 ± 6.69	169.83 ± 93.77	69.38 ± 14.66
Bryozoa	1.00 ± 0.00	NA	2.20 ± 0.37	12.83 ± 3.72
Chordata	1.33 ± 0.33	1.00 ± 0.00	99.00 ± 0.00	8.20 ± 2.75
Cnidaria	1.00 ± 0.00	5.00 ± 0.77	1.00 ± 0.00	2.00 ± 0.00
Echinodermata	1.00 ± 0.00	1.50 ± 0.50	1.00 ± 0.00	7.00 ± 6.00
Mollusca	540.50 ± 225.05	500.17 ± 105.43	193.50 ± 33.56	71.00 ± 21.03
Nematoda	291.67 ± 68.89	20.33 ± 10.09	206.17 ± 137.44	4.00 ± 2.00
Nemertea	5.50 ± 1.48	3.67 ± 1.33	8.00 ± 2.47	NA
Platyhelminthes	1.00 ± 0.00	NA	1.00 ± 0.00	NA

5.1.4. Diversity development in Holbæk Fjord 1996-2025

In Holbæk Fjord, mean abundance (N) declined significantly from 101.07 ± 5.25 in 1996 to 42 ± 7.24 in 2025 ($p = 0.0065$) (table 4.5; fig. 4) while mean species richness showed a minor decline from 9.8 ± 0.64 to 9.1 ± 0.90 but was not significant ($p = 0.3606$) although there was an observed reduction in total species numbers of -8 species (table S1). Margalef's index increased from 2.3 ± 0.12 in 1996 to 2.6 ± 0.13 in 2025 but was not significant ($p = 0.1005$). The ES10 also showed a slight decrease from 4.9 ± 0.17 to 4.8 ± 0.27 in 2025 but like the Margalef's index (D), this was not significant ($p = 0.6027$). Shannon diversity (H') showed a minor decrease between (2.4 ± 0.09 to 2.3 ± 0.14) but no significance was found ($p = 0.8602$). The evenness and both Simpson's index's (L1, L2) remained the same during the 29-year period but was only significant for evenness (J') ($p = 0.0211$) and L2 ($p = 0.0029$), indicating a more even distribution of individuals among species in 2025, suggesting that overall community diversity remained stable over time.

5.1.5. Change in community structure

As in Lammefjord, a similar decline in mean abundance across several phyla was also observed in Holbæk Fjord. Highest reductions were observed in Nematoda (206.17 ± 137.44 to 4.00 ± 2.00), Chordata (99.00 ± 0.00 to 8.20 ± 2.75), Annelida (236.83 ± 107.33 to 76.50 ± 21.23), Mollusca (193.50 ± 33.56 to 71.00 ± 21.03) and Arthropoda (169.83 ± 93.77 to 69.38 ± 14.66) (figure 5; tab. 6). A minor increase was observed for Bryozoa (2.20 ± 0.37 to 12.83 ± 3.72), Echinodermata (1.00 ± 0.00 to 7.00 ± 6.00) and Cnidaria (1.00 ± 0.00 to 2.00 ± 0.00). Platyhelminthes and Nemertea were not observed in 2025. 40 species were lost from 1996 to 2025, including taxa such as *Alderia modesta*, *Ampharete acutifrons*, *Macoma balthica*, *Nephtys hombergii*, and *Corbula gibba*. 32 new species were gained in 2025, such as *Ericthonius brasiliensis*, *Streblospio shrubsolii*, *Bittium reticulatum*, *Carcinus maenas*, and *Spirorbis spirorbis.* Between the two sampling years, 29 species were still present, including *Capitella capitata*, *Arenicola marina*, *Pygospio elegans*, *Mytilus edulis*, and *Heteromastus filiformis.* Most dominant species in 1996, were *Nematoda indet.* (1237 ind/m^{-2}), *Pusillina sarsii* (516 ind/m^{-2}), *Chironomus salinarius* (481 ind/m^{-2}.) og *Tubificoides benedii* (373 ind.), *Monocorophium insidiosum* (305 ind/m^{-2}), *Capitella capitata* (280 ind/m^{-2}), *Peringia ulvae* (224 ind/m^{-2}), *Polydora cornuta* (220 ind/m^{-2}*), Scoloplos armiger* (154 ind/m^{-2}) and *Littorina saxatilis* (111 ind/m^{-2}). In 2025 the community was dominanted by *Peringia ulvae* (331 ind ind/m^{-2}) and *Spirorbis spirorbis* (317 ind/m^{-2}), followed by *Microdeutopus gryllotalpa* (187 ind/m^{-2}), *Ericthonius brasiliensis* (137 ind/m^{-2}), *Monocorophium insidiosum* (131 ind/m^{-2}), *Spirorbis corallinae* (101 ind/m^{-2}), *Einhornia crustulenta* (76 ind/m^{-2}), *Gammarus locusta* (72 ind/m^{-2}), *Bittium reticulatum* (62 ind/m^{-2}) and *Pygospio elegans* (60 ind/m^{-2}).

5.2. Effect of dredging on diversity

5.2.1. Swept area ratio (SAR)

The results of the swept area ratio showed variation among stations. Station 10052 had the highest swept area ratio (153%), followed by station 10055 (53%), station T2 (39%) and station 10053 (14%), indicating relatively high dredging pressure in these areas, in 2024. Station 10050 exhibit a dredging intensity at (2%), 10002 (1%). Stations 10056 and 10057 showed no recorded dredging while stations 10058, 10059, 10060, and 10061 exhibited only minimal activity (0%). No dredging activity was observed in Holbæk Fjord, in 2024 (figure 6).

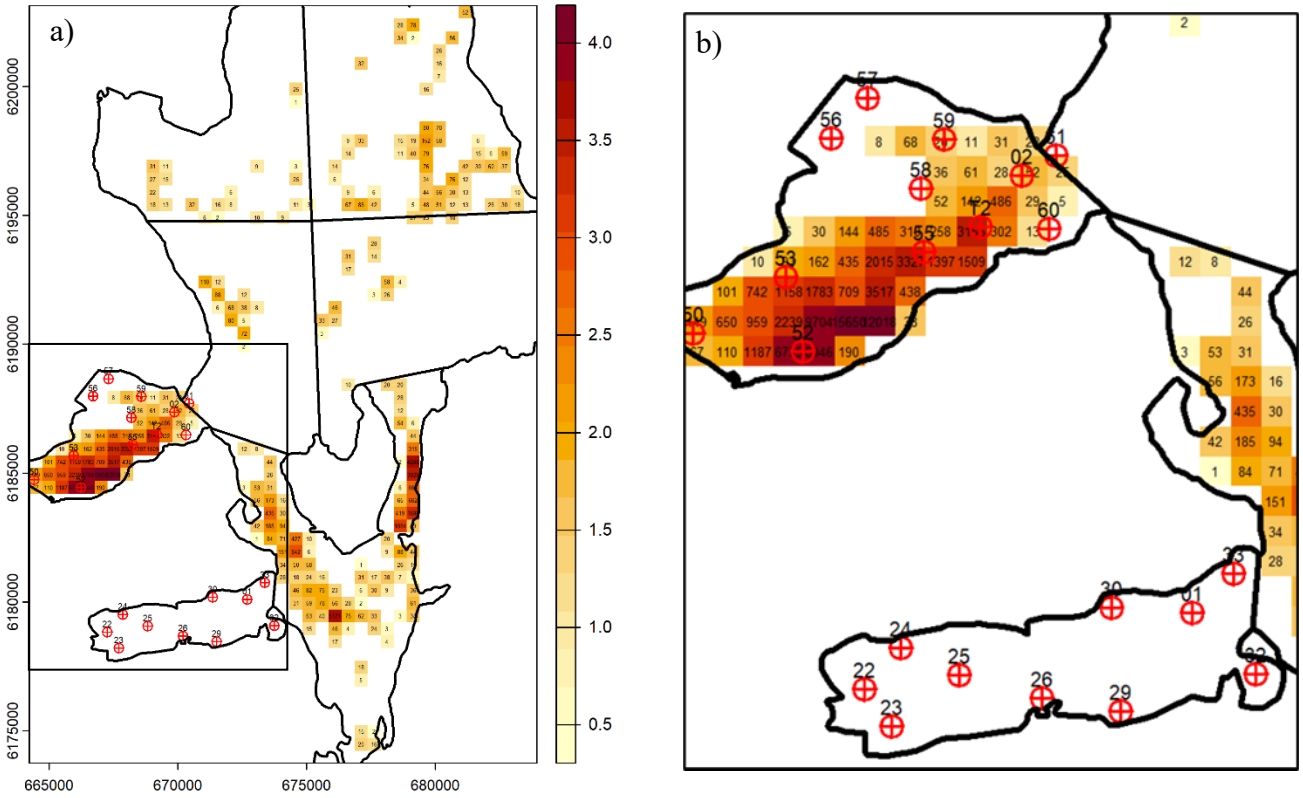


Figure 6a.b. Log10 SAR, VMS ping count from Isefjorden, Lammefjord and Holbæk Fjord, May 2023 - June 2024.

5.2.2. Station-level univariate analysis

The station-level analysis revealed measurable effects of dredging on both spatial and temporal scale (table 6,7; figure 5, 6). Both fjords exhibited spatial variability and temporal changes. Furthermore, the ANOSIM showed a significant relationship between (SAR) and the diversity indices among stations within Lammefjord in 2025 ($p<0.001$).

5.2.3. Station-level univariate analysis

The Lammefjord showed a higher number of stations with significant declines between 1996 and 2025 in richness and diversity accompanied by increased dominance (table 6.7; fig. 5), whereas significant changes in Holbæk Fjord were fewer and more restricted, with serval stations maintaining stable community structure despite reductions in abundance (table 6, and7; fig. 6). The changes in mean diversity metrics and results of Wilcoxon rank-sum test revealed that station 10002 in the Lammefjord (SAR=0.01) showed a significant decline in almost all diversity mean parameters and an increase in Simpson's dominance (L1, L2). Additionally, station 10052 (SAR=1.53) also showed significant negative changes in species richness (-6,17, p = 0.0099), abundance (-111.17, p = 0.005),

Shannon diversity (H') (-0.86, p = 0.026). Similarly, station 10053 (SAR=0.14) exhibited significant declines in species richness (p = 0.0333), ES10 (p = 0.0173), Shannon diversity (p = 0.0043), and increase in Simpson's indices (p = 0.0087), reflecting increased dominance and reduced diversity. The most significant changes were observed at station 10058 (SAR = 0), where all diverse metrics showed significant temporal differences (table 7). In contrast, station 10050 (SAR = 0.02), 10056 (SAR = 0), 10057 (SAR = 0), 10059 (SAR = 0), and 10060 (SAR = 0), showed few or no significant changes across metrics, suggesting relative stability at these locations.

In contrast, Holbæk Fjord exhibited fewer and more spatially restricted significant changes compared to Lammefjord. Station 10001 (SAR = 0) showed significant differences in species richness (-5.17, p = 0.0149), abundance (-14.07, p = 0.0043), ES10 (-2.82, p = 0.0151), Shannon diversity (-1.26, p = 0.0173), and Simpson's L1 (+0.26, p = 0.0151), indicating localized decline in diversity. Station 10026 (SAR = 0) showed significant changes in species richness (-4.70, p = 0.0169) and abundance (-52.80, p = 0.0135) while other diversity indices remained significantly stable across years. Station 10032 (SAR = 0) showed an increase in almost all diversity parameters, but only significant in Margalef's index (D) (p = 0.0043) and Simpson's indices (p = 0.0173). Station 10030 (SAR = 0) and 10033 (SAR = 0) were the only observed with no significant temporal changes across any diversity metrics (table 7.8).

Table 7. Mean values of abundance (N), species richness (S), Margalef's index (D), estimated species richness (ES10), Shannon diversity (H′), Evenness (J'), and Simpson's index (L1, L2) for each sampling station in Lammefjorden (Lf) and Holbæk Fjord (Hf) in 2025. Δ represents the change between the two sampling years (1996-2025). NA is due to missing matching station numbers for comparison data. Brackets are for highlighting stations with most significant effects.

Fjord	Station	SAR%	N	ΔN	S	ΔS	D	ΔD	J'	ΔJ'	ES10	ΔES10	H	ΔH	L1	ΔL1	L2	ΔL2
Lf	10002	0.01	9.33	-13.33	2	-6.17	0.46	-1.95	0.59	-0.28	1.67	-4.18	0.46	-2.14	0.81	+0.60	0.23	-0.60
Lf	10050	0.02	7.4	-30.27	4	-3.00	1.86	+0.10	0.88	+0.09	3.72	-0.81	1.54	-0.62	0.46	+0.16	0.81	+0.07
Lf	10052	1,.53	10.33	-111.17	4.67	-6.17	1.6	-0.46	0.91	+0.16	3.76	-1.05	1.69	-0.86	0.41	+0.18	0.71	-0.07
Lf	10053	014	33	-53.50	7	-5.17	1.9	-0.62	0.82	0.00	4.34	-1.30	2.08	-0.85	0.3	+0.13	0.77	-0.07
Lf	10055	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lf	10056	0	204	-27.50	11	+2.17	1.89	+0.40	0.42	-0.21	3.07	-0.60	1.48	-0.45	0.58	+0.23	0.43	-0.23
Lf	10057	0	12.8	-21.03	5	-0.33	1.87	+0.53	0.88	+0.11	3.93	+0.29	1.84	+0.25	0.34	-0.11	0.84	+0.26
Lf	10058	0	307.2	-1462.13	11.6	-14.73	1.85	-1.61	0.3	-0.28	2.44	-2.33	1.09	-1.65	0.7	+0.46	0.3	-0.46
Lf	10059	0	9.8	-18.20	5	-3.17	1.68	-0.62	0.83	-0.03	4.53	-0.82	1.83	-0.65	0.38	+0.15	0.69	-0.12
Lf	10060	0	102.8	-112.03	13	+0.33	2.77	+0.60	0.71	-0.03	4.96	-0.04	2.52	-0.18	0.28	+0.07	0.74	-0.06
Lf	10061	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

Lf	T2	0.39	102.67	NA	11	NA	2.28	NA	0.71	NA	4.9	NA	2.42	NA	0.31	NA	0.71	NA
Hf	10001	0	3.6	-14.07	3	-5.17	1.79	-0.73	0.96	+0.07	3	-2.82	1.34	-1.26	0.47	+0.26	0.92	+0.07
Hf	10022	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Hf	10023	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Hf	10024	0	116.2	NA	16.6	NA	3.33	NA	0.7	NA	5.19	NA	2.84	NA	0.22	NA	0.78	NA
Hf	10025	0	43.33	-26.50	13.33	+2.83	3.86	+1.59	0.83	+0.07	5.62	+0.78	2.72	+0.21	0.3	+0.06	0.86	+0.09
Hf	10026	0	10.2	-52.80	5.8	-4.70	2.17	-0.31	0.9	+0.11	5.17	-0.17	2.2	-0.48	0.27	+0.06	0.85	+0.04
Hf	10029	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Hf	10030	0	21.8	-35.87	6.6	-0.90	2.02	+0.24	0.87	+0.09	5.15	+1.23	2.32	+0.38	0.25	-0.11	0.82	+0.14
Hf	10032	0	99.67	+28.33	13.33	+5.00	3.14	+1.28	0.75	+0.06	4.68	+0.51	2.51	+0.47	0.18	-0.16	0.82	+0.15
Hf	10033	0	24.83	-2224.17	7.83	-20.17	2.13	-1.36	0.82	+0.17	5.03	-0.59	2.4	-0.74	0.25	+0.06	0.79	-0.02
Hf	J	0	7.8	NA	5	NA	2.32	NA	0.93	NA	4.61	NA	1.87	NA	0.38	NA	0.89	NA

Tabel 8. Compared diversity measures between stations in Lammefjord and Holbæk Fjord with a paired Wilcoxon rank-sum test, between Lammefjord and Holbæk fjord 1996 to 2025. Significance levels: * p <0.05, ** p <0.01, *** p <0.001, ns = not significant. NA is due to missing matching station numbers for comparison data. Brackets are for highlighting stations with most significant effects.

Fjord	Station	SAR%	S	N	D	E	ES10	H	L1	L2
Lf	10002	0.01	0.0275 *	0.2433 ns	0.0238 *	0.1429 ns	0.0275 *	0.0238 *	0.0238 *	0.0238 *
Lf	10050	0.02	0.1027 ns	0.0173 *	0.9143 ns	0.4762 ns	0.7837 ns	0.2468 ns	0.329 ns	0.6095 ns
Lf	10052	1.53	0.0099 **	0.005 **	0.3095 ns	0.0087 **	0.4704 ns	0.026 *	0.0649 ns	0.1797 ns
Lf	10053	0.14	0.0333 *	0.0519 ns	0.1198 ns	0.7922 ns	0.0173 *	0.0043 **	0.0087 **	0.0303 *
Lf	10055	0.53	NA	NA	NA	NA	NA	NA	NA	NA
Lf	10056	0	0.2678 ns	1 ns	0.1255 ns	0.0823 ns	0.1775 ns	0.1255 ns	0.1255 ns	0.1255 ns
Lf	10057	0	0.8514 ns	0.1699 ns	0.3602 ns	0.2948 ns	0.7832 ns	0.4642 ns	0.5368 ns	0.1198 ns
Lf	10058	0	0.0358 *	0.0357 *	0.0357 *	0.0357 *	0.0357 *	0.0357 *	0.0357 *	0.0357 *
Lf	10059	0	0.1182 ns	0.0988 ns	0.2468 ns	0.9307 ns	1 ns	0.2468 ns	0.2468 ns	0.4286 ns
Lf	10060	0	0.7131 ns	0.1255 ns	0.0823 ns	0.7922 ns	0.7922 ns	0.329 ns	0.5368 ns	0.6623 ns
Lf	10061	0	NA	NA	NA	NA	NA	NA	NA	NA
Lf	T2	0.39	NA	NA	NA	NA	NA	NA	NA	NA
Hf	10001	0	0.0149 *	0.008 **	0.0871 ns	0.1645 ns	0.0151 *	0.0173 *	0.0173 *	0.2395 ns
Hf	10022	0	NA	NA	NA	NA	NA	NA	NA	NA
Hf	10023	0	NA	NA	NA	NA	NA	NA	NA	NA
Hf	10024	0	NA	NA	NA	NA	NA	NA	NA	NA
Hf	10025	0	0.2207 ns	0.2403 ns	0.0087 **	0.1255 ns	0.0649 ns	0.1797 ns	0.3939 ns	0.0823 ns
Hf	10026	0	0.0169 *	0.0135 *	0.2468 ns	0.1255 ns	0.7922 ns	0.2468 ns	0.329 ns	0.6623 ns

Hf	10029	0	NA	NA	NA	NA	NA	NA	NA	NA
Hf	10030	0	0.7138 ns	0.583 ns	0.5368 ns	0.1775 ns	0.1775 ns	0.4286 ns	0.1775 ns	0.0823 ns
Hf	10032	0	0.0632 ns	0.3095 ns	0.0043 **	0.5368 ns	0.1797 ns	0.0649 ns	0.0173 *	0.0303 *
Hf	10033	0	0.2072 ns	0.2857 ns	0.2857 ns	0.2857 ns	0.2857 ns	0.2857 ns	0.2857 ns	0.8571 ns
Hf	J	0	NA	NA	NA	NA	NA	NA	NA	NA

5.3. Species accumulation curve (SAC)

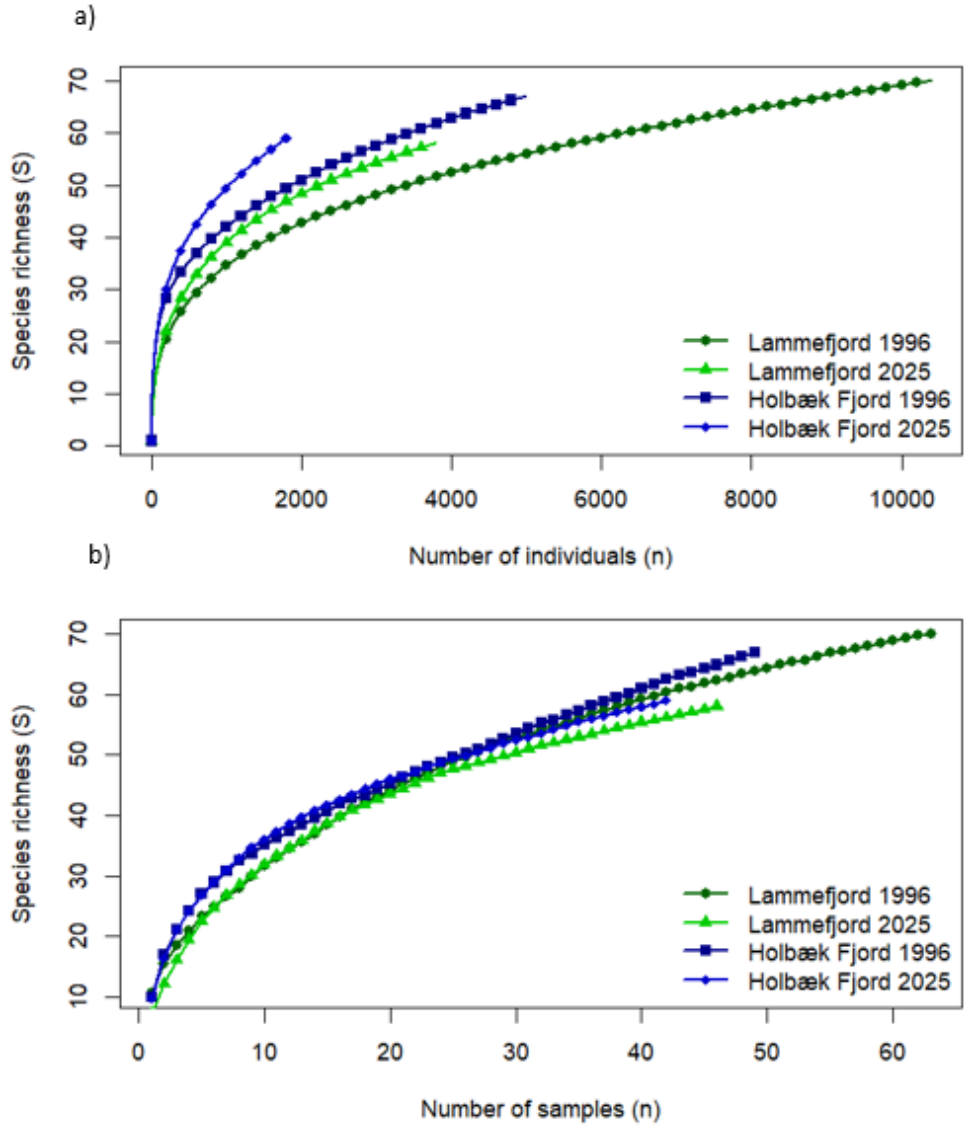


Figure 7. Species accumulation curve (SAC) on individual-based level (a) and sample-base level (b). Curves representing Lammefjord (green) and Holbæk Fjord (blue colors) in 1996 and 2025.

The SAC curves showed higher species richness in Holbæk Fjord compared to Lammefjorden in both 1996 and 2025 (Figure 7a.b). In both fjords, species richness was generally lower in 2025 than in 1996. Holbæk Fjord exhibited higher species richness at comparable numbers of individuals, in the individual-based rarefaction curves, while Lammefjorden reached a higher total species richness at larger sample sizes, reflecting a greater total number of individuals rather than higher diversity per sample. This pattern was consistent across both individual-based and sample-based rarefaction curves.

5.4. Biomass

5.4.1. Fjord-scale spatial and temporal comparison

Due to scarce data from 1996, results should be interpreted carefully. The geometric mean biomass for Lammefjord showed a minor increase from 34.0 g/m² in 1996 to 43.0 g/m² in 2025, and a decline in mean biomass for Holbæk Fjord from 35.9 g/m² in 1996 to 9.45 g/m² in 2025.

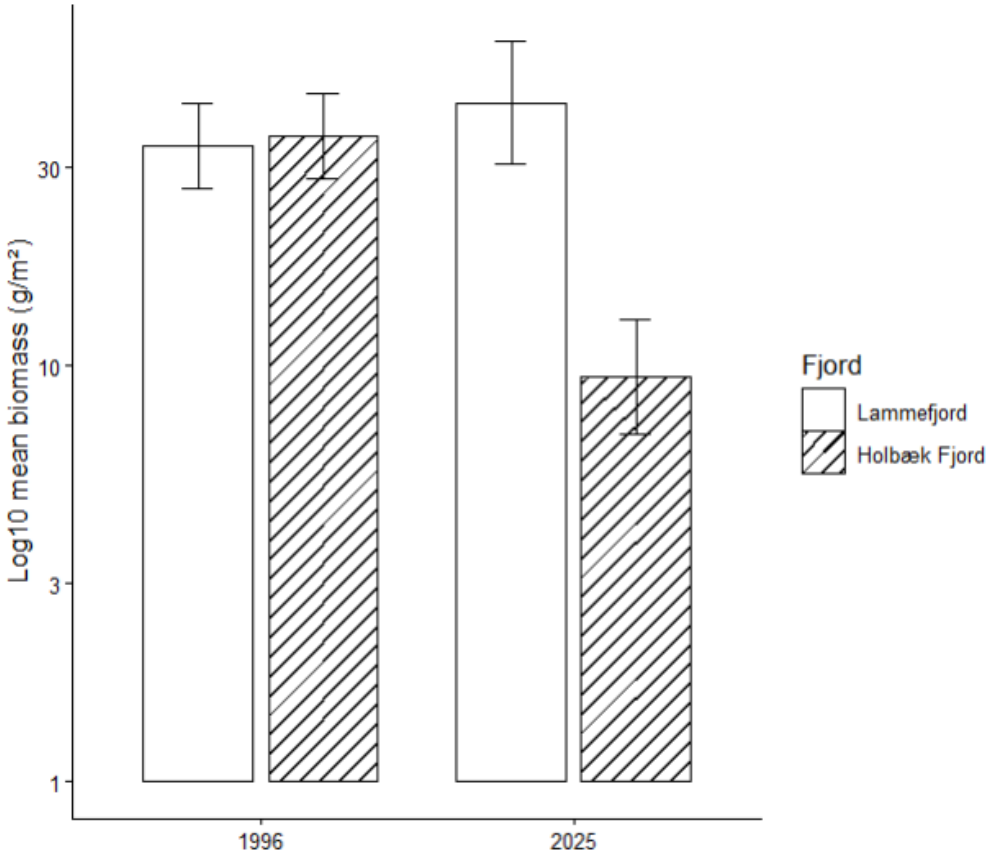


Figure 8. Mean ± SE biomass (g/m²) in Lammefjorden and Holbæk Fjord in 1996 and 2025 on a $\log_{10}$ scale.

5.4.2. Biomass at station level and comparison

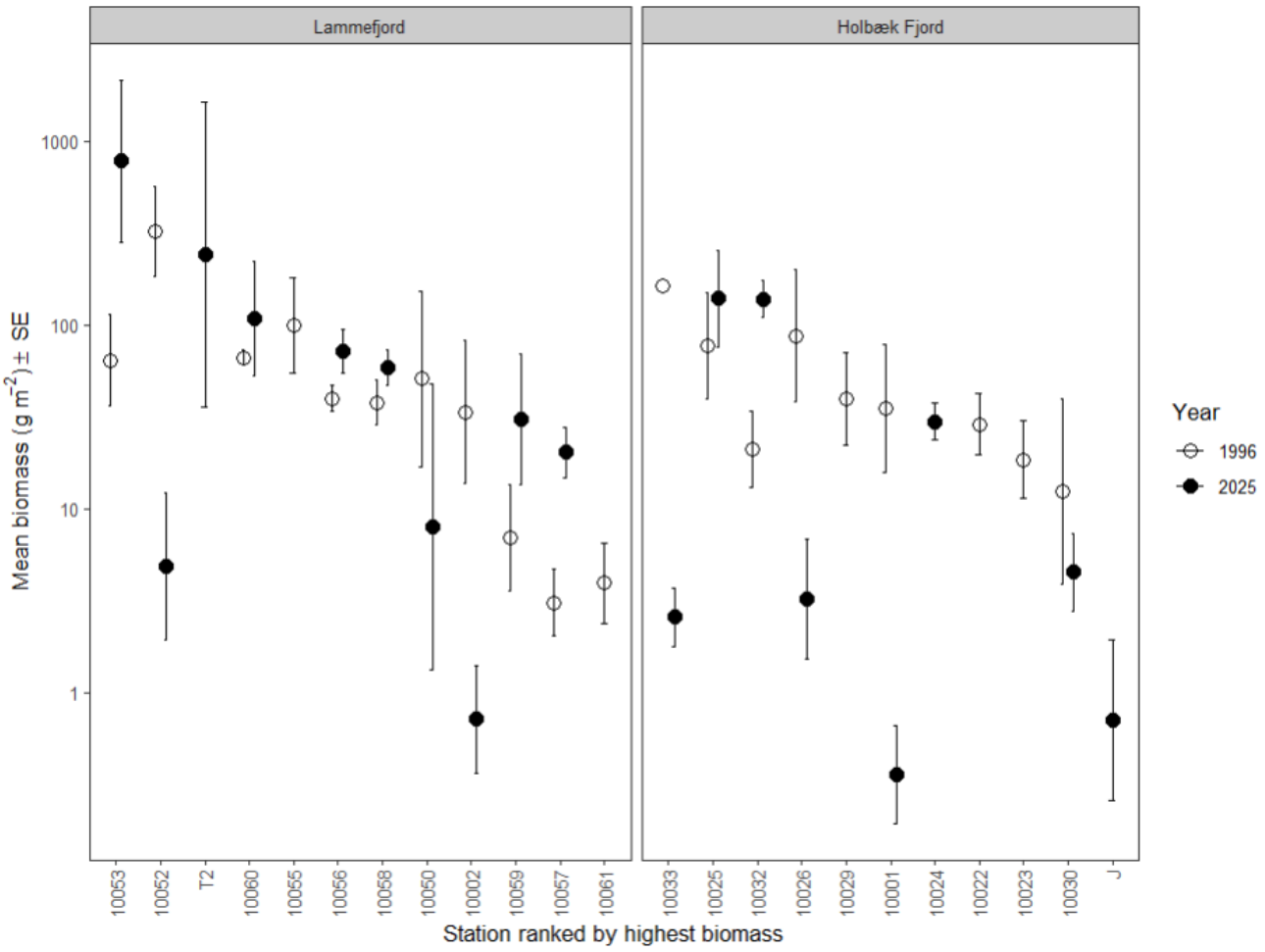


Figure 9. Comparison of geometric mean ± SE biomass (g/m²) at station level in Lammefjord and Holbæk Fjord between 1996 and 2025. Open circles represent stations sampled in 1996, while filled circles represent stations sampled in 2025. Error bars indicate standard error among samples. The y-axis is displayed on a logarithmic scale.

The Spearman correlations test showed no significant relationships between dredging intensity (SAR) and total biomass among stations in Lammefjord in 2025 ($p > 0.05$). The biomass showed only a very weak relationship with SAR ($\rho = -0.06$, $p = 0.86$).

A reduction in biomass was observed for both fjords between 1996 and 2025. The highest reduction in Lammefjorden was observed at station 10052, where biomass decreased from 324.38 ± 0.24 g/m² to 4.88 ± 0.40 g/m², followed by station 10050, which declined from 50.89 ± 0.48 g/m² to 7.94 ± 0.78

g/m², and station 10002, where biomass decreased from 33.58 ± 0.39 g/m² to 0.71 ± 0.29 g/m² (figure 9). In contrast six out of ten stations exhibited an increase in biomass. This accounted for station 10053, where biomass increased from 64.00 ± 0.25 g/m² to 775.59 ± 0.44 g/m² in 2025, as for station 10060 (66.36 ± 0.04 g/m² to 108.96 ± 0.31 g/m²), station 10056 (39.76 ± 0.07 g/m² to 71.94 ± 0.12 g/m²), station 10058 (37.87 ± 0.12 g/m² to 58.32 ± 0.09 g/m²), station 10059 (6.94 ± 0.29 g/m² to 30.61 ± 0.35 g/m²) and at station 10057 (3.07 ± 0.18 g/m² to 20.22 ± 0.14 g/m²). Stations 10055 and 10061 were only present in the 1996 dataset, while station T2 was only present in 2025 but with a particular high biomass at 239.49 ± 0.83 g/m²).

The same accounted for Holbæk Fjord, where four stations showed a reduction in biomass between 1996 and 2025. The highest reduction was observed at station 10033, where biomass decreased from 162.71 g/m² to 2.57 ± 0.16 g/m² in 2025, followed by station 10026, where the biomass declined from 87.17 ± 0.36 g/m² to 3.23 ± 0.33 g/m², and station 10001, which decreased from 35.33 ± 0.35 g/m² to 0.36 ± 0.26 g/m². A minor reduction was observed at station 10030, where biomass decreased from 12.42 ± 0.50 g/m² to 4.52 ± 0.21 g/m² in 2025.

Three stations exhibited an increase in biomass. This was observed at 10032 (21.06 ± 0.21 g/m² to 138.26 ± 0.10 g/m² in 2025, as for 10025 (76.44 ± 0.29 g/m² to 139.15 ± 0.26 g/m²). Stations 10022, 10023 and 10029 were only present in 1996 and could therefore not be compared. The biomass at these stations was 28.80 ± 0.16 g/m², 18.44 ± 0.21 g/m² and 39.67 ± 0.25 g/m². The same accounted for station 10024 and station J which only occurred in 2025, with biomasses of 29.81 ± 0.10 g/m² and 0.71 ± 0.44 g/m².

5.4.3. Biomass of *Mytilus edulis*

The temporal development of *M. edulis* in both fjords showed a reduction in the biomass with a highest reduction observed in Holbæk Fjord from 558.81 ± 0.19 g/m² in 1996 to 0.05 ± 0.33 g/m² in 2025. The biomass of *M. edulis* also decreased in Lammefjorden from 729.83 ± 0.33 g/m² to 222.23 ± 0.93 g/m² between 1996 and 2025, but not as profound as in Holbæk.

Station	Depth (m)	SAR (%)	*M. edulis* 1996 (g/m²)	*M. edulis* 2025 (g/m²)
Lammefjord				
10002	10.0	1	11.06	0.00
10050	5.2	2	1550.54	4201.46
10052	4.0	153	147.37	0.20
10053	5.0	14	52.68	2634.60
10055	9.1	53	36.02	–
10056	1.8	0	0.00	0.45
10057	2.3	0	0.00	0.04
10058	3.0	0	0.18	9.94
10059	6.3	0	0.08	0.00
10060	3.6	0	0.04	44.87
10061	11.5	0	0.34	–
T2	NA	39	–	10770.63
Holbæk Fjord				
10001	9.0 / 8.1	0	0.00	0.00
10022	0.8	0	8.76	–
10023	1.5	0	0.00	–
10024	2.0	0	–	0.11
10025	3.5	0	111.80	0.00
10026	3.6	0	129.24	0.00
10029	3.0	0	0.00	–
10030	2.2	0	184.63	0.00
10032	1.2	0	0.00	0.02
10033	3.5	0	0.08	0.00
J	NA	0	–	0.00

Table 9. Geometric means biomass of *Mytilus edulis* at station level from both fjords and sampling years.

The biomass at station level revealed a substantial spatial variation in Lammefjorden. Highest biomass was observed at stations 10050 (1550.54 g/m²), 10052 (147.37 g/m²) and 10053 (52.68 g/m²). Highest biomasses in 2025 were observed at stations T2 (10770.63 g/m²), 10050 (4201.46 g/m²) and 10053 (2634.60 g/m²), while the highest decline was observed at station 10052, where

biomass decreased from 147.37 g/m² to 0.20 g/m². In contrast, the biomass of *M. edulis* in Holbæk Fjord was more evenly distributed in 1996, with the highest observed biomass at stations 10030 (184.63 g/m²), 10026 (129.24 gm²) and 10025 (111.80 g/m²), while in 2025*, M. edulis* was only observed at stations 10024 (0.11 g/m²) and 10032 (0.02 g/m²).

M. edulis therefore remained abundant at several stations in Lammefjorden though the fjord experienced varying dredging activities, while it almost disappeared from Holbæk Fjord between 1996 and 2025. This could imply that other factors than dredging alone influenced the distribution and biomass of *M. edulis*.

5.4.4. Species with highest contributing biomasses

The most dominant species in biomass in Lammefjord 1996, were *M. edulis* (729.83 ± 0.33 g/m²), *Alitta virens* (188.81 g/m²) and *Capitella capitata* (82.86 ± 0.02 g/m²). Other species such as *Macoma calcarea* (79.11 g/m²), *Macoma balthica* (52.03 ± 0.06 g/m²) and *Chironomus salinarius* (38.05 ± 0.02 g/m²) exhibited an intermediate biomass, while the lowest biomasses was observed for *Corbula gibba* (20.77 ± 0.34 g/m²), *Pusillina sarsii* (20.30 ± 0.29 g/m²) and *Nephtys hombergii* (17.76 ± 0.07 g/m²).

In 2025, *Carcinus maenas* exhibited the highest biomass of 3113.09 g/m², followed by *M. edulis* (222.23 ± 0.93 g/m²) and *Tritia reticulata* (109.72 ± 0.14 g/m²). Intermediate biomasses were observed for *Asterias rubens* (71.77 ± 0.15 g/m²), *Balanus improvisus* (59.73 ± 0.37 g/m²) and *Ciona intestinalis* (47.03 g/m²), while the lowest biomasses were observed of *Peringia ulvae* (20.85 ± 0.38 g/m²), *Alitta succinea* (20.26 ± 0.31 g/m²) and *Nephtys hombergii* (16.73 ± 0.30 g/m²).

In Holbæk Fjord, 1996, *Mytilus edulis* also exhibited the highest biomass of 558.81 ± 0.19 g/m², followed by *Scrobicularia plana* (242.60 g/m²) and *Macoma balthica* (120.97 ± 0.29 g/m²), *Cerastoderma glaucum* (84.64 ± 0.33 g/m²) and *Dendrodoa grossularia* (40.67 g/m²). The lowest biomasses were observed for *Chironomus salinarius* (15.45 ± 0.13 g/m²), *Pusillina sarsii* (12.77 ± 0.06 g/m²), *Scoloplos armiger* (11.92 ± 0.14 g/m²) and *Littorina littorea* (11.17 g/m²).

As in Lammefjord, *Carcinus maenas* exhibited the highest biomass in 2025 of 666.09 g/m², followed by *Asterias rubens* (346.24 g/m²) and *Littorina littorea* (179.24 g/m²). Intermediate biomasses were observed for *Tritia reticulata* (36.60 ± 0.09 g/m²), *Botryllus schlosseri* (36.39 g/m²) and *Einhornia crustulenta* (26.75 ± 0.26 g/m²), and the lowest biomasses for *Electra crustulenta*

(23.24 g/m²), *Ericthonius brasiliensis* (9.22 ± 0.48 g/m²), *Peringia ulvae* (5.38 ± 0.20 g/m²) and *Praunus inermis* (4.96 ± 0.88 g/m²).

5.4.5. Comparison to Isefjord Yderbredning

In Isefjord Yderbredning, biomass composition also changed between 1996 and 2024. In 1996, the species with highest biomasses were *Alitta succinea* (10.31 ± 0.18 g/m²), *Scoloplos armiger* (8.63 ± 0.04g/m²), and *Corbula gibba* (4.92 ± 0.11g/m²). Other high biomasses were observed for *Turritella communis* (1.20 ± 0.19 g/m²), *Mediomastus sp.* (0.96 ± 0.07 g/m²), *Microdeutopus gryllotalpa* (0.75 g/m²), *Corophium volutator* (0.74 ± 0.12 g/m²), and *Parvicardium sp.* (0.61 ± 0.16 g/m²), while lower biomasses were observed for *Harmothoe imbricata* (0.50 g/m²) and *M. arenaria* (0.49 ± 0.57 g/m²).

In 2024, biomass was mostly dominated by *M. edulis* (1936.36 g/m²), followed by *Tritia reticulata* (329.45 g/m²), *Peringia ulvae* (69.98 g/m²), and *Balanus crenatus* (69.93 g/m²), *C. gibba* (19.55 g/m²) and *Polydora cornuta* (14.22 g/m²).

5.5. Community trait analysis

Both the AMBI and the CWM analysis of functional traits showed an alteration in community structure between both fjords and sampling years.

5.5.1. Spatial and temporal comparison of AMBI 2025

In 2025, group III species was the dominating group of the community in both fjords (Lammefjord: 74.5%; Holbæk Fjord: 61.7%) (table 10). The combined proportion of group I-II was higher in Holbæk Fjord (31.1%), than in Lammefjord (20.8%). Groups IV-V accounted for ≤6.4% in both fjords. From 1996-2025, both fjords exhibited clear alterations in ecological group distribution, characterised by an increase in group III and a reduction in groups IV-V (Table 10; fig. 19.20). Group III species increased in Lammefjord 43.6% to 74.5% (+30.9%), while group IV-V decreased from 25.6% to 3.8% (-21.8%) and from 15.3% to 1.0% (-14.3%), respectively. In Holbæk Fjord, group III species increased from 45.6% to 61.7% (+16.1%), while group IV-V decreased from 13.4% to 3.4% (−10.0%) and from 11.5% to 3.0% (−8.5%). Group I decreased in both fjords as well (Lammefjord: 12.7% to 6.9%; Holbæk Fjord: 20.6% to 14.2%), while an increase in group II species was observed (Lammefjord: 2.8% to 13.9%; Holbæk Fjord: 8.9% to 17.9%) (table 10).

Tabel 10. Temporal development of the abundance of category I-V species, in Lammefjord and Holbæk Fjord between 1996-2025.

Fjord	Group	1996	2025	Change
Lammefjord				
	I	12.7%	6.9%	−5.8%
	II	2.8%	13.9%	+11.1%
	III	43.6%	74.5%	+30.9%
	IV	25.6%	3.8%	−21.8%
	V	15.3%	1.0%	−14.3%
Holbæk Fjord				
	I	20.6%	14.2%	−6.4%
	II	8.9%	17.9%	+9.0%
	III	45.6%	61.7%	+16.1%
	IV	13.4%	3.4%	−10.0%
	V	11.5%	3.0%	−8.5%

5.5.2. AMBI analyses

The AMBI analysis in figure 10,11 shows a clear improvement in ecological conditions at all stations. The proportion of slightly disturbed stations increased from 1996 to 2025 in both fjords. In Lammefjord ∼73% of stations were classified as moderately disturbed in 1996, improving to 100% being slightly disturbed in 2025. In Holbæk ∼66% of stations were classified as moderately disturbed whereas all stations were categorized as 100% slightly disturbed in 2025.

There was no clear pattern with dredging intensity and AMBI values at the different stations, except for station 10052, which exhibited highest proportions of tolerant and opportunistic species (EG III) and highest dredging activity (SAR=1.53%). The results of the swept area ration showed variation among stations. But a clear trend was observed between Lammefjord and Holbæk Fjord, with Holbæk Fjord containing more sensitive species (EG I-II), in several stations (figure 10,11).

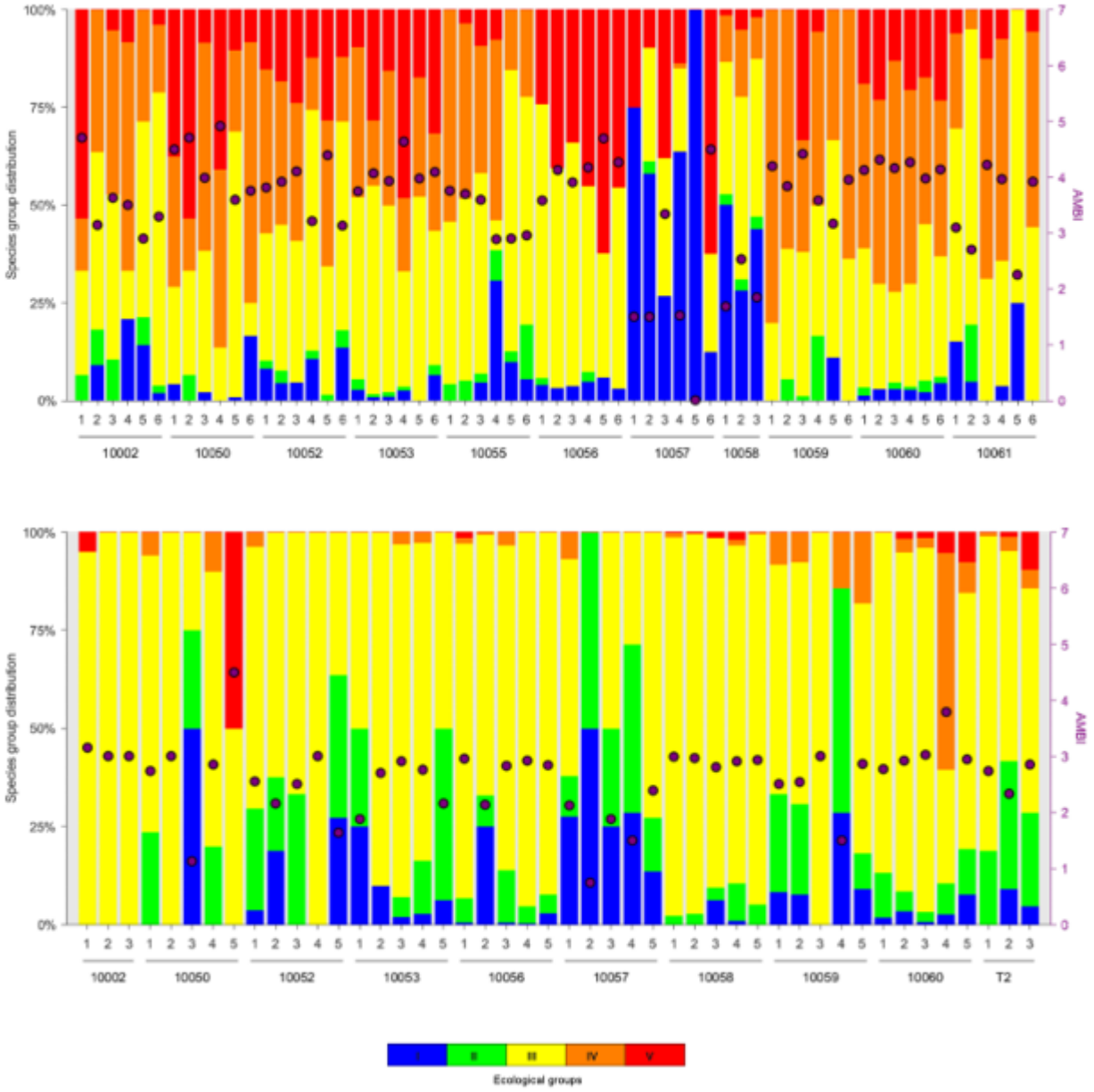


Figure 10. Represents the ecological condition and development of Lammefjord on a temporal scale from 1996 (upper graph) to 2025 (bottom graph). Colours indicate ecological groups of the species present within each sample and station, as for their abundances. The classification is categorised into five groups I-V in relation to tolerance of disturbance.

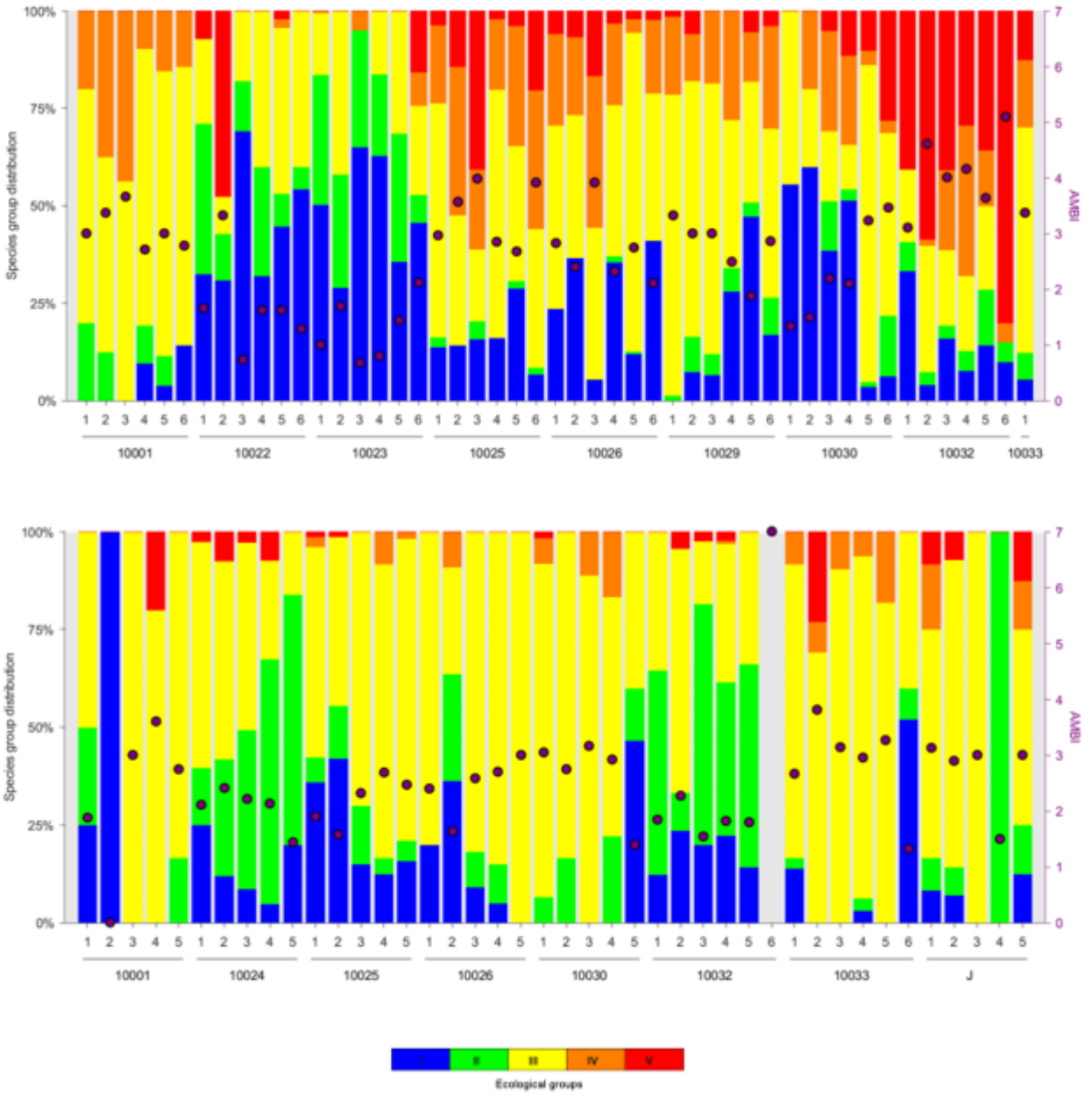


Figure 11. Represents the ecological condition and development of Holbæk Fjord on a temporal scale from 1996 (upper graph) to 2025 (bottom graph). Colours indicate ecological groups of the species present within each sample and station, as for their abundances. The classification is categorised into five groups I-V in relation to tolerance of disturbance.

5.5.3. CWM Analysis

A clear temporal shift in functional traits was observed in the community-weighted mean (CWM) analyses for both fjords (figure 12; table 12).

In Lammefjord, the relative abundance of planktotrophic larvae increased significantly from 28-84% (p=0.001), while lecithotrophic decreased with (33-3%, p = 0.007). Individuals with direct development decreased with 40-13% but was not significant (p = 0.179). Infaunal individuals increased with 70 to 88% while epifaunal individuals decreased with 30 to 12%, but neither of these was significant (p = 0.502, p = 0.316). The relative abundance of deposit-feeders showed a slight increase from 62 to 77%, while grazers exhibited a high decline from 25 to 1%, but both was not significant (p = 0.455, p = 0.203). Suspension feeding increased from 9-16% but was not significant (p = 0.888). A minor increase in predators/scavengers was observed from 2 to 3% (p = 0.004). Individuals with very short longevity (<1yr), decreased significantly from 28% to 4% (p >0.001), while a significant increase in short-lived (1-3 yr), was observed from 66% to 84% (p <0.001). A minor significant increase in individuals with medium longevity (3-10yr) was also observed (3-14%, p = 0.020), while long living individuals (>10) remained stable.

In Holbæk Fjord, same patterns for larvae development were observed. Planktotrophic larvae increased significantly from 32 to 61% (p = 0.018), while lecithotrophic larvae decreased from 18 to 8% (p <0.001). Individuals with direct development also decreased 49% to 32% and was close be significant (p = 0.057). On the contrary to Lammefjord, epifaunal individuals increased from 25 to 49% while infaunal individuals decreased (75-51%), but both observations were not significant (p = 0.414, p = 0.835). The relative abundance of deposit feeders decreased from 69 to 54% (p = 0.165), while suspension-feeders increased significantly from 9 to 34% (p <0.001). Grazers also declined significantly (15-7%, p = 0.002). Individuals with very short longevity remained relatively stable, while the relative abundance of short-lived individuals showed a minor increase from 50 to 59% (p = 0.019). Individuals with medium longevity decreased significantly from 11 to 3% (p = 0.014), while long-lived individuals also remained relatively stable.

Table 11. Community-weighted mean (CWM) values of functional traits based on relative abundance for Lammefjord (1996 and 2025) and Holbæk Fjord (1996 and 2025). Values represent the mean relative contribution of each trait to the community and range from 0 to 1 (100%), indicating the proportional contribution of each trait category to the total community abundance.

Trait group	Trait	LF 1996	LF 2025	HF 1996	HF 2025
Longevity	Long	0.03	0.08	0.01	0.01
Longevity	Medium	0.03	0.03	0.11	0.03
Longevity	Short	0.66	0.84	0.50	0.59
Longevity	VeryShort	0.28	0.04	0.38	0.37
Larvae	Direct	0.40	0.13	0.49	0.32
Larvae	Lecithotrophic	0.33	0.03	0.18	0.08
Larvae	Planktotrophic	0.28	0.84	0.32	0.61
Habitat	Epifauna	0.30	0.12	0.25	0.49
Habitat	Infauna	0.70	0.88	0.75	0.51
Feeding type	Deposit	0.62	0.77	0.69	0.54
Feeding type	Grazer	0.25	0.01	0.15	0.07
Feeding type	Omnivore	0.02	0.02	0.05	0.03
Feeding type	Parasite	NA	0.01	NA	0.01
Feeding type	Predator/Scavenger	0.02	0.03	0.03	0.02
Feeding type	Suspension	0.09	0.16	0.09	0.34

Comparisons between fjords in 2025 showed a significant difference of direct development with the trait being more abundant in Holbæk Fjord (32%%) than Lammefjord (13%) ($p = 0.004$). In contrast, planktotrophic larvae were significantly more abundant in Lammefjord (84%) compared to Holbæk Fjord (51%) ($p = 0.003$). Furthermore, the long-lived individuals also exhibited a minor higher relative abundance in Lammefjord (8%), compared to Holbæk Fjord (1%) ($p=0.036$), while individuals with very short longevity were significantly more abundant in Holbæk Fjord (37%) compared to Lammefjord (4%) ($p = 0.003$).

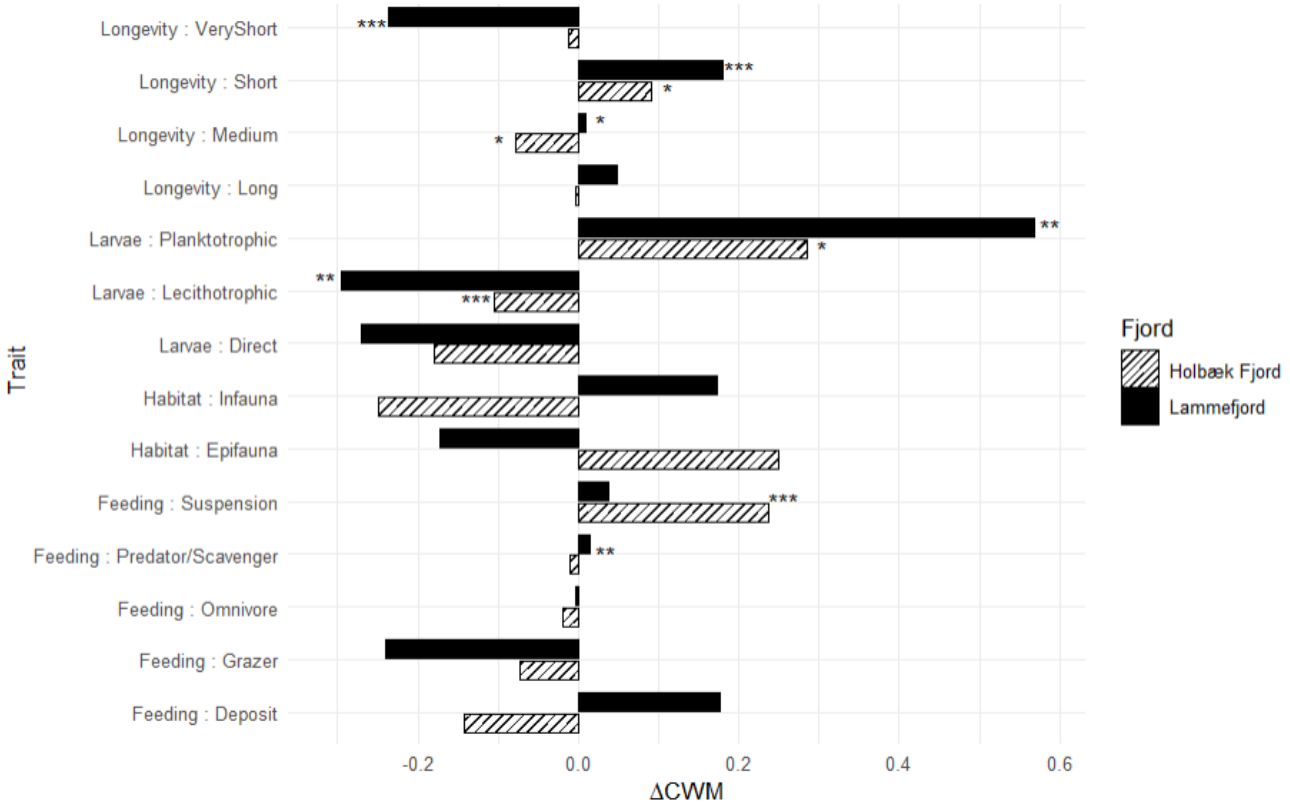


Figure 12. CWM analysis revealing change in functional traits from 1996 to 2025 in Lammefjord and Holbæk Fjord. Values are calculated based on species-composition weighted by trait-abundance. The x-axis represents the proportional change in the relative abundances of trait. The y-axis represents different trait categories. Solid bars represent Lammefjord while hatched bars represent Holbæk Fjord. Positive values indicate an increased relative dominance of trait. Negative values indicate a decrease.

Tabel 12. Kruskal–Walli's test results comparing CWM trait values between fjords and years. Mean values group_1 and group_2, p-values are shown. Significance levels: * p <0.05, ** p <0.01, *** p <0.001, ns = not significant.

Comparison	Trait group	Trait	Mean 1	Mean 2	p-value	Significane
LF 1996 vs LF 2025	Feeding	Deposit	0.73	0.65	0.455	ns
LF 1996 vs LF 2025	Feeding	Grazer	0.15	0.06	0.316	ns
LF 1996 vs LF 2025	Feeding	Omnivore	0.06	0.09	0.888	ns
LF 1996 vs LF 2025	Feeding	Parasite	NA	0.03	NA	NA
LF 1996 vs LF 2025	Feeding	Predator/Scavenger	0.04	0.16	0.004	**
LF 1996 vs LF 2025	Feeding	Suspension	0.15	0.18	0.888	ns
LF 1996 vs LF 2025	Habitat	Epifauna	0.22	0.32	0.260	ns
LF 1996 vs LF 2025	Habitat	Infauna	0.83	0.76	0.502	ns

LF 1996 vs LF 2025	Larvae	Direct	0.31	0.25	0.179	ns
LF 1996 vs LF 2025	Larvae	Lecithotrophic	0.27	0.18	0.007	**
LF 1996 vs LF 2025	Larvae	Planktotrophic	0.50	0.69	0.001	**
LF 1996 vs LF 2025	Longevity	Long	0.12	0.11	0.685	ns
LF 1996 vs LF 2025	Longevity	Medium	0.05	0.14	0.020	*
LF 1996 vs LF 2025	Longevity	Short	0.59	0.78	<0.001	***
LF 1996 vs LF 2025	Longevity	VeryShort	0.33	0.09	<0.001	***
HF 1996 vs HF 2025	Feeding	Deposit	0.59	0.68	0.165	ns
HF 1996 vs HF 2025	Feeding	Grazer	0.32	0.11	0.002	**
HF 1996 vs HF 2025	Feeding	Omnivore	0.06	0.07	0.603	ns
HF 1996 vs HF 2025	Feeding	Parasite	NA	0.05	NA	NA
HF 1996 vs HF 2025	Feeding	Predator/Scavenger	0.05	0.06	0.850	ns
HF 1996 vs HF 2025	Feeding	Suspension	0.10	0.26	<0.001	***
HF 1996 vs HF 2025	Habitat	Epifauna	0.37	0.43	0.414	ns
HF 1996 vs HF 2025	Habitat	Infauna	0.66	0.68	0.835	ns
HF 1996 vs HF 2025	Larvae	Direct	0.33	0.44	0.057	ns
HF 1996 vs HF 2025	Larvae	Lecithotrophic	0.33	0.13	<0.001	***
HF 1996 vs HF 2025	Larvae	Planktotrophic	0.39	0.51	0.018	*
HF 1996 vs HF 2025	Longevity	Long	0.05	0.04	0.877	ns
HF 1996 vs HF 2025	Longevity	Medium	0.17	0.08	0.014	*
HF 1996 vs HF 2025	Longevity	Short	0.61	0.73	0.019	*
HF 1996 vs HF 2025	Longevity	VeryShort	0.26	0.29	0.850	ns
LF 2025 vs HF 2025	Feeding	Deposit	0.65	0.68	0.953	ns
LF 2025 vs HF 2025	Feeding	Grazer	0.06	0.11	0.203	ns
LF 2025 vs HF 2025	Feeding	Omnivore	0.09	0.07	0.893	ns
LF 2025 vs HF 2025	Feeding	Parasite	0.03	0.05	0.492	ns
LF 2025 vs HF 2025	Feeding	Predator/Scavenger	0.16	0.06	0.163	ns
LF 2025 vs HF 2025	Feeding	Suspension	0.18	0.26	0.120	ns
LF 2025 vs HF 2025	Habitat	Epifauna	0.32	0.43	0.120	ns
LF 2025 vs HF 2025	Habitat	Infauna	0.76	0.68	0.335	ns
LF 2025 vs HF 2025	Larvae	Direct	0.25	0.44	0.004	**
LF 2025 vs HF 2025	Larvae	Lecithotrophic	0.18	0.13	0.953	ns
LF 2025 vs HF 2025	Larvae	Planktotrophic	0.69	0.51	0.003	**
LF 2025 vs HF 2025	Longevity	Long	0.11	0.04	0.036	*
LF 2025 vs HF 2025	Longevity	Medium	0.14	0.08	0.402	ns
LF 2025 vs HF 2025	Longevity	Short	0.78	0.73	0.492	ns
LF 2025 vs HF 2025	Longevity	VeryShort	0.09	0.29	0.003	**

5.6. Multivariate analysis

The results of the dredging impact on species composition between dredged and non-dredged areas, revealed a significant difference in community structure (ANOSIM: $p < 0.001$). This explains that the observed differences in benthic assemblages differed consistently between areas exposed to mussel dredging in 2024 and areas without recorded dredging activity. Additionally, the SIMPER analysis showed that the dissimilarity between dredged and non-dredged stations was primarily driven by differences in the abundance of *Peringia ulvae*, *Pygospio elegans, Microdeutopus gryllotalpa, Tritia reticulata, Mya arenaria,* and *Mytilus edulis* (Table 13). Among these, *P. ulvae* contributed most strongly to the observed dissimilarity, accounting for 23.98% of the total variation between groups.

Tabel 13. SIMPER analyses of species dissimilarity between dredged and non-dredged areas in Lammefjord 2025. Species are ranked regarding to percentage contribution to total community dissimilarity.

Species	Av. Abund (Dredged)	Av. Abund (Non-dredged)	Av. Diss	Diss/SD	Contrib. %	Cum. %
Peringia ulvae	1.30	6.92	19.59	1.35	23.98	23.98
Pygospio elegans	0.11	2.07	6.04	1.21	7.39	31.36
Microdeutopus gryllotalpa	0.66	1.24	5.88	0.80	7.20	38.56
Tritia reticulata	0.52	0.84	4.46	0.75	5.46	44.02
Mya arenaria	0.26	1.37	4.12	0.99	5.04	49.05
Hydrozoa indet.	0.43	0.68	3.94	0.74	4.82	53.87
Mytilus edulis	0.66	0.88	3.57	0.90	4.37	58.25
Polydora cornuta	0.20	0.87	3.32	0.71	4.06	62.31
Harmothoe imbricata	0.53	0.51	2.89	0.73	3.53	65.84
Alitta succinea	0.34	0.63	2.78	0.64	3.40	69.24
Balanus improvisus	0.67	0.00	2.01	0.39	2.46	71.69

Species associated with non-dredged stations generally exhibited higher average abundances compared to dredged stations, suggesting reduced community complexity and altered species composition in dredged areas.

5.6.1. Lammefjord and Holbæk Fjord 1996-2025

The non-metric multidimensional scaling (nMDS) based on Bray-Curtis similarity did not show a clear distinguishment of benthic community structure, between Lammefjord and Holbæk Fjord on a spatial scale for 2025 and 1996, but on the contrary, a clear difference was observed on a temporal scale (figure 13), suggesting a community shift over time. Samples from the two survey years formed distinct clusters in the ordination space, indicating that the benthic assemblages in both fjords have undergone compositional alterations between the two sampling periods. The similarity stress level (0.24) indicates that ordination provides a moderate representation of the community composition and should be interpreted in terms as a general pattern rather than fine-scale differences among samples.

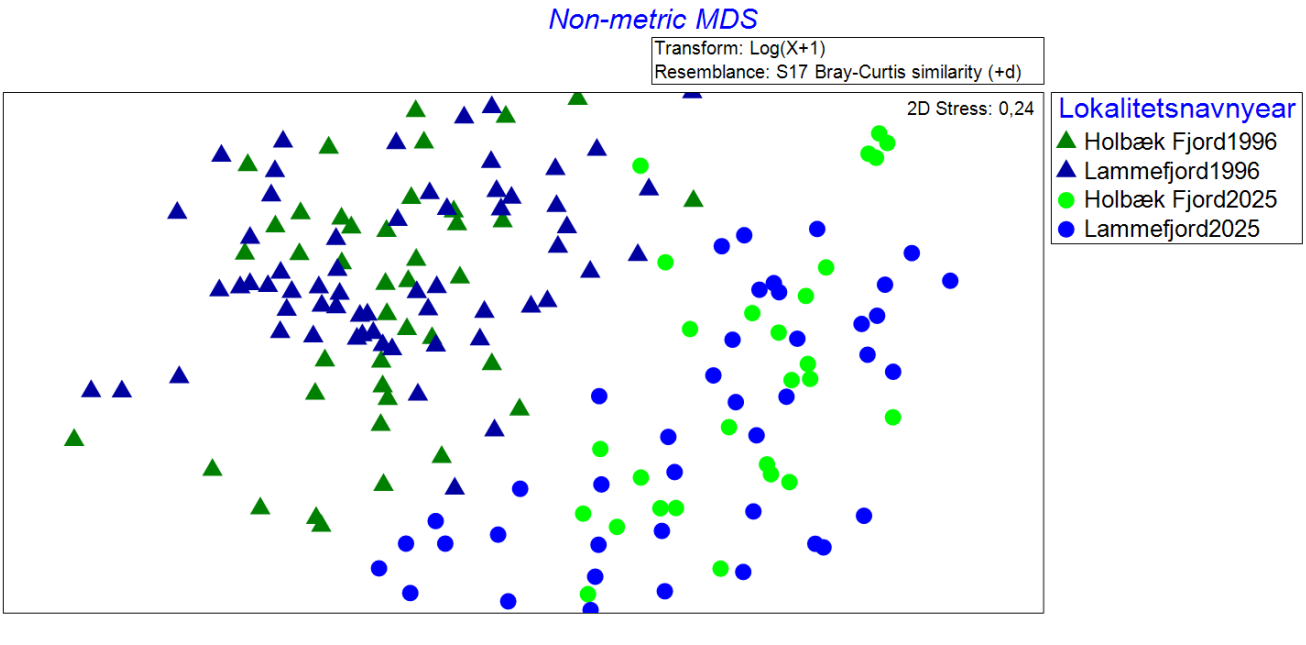


Figure 13. nMDS on a Log(x+) scale representing Lammefjord and Holbæk fjord stations on a temporal scale 1996-2025.

5.6.1. Comparison of stations between Lammefjord and Holbæk Fjord 1996-2025

The nMDS ordination for 1996 showed a compact distribution of samples with minor overlapping communities among stations, from both Lammefjord and Holbæk Fjord (figure 14). The lack of clear clustering indicates a more homogenic benthic community composition across the study area during this period. On the contrary, samples from both fjords in 2025, shows a more spatial distributed pattern, being more scattered across the study area (figure 15).

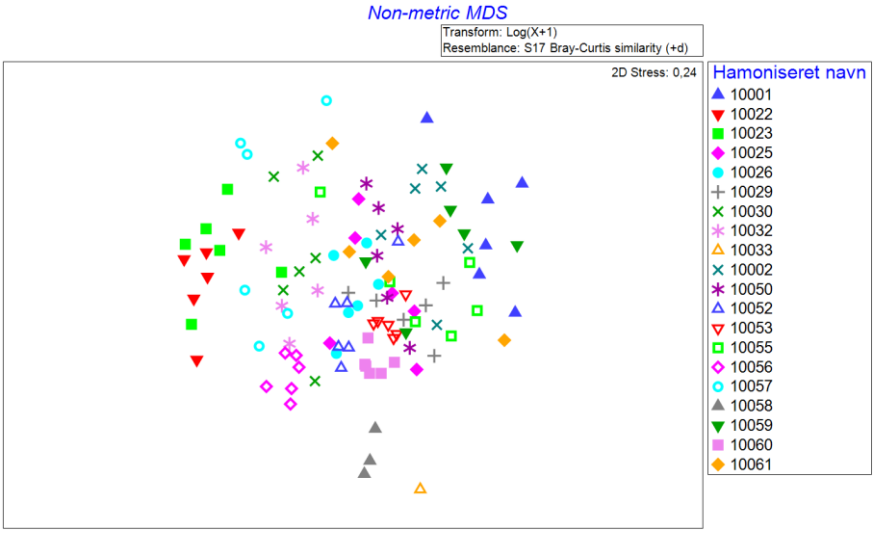


Figure 14. nMDS on a Log(x+) scale representing Lammefjord and Holbæk fjord 1996, on a local scale, by stationID including samples n=6.

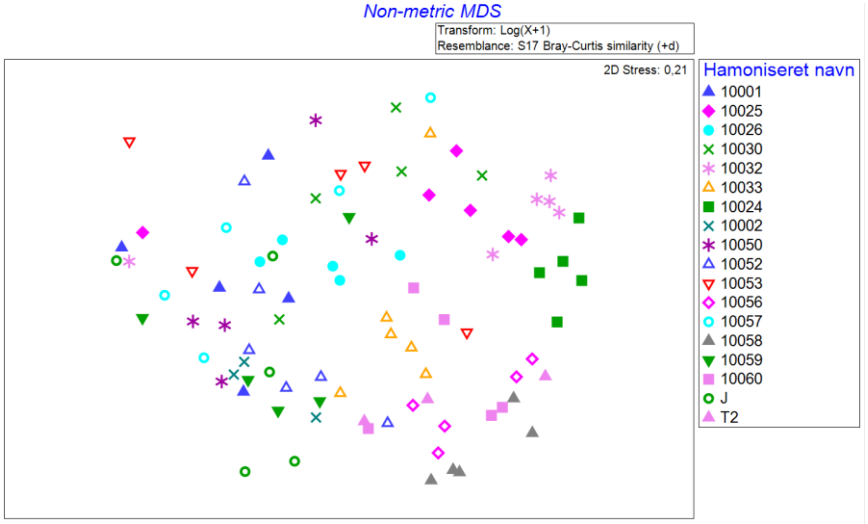


Figure 15. nMDS on a Log(x+) scale representing Lammefjord and Holbæk fjord 2025, on a local scale, by stationID including samples n=3-6.

5.6.2. Metapopulation connetivity

The connecivity of Lammefjord with a potential source popoulation in Kattegat is represented in figure 16-19, connecting potential propagule distribution. The figures shows a clear gradient of community overlap from being slighty overlapping between Lammefjord and Isefjorden (Inner bredning), while gradually increase in overlap was observed porportionally with distance. This indicates a connectivity between metapopulations from the inner part of Isefjorden and its sub-fjords, being more connected with sourcepopulations in Kattegat.

Lammefjord - Isefjord Inderbredning

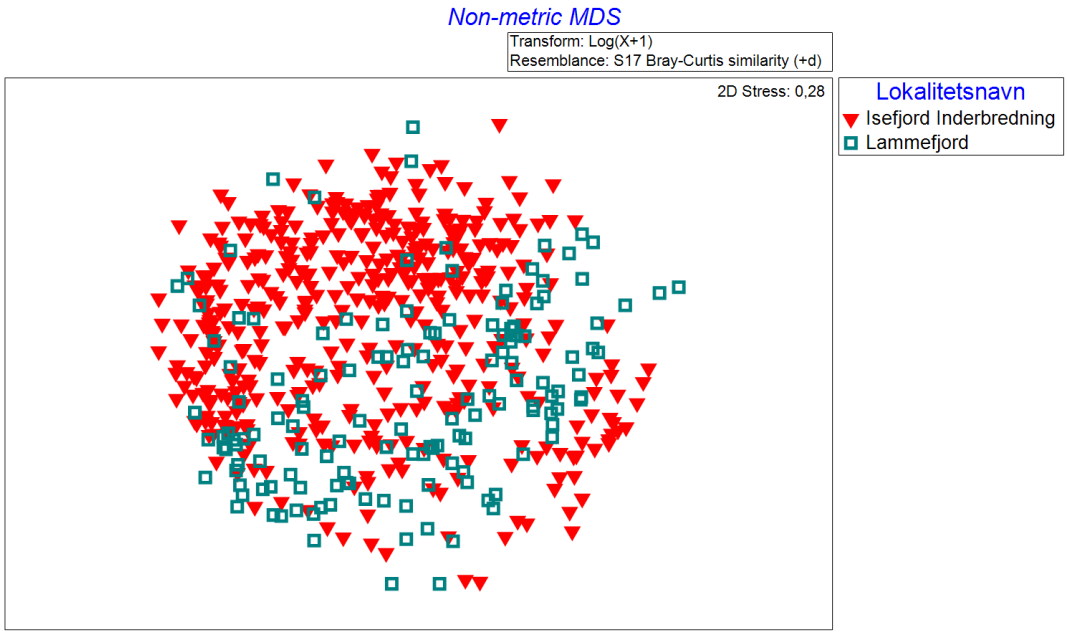


Figure 16. nMDS on a Log(x+) scale representing all stations of the entire Lammefjord and Isefjord Inderbredning, on a temporal scale 1988-2025.

Isefjord Inderbredning - Isefjord Ydrebredning

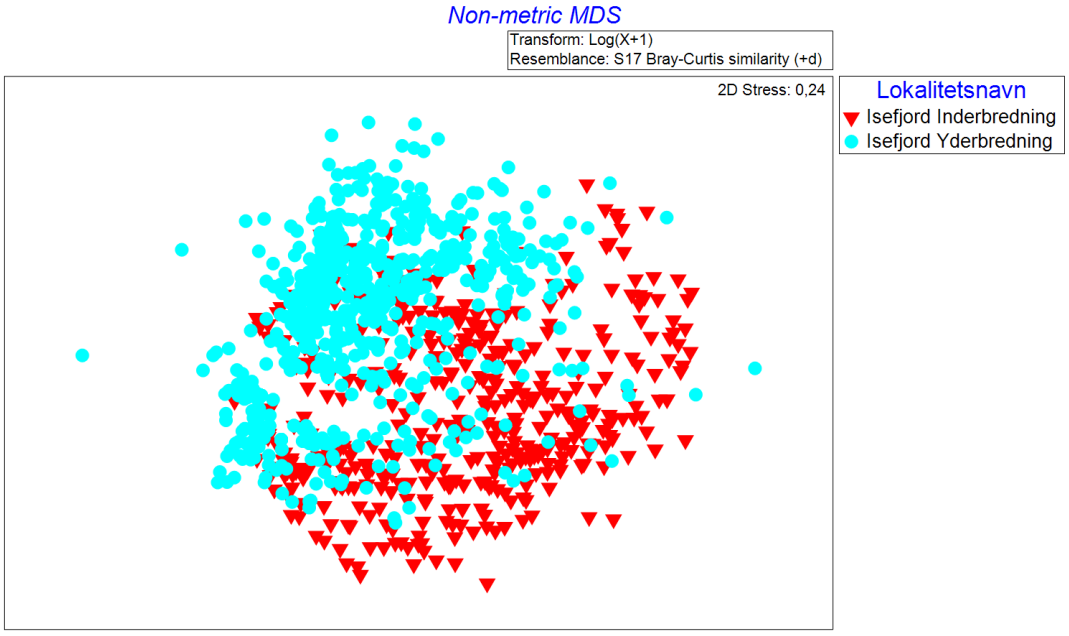


Figure 17. nMDS on a Log(x+) scale representing all stations of the entire Isefjord Inderbredning and Isefjord Ydrebredning, on a temporal scale 1989-2024.

Isefjord Ydrebredning - Hesselø Bay

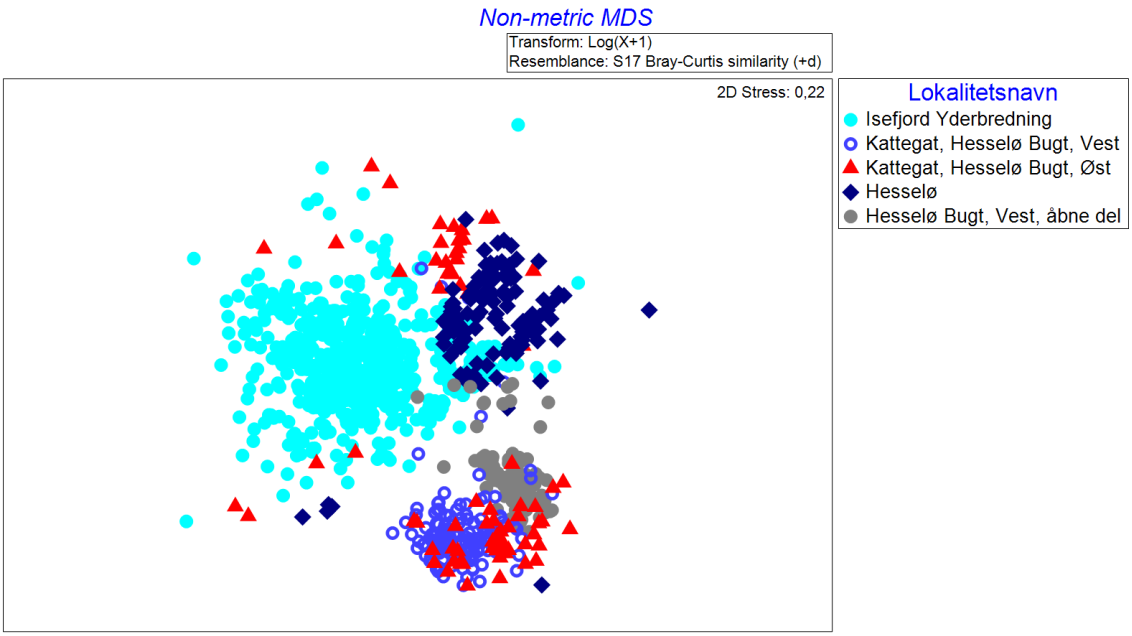


Figure 18. nMDS on a Log(x+) scale representing all stations of the entire Isefjord Yderbredning and Hesseløbugten, during 1989-2025.

Hesselø Bay- Kattegat - Anholt

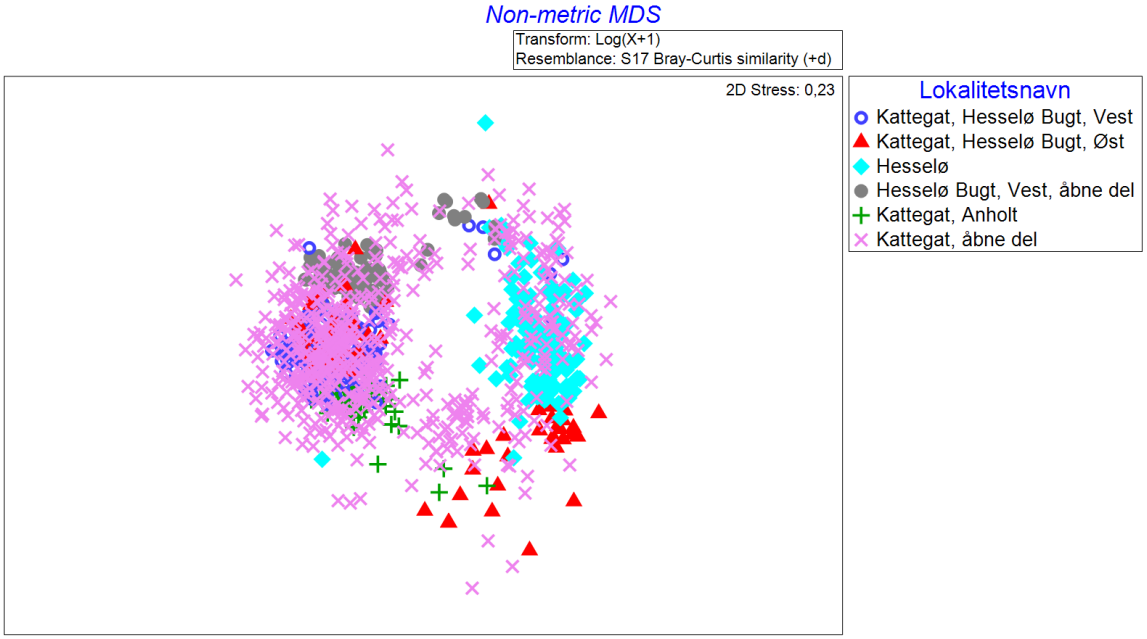


Figure 19. nMDS on a Log(x+) scale representing all stations of the entire Hesselø Bay and Kattegat on a temporal scale 1989-2025.

6. Discussion

6.1. Diversity

6.1.1. Diversity response to dredging

The results of the univariate analysis revealed that the fjords exhibited different developments in diversity and community structure, despite both showing a strong temporal decline in abundance between 1996-2025 (table 4.5; figure 4). In Lammefjord, a clear decline in species richness (S) Margalef's index (D), Shannon diversity (H'), ES10 and evenness, combined with increased dominance (L1, L2), indicates a shift toward a more homogenized and disturbed benthic habitat. In contrast, Holbæk fjord exhibited a clear stable diversity over the 29-years period, despite mean abundance declined significantly over the 29-year period (table 4.5). The stable Shannon diversity and evenness indicated that individuals remained more evenly distributed among species, preventing strong dominance by only a few opportunistic species as in Lammefjord. Ecological resilience describes the ability of a community to resist or recover from environmental disturbance while maintaining overall ecosystem structure and function. Furthermore, the absence of recorded dredging activity in Holbæk Fjord 2024 and at least the past five years according to lading data, may explain the more stable diversity patterns observed in 2025 (figure 4). Species richness can often be difficult to measure, since richness typically is strongly influenced by sample size and number of individuals, with more individuals increasing the number of species (Hansen and Josefson, 2024; Krebs, 2014). Therefore, diversity metrics such as Shannon diversity, Simpsons' dominance and evenness, can be good representatives of diversity, as they account for both how evenly the species are distributed within a sample (dominance) and between samples (evenness) (Clarke and Warwick 2001; Hansen and Josefson 2004).

Several studies have demonstrated that dredging results in increased dominance of opportunistic species which rapidly colonize and dominate the areas (Tillin et al., 2006; Zhang et al., 2024). This may explain the observed lower Shannon diversity and evenness, as for the increased Simpsons index, in Lammefjorden, indicating that this fjord experienced more frequent disturbances, than Holbæk, where less species became more dominant over time. The species accumulation curves further supported these findings, showing that Holbæk Fjord maintained higher diversity at comparable numbers of individuals, whereas Lammefjord reached higher total richness primarily due to high abundances of a limited number of dominant species (figure 7). This implies that the higher total

abundance observed in Lammefjord does not reflect a higher diversity but rather increase dominance by fewer opportunistic species.

6.1.2. Beta-diversity and dredging

The diversity at station scale represents beta-diversity (Krebs, 2014) and can further explain a more complex diversity pattern and shift in community composition. The station-level analysis revealed measurable effects of dredging on both spatial and temporal scale, in both fjords (table 6,7; figure 5, 6). The multivariate analysis and Wilcoxon rank-test (table 7) showed a significant difference in species composition between dredged and non-dredged areas (ANOSIM, $p < 0.001$). This indicates that the effect of dredging may be reflected in community composition rather than diversity metrics alone. The SIMPER analysis further revealed that the dissimilarity between dredged and non-dredged stations was mostly driven by opportunistic and disturbance tolerant species such as *Peringia ulvae*, *Pygospio elegans*, *Microdeutopus gryllotalpa*, *Mya arenaria* and *Polydora cornuta*. Especially *P. ulvae* contributed with ~24% of the total dissimilarity between station groups (table 13). Additionally, several stations in Lammefjord (10002, 10052, 10053 and 10058) exhibited significantly lower diversity than the rest of the stations in Lammefjord 2025 (table 8, 9). These stations also had the lowest density (ind/m^2) compared to non-dredged stations, except for station 10059 (9.8 ind/m^2). Station 10058 exhibited the most significant decline with a mean reduction of 1462.13 ind/m^2, but with a SAR = 0% (table 8). A similar observation was also found in Holbæk Fjord at station 10001 with a significant decline in all diversity indices and abundance with a SAR = 0%. This observation in Holbæk fjord, might be explained by another type of physical disturbance in terms of maintenance of the navigation channel in the area (Tænketanken Hav, 2025) since it was the deepest station in Holbæk (8.1 m), and with the lowest diversity of all stations.

6.2. Biomass

6.2.1. Fjord scale

At fjord scale, different temporal observations were found between the Lammefjord and Holbæk Fjord (figure 8). An increase in biomass was observed in Lammefjord 34.0 g/m² in 1996 to 43.0 g/m² in 2025, while a reduction from 35.9 g/m² to 9.45 g/m² was observed in Holbæk. These differences could be explained by limited data in 1996, especially for Holbæk Fjord, and direct comparison between sampling years should therefore be interpreted with caution. Only spatial variation in 2025 at station-level is quantitatively comparable. Additionally, the effect of dredging on biomass showed no clear relationship between SAR and mean biomass between stations in

Lammefjord (Spearman correlation, p = 0.86), indicating that dredging alone did not explain spatial variation in biomass. However, the analysis at station scale showed a spatial response in dredging.

For the biomass of *M. edulis* a reduction in both fjords were observed between 1996 and 2025. Especially in Lammefjord where the biomass decreased from 729.83 ± 0.33 g/m² to 222.23 ± 0.93 g/m², corresponding to a reduction of approximately 70%. A higher reduction was found in Holbæk Fjord, with biomass decreasing from 558.81 ± 0.19 g/m² to 0.05 ± 0.33 g/m². This finding is particularly important because no dredging activity was recorded in Holbæk Fjord in 2024, suggesting that the decline of *M. edulis* might not be explained by dredging alone.

6.2.2. Station scale

The clearest indication of a dredging effect, was observed at station 10052, which exhibited the highest SAR value (1.53%) and reduction in biomass (324.38 ± 0.24 g/m² to 4.88 ± 0.40 g/m²) in 2025, as for a high reduction in the biomass of *M. edulis* 147.37 g/m² to 0.20 g/m² in 2025 (figure 9, table 13). This observation could imply that repeated dredging may have negatively affected the benthic biomass over time. A reduction was also observed at 10002 (33.58 ± 0.39 g/m² to 0.71 ± 0.29 g/m², SAR = 1%) and 10050 (50.89 ± 0.48 g/m² to 7.94 ± 0.78 g/m², SAR = 2%). Corresponding, an increase was also found in the biomass of *M. edulis* at 10050 (1550.54 g/m² to 4201.46 g/m²).

Other patterns were in contrast observed at several stations. The biomass increased at station 10053 from 64.00 ± 0.25 g/m² to 775.59 ± 0.44 g/m², despite a SAR value of 14%. A high biomass was also observed at station T2 (239.49 ± 0.83 g/m²) in contrast of a SAR value of 39%. At these stations, a corresponding high biomass was observed of *M edulis* (52.68 g/m² to 2634.60 g/m²) and (10770.63 g/m²). Five stations (10056, 10057, 10058, 10059, 10060) in Lammefjorden, exhibited a minor increase in biomass corresponding to no dredging activity. The biomass of *M. edulis* did similarly exhibit a minor increase in biomass, but far below the high- and intermediate dredging activities, observed at stations 10052, T2 and 10002. This pattern might indicate that *M. edulis* is relatively tolerant to physical disturbance, since they often are found in dynamic coastal environments, attached to hard surfaces through byssus threads, and thereby being adapted and tolerant to disturbed areas with high variation of both water level and wave action. Their high reproductive rate and rapid growth may further lead to fast recover of populations following a dredging activity compared to other species.

The results of biomass at station scale in Lammefjord may be connected directly to dredging, although this disturbance alone might not fully explain the spatial and temporal patterns observed in Lammefjord. Instead, local environmental conditions such as depth, sediment composition, or patchy recruitment may have influenced biomass distribution among stations as well. In this study, depth can be difficult to couple since some stations with great depths and low dredging activities exhibit a decline in biomass, whereas some stations with great depths experience an increase in biomass. The only station where depth could be the other explanatory factor is station 10002 (10 m, SAR = 1%), where a decrease in both biomass for the entire community at that station, as well for *M edulis* alone was observed.

6.3. Community shift and functional diversity

The diversity indices alone may not fully explain the observed changes in community structure. Therefore, the species turnover rate may provide additional insight into underlaying patterns and an important indicator of chronic long-term disturbance. The observed species turnover rates indicate a temporal community shift in both fjords, between 1996 and 2025. The turnover rate of 55% in Lammefjorden suggests that approximately half of the community changed over the 29-year period, despite the minor observed net loss of 12 species. The same accounts for Holbæk Fjord, which exhibited a turnover rate of 56% and net loss of 8 species, indicating a high turnover as in Lammefjorden (table S2). However, the change in community composition was further observed in the shift in dominance structure as well for functional composition.

In Lammefjorden, the community shifted from being dominated by annelids, arthropods and nematodes in 1996, towards a mollusca dominated system in 2025 (figure 5.a.b). Several species associated with organic rich sediments, exhibited a high reduction in abundance, such as *Capitella capitata*, *Chironomus salinarius, Monocorophium insidiosum, Tubificoides benedii, Polydora cornuta* as for the Mollusca *Pusillina sarsii* (figure 5.a, b; table S1). Instead, the community became dominated by opportunistic, fast-colonizing and disturbance tolerant species such as *Peringia ulvae* (n=2462), a highly dominating opportunistic-tolerant gastropod, often associated with disturbed sediments and very characteristic of subtidal blue mussel beds (McLaverty, C., et al. (2024)*, Pygospio elegans* (n=218), *Mya arenaria* (n=162), *Mytilus edulis* (n=134) and *Microdeutopus gryllotalpa* (n=128). The multivariate analysis supported these findings, as the ANOSIM analysis showed that dredging had a significant difference in species composition between dredged and non-dredged areas in Lammefjord ($p < 0.001$), while the SIMPER analysis explained the observed dissimilarity and

community shift was driven by *P. ulvae* which contributed with ~24% of the total dissimilarity, followed by *P. elegans* ~7.4%, *M. gryllotalpa* ~7.2%, *Tritia reticulata* ~5.5% and *M. arenaria* ~5% (table 13).

Although Holbæk Fjord did not experience the same intensive dredging activity in 2024, the turnover rates for were similar as in Lammefjorden, but with a different pattern of alteration in community structure. A similar decline in annelids and nematodes was observed, but with a more even distribution among phyla compared to Lammefjorden. The community became more dominated by *Peringia ulvae* (n=331), *Spirorbis spirorbis* (n=317), *Microdeutopus gryllotalpa* (n=187), *Monocorophium insidiosum* (n=131), *Spirorbis corallinae* (n=101), *Ericthonius brasiliensis* (n=74), and *Gammarus locusta* (n = 72). Several of these species are characterized by being epifaunal, mobile and associated with vegetated habitats such as macroalgae or eelgrass beds. This could indicate that an improvement in nutrient loading rather than dredging, could have caused the community shift in Holbæk Fjord, compared to Lammefjorden. In this analysis, a longer and more comprehensive time series of data would have provided additional insight into when most of the community shift occurred in response to chronic dredging disturbance. Therefore, advocating for more monitoring is an important step in understanding these underlying mechanisms better.

6.3.1. AMBI

Both fjords exhibited a similar temporal shift in community composition (table 10; figure 10,11) with a decline in most disturbance tolerant species (EG IV-V) and an increase in dominance of moderate tolerant species (EG III) to 74.5% in Lammefjord and 61.7% in Holbæk Fjord. Despite the improvement in ecological condition (figure 10,11), spatial differences were observed between the two fjords in 2025. Lammefjord exhibited 50% less of most sensitive species (6.9%) compared to Holbæk fjord (14.2%), as well as Holbæk Fjord containing more stations with higher ecological conditions (figure 10, 11). Although AMBI is generally linked to nutrient pollution and organic enrichment (Borja et al., 2000; van der Linden et al., 2016; Hansen and Andersen, 2024) both fjords would have been expected to exhibit the same improvement in water quality, if nutrient loading alone explained the observed patterns (table 11; figure 10, 11). Since 1996, both fjords have experienced a threefold reduction in nutrient loading (Pers. Com. Hansen, 2026). Therefore, with Lammefjord exhibiting a minor lower ecological quality and higher proportions of EG III species than Holbæk Fjord, this observation could imply that Lammefjord would experience another type of disturbance, than nutrient pollution, such as dredging. This interpretation could further explain the observation at

station 10052, which exhibited both the highest dredging intensity (SAR = 1.53%) and the highest proportion of tolerant EG III species (figure 10), although the relationship was not statistically tested.

These findings can be difficult to interpret since no statistical test was made, and since Danish coastal waters have a long history of eutrophication. Therefore, direct coupling to dredging can be difficult. A study by Pommer et al. (2016) demonstrated that chronic mussel dredging reduced sensitive species and promoted dominance of disturbance-tolerant species through sediment homogenization and habitat alteration. On the other hand, another study by McLaverty et al. (2024) found that the impact of mussel dredging has shown to be difficult to detect since nutrient pollution can disrupt the observable effects of dredging, and that eutrophication might contribute to a synergy effect, rather than dredging alone, explaining the reduced diversity. The observed AMBI patterns may therefore reflect partial recovery from historical nutrient enrichment, while such an effect could have been counteracted continued moderate physical disturbance, and might explain the observed patterns, where AMBI have narrowed in the middle of the spectrum (i.e. group III) particularly in Lammefjord. A further investigation of the historic development in primary production and oxygen content might have explained these observations better than dredging.

6.3.2. Mechanisms of sediment disturbance and functional homogenization

AMBI can also be used in combination with diversity indices to analyze the development of diversity. Analysis of the Kattegat bottom fauna has found that when diversity increased, it was caused by an increase in category (IV-V) species which typically feeds on the organic material on the surface such as the ones reduced in Lammefjord 2025 (Pers. Com. Hansen 2026). Such species would be *C. capitata*, *S. armiger* and *Arenicola marina* which thrive in organically enriched sediments and pollution tolerant species (McLaverty et al., 2024).

The organic carbon (OC) content in the surface sediments is an essential food resource for many benthic species and plays an important role in the benthic pelagic coupling (Høgslund et al., 2019; Zhang et al., 2024). OC produced in the plankton, falls to the seafloor and undergoes a series of resuspension, deposition processes, before it stores in the sediment (Zhang et al., 2024). When stored, this OC is being remineralized by benthos and microorganisms through these burial and transport processes (Zhang et al., 2024). Hence, bioturbating fauna plays a crucial role of mineralizing and preserving OC as a stable food source available for the entire benthic ecosystem (Josefson & Hansen 2003; Høgslund et al., 2019; Zhang et al., 2024). Physical disturbance from bottom dredging may disrupt these sedimentary processes through sediment resuspension, homogenization of substrate type

and oligotrophication of sediments (Petersen et al., 2024). A study from the North Sea by Zhang et al. (2024), demonstrated that intensively dredged muddy sediments (SAR > 1 yr^{-1}) experienced highest reduction in OC (10-25%), compared to the non-dredged areas, and that sandy areas experienced an OC reduction by 5-10% OC. Similar dredging intensities were observed at several stations in Lammefjord 2024, including 10052 (SAR=1.53%) which exhibited reduced diversity, low biomass and increased dominance of moderate opportunistic species (EG III). Although, the OC content was not measured in this study, sediment characterization of both fjords was described by silty-sandy substrate, while Holbæk Fjord additionally contained a higher proportion of eelgrass beds. Eelgrass have previously been demonstrated to enhance sediment stability and carbon retention (Bijak and Smyth, 2023). Furthermore, the grain sizes of substrates are also of importance in benthic ecosystems, since different species use specific grain size or building protecting tubes, such as infaunal polychaetes like spionids. Hence, sediment composition is an important factor regarding to biodiversity (Høgslund et al., 2019). Furthermore, other studies explain that species such as *Macoma balthica* and *Corophium volutator* can be observed in high densities with high organic content in the sediment and are important secondary producers and important fish food (Bertness, 2007; Kaiser et al., 2011; McLusky and Elliott, 2007). *Corophium* sp. often coexists in sediments with the snail *P. ulvae*, but competition is minimized by the selection of particles for feeding of different sizes, with *Hydrobia* sp. taking the larger particles, and *Corophium* sp. the smaller (Bertness, 2007; Kaiser et al., 2011; McLusky and Elliott, 2007).

6.3.3. Functional traits

The observed shift in functional traits from the CWM analysis in figure 12 and table 11, 12 further indicates that both fjords underwent a temporal shift in community structure as for the phyla, AMBI and SIMPER analysis revealed.

A clear shift was observed in Lammefjorden, with a high dominance of traits such as short-lived (1-3yr) infaunal, deposit -and suspension feeding species, with planktotrophic larvae development. These findings correspond well with the SIMPER analysis with *P. ulvae* contributing most to the difference to the community as for *P. elegans*, *M. gryllotalpa, Tritia reticulata* and *M. arenaria* and *Microdeutopus* sp. These species have especially been linked to being less affected in disturbed areas such as dredged areas (McLaverty et al., 2024). The increasing dominance of the infaunal individuals from 70 to 88% and reduction of epifauna (30 to 12%) might be due to their reproduction and recruitment strategies rather than habitat position a since mussel dredges are one

of the types of bottom fishing gear that penetrates deepest into the sediments. The increase of deposit-feeders by 62 to 77% could be explained by resuspended rich organic sediments, caused by dredging which fits well with the high abundance of *P. ulvae* and *S. armiger*, *M. gryllotalpa*, as they are associated with unstable and organic rich environments, and fast colonizers (Whitlatch and Zajac, 1985). Additionally, the high decline in epifaunal grazers could indicate reduced habitat complexity with reduced macroalgae and eelgrass beds, which may have declined over time.

The high relative abundance of suspension-feeders in Lammefjord can be explained by the high proportions of *M. edulis* and *M. arenaria* (table S1). Additionally, *M. arenaria* has been described to be a species with a long lifespan (>10 years) (Tyler-Walters, 2003), and it has a rapid growth rate under optimal conditions. In this study all *M. arenaria* individuals showed an average size of ~4.5mm, approximately 1.5yr post settled individuals from 2024 (Gerasimova and Maximovich, 2014; Tyler-Walters, 2003), which has been described to typically occur in the upper 2 cm (Zwarts and Wanink, 1989). This life-strategy of initial rapid growth allows them to outcompete smaller individuals and help juvenile individuals to avoid size-specific predation (Du Clos and Jiang, 2018). Furthermore, the observed increase in predators/scavengers also fits well with the high abundance of *Tritia reticualta* and *Harmothoe imbricanta* as these species typically feed on dead and decaying organisms (Person and Rosenberg, 1978). The increase in abundance of individuals with these traits has previously been demonstrated by Sparks-McConkey and Watling (2001), where the abundance of scavengers and predations increases after a dredging activity, due to a high amount of damaged and dead organisms.

In contrast to Lammefjord, the high amount of suspension feeders in Holbæk Fjord, can be related to a high abundance of the bryozoan *Einhornia crustulent*, amphipods, ascidians and the polychaete *Spirorbis* sp., which also are epifaunal species that inhabit macroalgae and eelgrass beds. Especially ascidian have been linked to areas with lower mussel dredging activity (MacLaverty et al., 2024). The high decline in deposit feeders in both fjords is due to the reduced populations on *C. capitata*, Nematoda and *Chironomus salinarius* as seen in the AMBI analysis. These species are all highly associated with organic rich sediments, in which the AMBI analysis revealed a reduction in nutrient enrichment, since 1996 (figure 10,11). The observation from the analysis has previously been found in other studies (Tillin et al., 2006), which also demonstrated that larger, epifaunal, filter-feeding species were more abundant in lightly dredged areas, while areas with higher dredging activity were characterized by higher biomass of mobile animals and infaunal and scavenging invertebrates.

Furthermore, the study also suggested that ecological features of suspending-feeding species could directly affect their vulnerability to dredging impacts, due to their habitat position. This study supports the observation by Tillin et al. (2006) that sedentary and emergent positions close to the sediment-water interface make this group particularly vulnerable to dredging. Therefore, higher amount of epifaunal abundance in Holbæk Fjord could be an indicator for less dredging activity, as in Lammefjord.

The significant increase in planktotrophic larvae from 28 to 84% ($p = 0.001$) and decrease in direct (40-13%) and lecithotrophic development (33-3%, $p = 0.007$), may be interpreted as an indicator of a distributed system by dredging as they have an advantage in dispersal and colonizing areas with frequent disturbances. In systems exposed to repeated dredging, traits associated with high dispersal, rapid growth and recruitment, are typically favored, while species with direct or lecithotroph development such as many amphipods and gastropods observed in Holbæk Fjord (table S1), would be reduced due to high mortality caused by dredging gear and sediment disturbance. In contrast, if the system is relatively stable, species with traits such as epifaunal habitat position and direct development would be more dominant, as they outcompete planktotrophic larvae for space. Typically, species with planktonic larvae development exhibit more fluctuating population densities than organisms with direct development due to a high predation pressure in the water column (Bertness, 2007; Kaiser et al., 2011; McLusky and Elliott, 2007; Thorson, 1950). However, species with planktotrophic larvae compensate for this through high productive rates and outputs like many bivalves and worms. These larvae may also avoid high mortality rates caused by direct contact with dreading gear due to late settlement, increasing the probability of higher recruitment in disturbed areas. The advantage of species with direct and lecithotrophic development on the other hand, is reduced mortality in the plankton as well as competition advantages for space due to larger body sizes.

In contrast, species with lecithotrophic and especially direct development, may benefit from reduced larval mortality as well with better competition abilities for space, but these traits have faced the cost of high parental investment resulting in fewer offsprings, lower fecundity and limited dispersal (Bertness, 2007; Kaiser et al., 2011; McLusky and Elliott, 2007). A consequence of this, populations with lecithotrophic and direct development may be vulnerable to repeated dredging as population mortality rates may exceed recovery and recruitment rates. The dominance of planktotrophic development observed in this study may therefore reflect a selective filter of high reproduction and

vast dispersal capacity, under long-term disturbance. This mechanism has also been explained in previous studies by Hansen and Andersen (2024) and Bendtsen and Hansen (2013).

6.4. Metapopulation connectivity

While a clear temporal distinction was found between both fjords in the nMDS plot in figure 13, a spatial difference within years was not found in nMDS plot (figure 13-15). The alteration in time underlines the community shift of both fjords, in the previous results, while the nMDS plots at sample-station level did not indicate a clear indication of dredging effect on the community. If dredging showed a clear effect on the community structure, a more separated clustering would be observed in the stations. The nMDS plots of Lammefjord and Isefjord showed different clustering with a minor overlap, which might indicate two different communities with a minor overlap. This could be explained by both fjords exhibiting dredging in several years, and that Isefjorden is placed in the more open part of the fjord experiencing other environmental and hydrographic conditions, while Lammefjorden geographically is placed in a semi-closed part. A more mixed cluster was also observed between Isefjord Inder (IIB) -and Yderbredning, (ISY) indicating that this part of the fjord, the populations might be more similar, than with Lammefjorden. A clear distinguishment was observed between ISY and the southern part of Kattegat in Hesselø Bay (figure 18) which potentially can be explained by the salinity gradient between the two systems with those stations clustering in the outer part of Hesselø Bay being more saline than Isefjorden. Some species have adapted to withstand such a salinity difference and may therefore be suitable for inhabiting different environments. A study by Josefson and Hansen (2004) and Bendtsen and Hansen (2013) have shown that Kattegat functions as a donor area to Isefjord providing the fjord system with propagules transported with ocean currents. Additionally, Person and Rosenberg (1978) have argued that timing of reproduction determines the succession of species in a disturbed area. Benthic macroinvertebrates reproductive activity takes place in spring, with planktotrophic larvae reproducing earliest, followed by lecithotrophic and last, species with direct development. Planktotrophic has been demonstrated in the CWM analysis, to support Isefjord and the adjunct fjord systems, providing populations with new propagules. Therefore, in fjord systems such as the Kattegat - Isefjord - Lammefjord, spatial connectivity between benthic populations is of high importance to maintain populations of certain species. If the connectivity is decoupled by dredging, the contributions with propagules will be cut off. The result of this analysis could therefore imply that absent traits such as low dispersal potential, late maturation and long lifespan (Pommer et al., 2016), might be explained by sensitivity of these traits due to long-term and intensified dredging. Dredging may have led to reduced local populations

within Lammefjord of especially species, with direct development, and recovery will therefore depend on recolonization from surrounding local populations.

Understanding the interaction between disturbance and metapopulation connectivity is therefore important for future management and conservation of these areas. Systems with limited connectivity may be particularly vulnerable to repeated disturbance because recolonization processes may be slower and more dependent on the availability of nearby source populations (van Denderen et al., 2022).

6.5. Benthic comparison with Isefjorden

To investigate whether the observed patterns in community biomass were due to natural population dynamics or were caused by mussel dredging, a comparison of dominating biomasses contributing species in Lammefjorden and Holbæk Fjord was made with those observed in Isefjord Yderbredning, where commercial mussel dredging also takes place. Comparable studies examining long-term changes in biomass were not found, making direct comparisons difficult. However, some similarities were observed between the two fjords.

In all three fjords, the community biomass was mostly characterized by deposit-feeding infaunal polychaetes and bivalves, and shifted toward a more similar community dominated by *Mytilus edulis*, *Tritia reticulata*, *Peringia ulvae* and *Balanus* spp. However, the biomass in Holbæk Fjord exhibited a higher contributor of epifaunal species.

6.5.1. Trophic interactions of ecological importance

The observed shift in benthic composition in Lammefjord may have important consequences for trophic interactions and ecosystem functioning within the Isefjord system. Similar patterns in both fjords imply that changes in the ecosystems are interconnected and may reflect a coherent response to long-term chronic disturbance and habitat alterations. A consequence of lower biomass and altered macrofaunal community composition would at first seem to result in lower food resources to demersal predatory fish populations such as plaice (*Pleuronectes platessa*), European flounder (*Platichthys flesus)* and dab (*Limanda limanda*). Since fish and stomach content was not investigated in this study, a direct coupling could not be made, but only assumptions and estimations based on the present and abundance of species and previous studies. Studies by Nissling et al. (2007) and Støttrup et al. (2019), have found that flatfish are highly dependent on benthic prey during their juvenile life stages of their development. The decline of key infaunal prey species, combined with increasing dominance of *M.*

edulis, could imply a reduced habitat suitability for several demersal fish species. A decline in flatfish landings in Isefjord was observed between 2013 and 2025. Mean landings declined from 3.70 tonnes yr^{-1} in 2013-2018 to 1.15 tonnes yr^{-1} in 2019-2025, corresponding to a reduction of approximately 69% (Ministry of Food, Agriculture and Fisheries (n.d.). Similar responses have been linked to bottom dredging in a previous study by Johnson et al. (2015) which demonstrated that chronic bottom dredging significantly reduced the biomass of prey species in the northeastern Irish Sea. This decline was observed in plaices (*Pleuronectes platessa*) and dab (*Limanda limanda*), altering prey composition and quality. Although, abundance of prey species remained the same, the reduction of high-energy prey negatively affected fish conditions and foraging efficiency (Johnson et al., 2015). The plaice undergoes an ontogenetic change in diet, feeding mainly on infaunal polychaetes and bivalves during juvenile stages before transitioning to epibenthic fauna such as crustaceans, small fish, and echinoderms, as adult (Støttrup et al., 2019). Important prey species have been shown to be the bivalve *Abra alba* and the high-energy resource *Nephtys* spp. Furthermore, Johnson et al. (2015) found that the polychaetes exhibited a reduced biomass in dredged areas but maintained the same abundance. This indicates that dredging indirectly affects demersal fish populations through reducing biomass of specific prey species and not solely of abundance (Johnson et al., 2015). Similar preferences have been described for juvenile turbot (*Scophthalmus maximus*) which typically consumes copepods, chironomids, amphipods such as *Bathyporeia pilosa* and mysids, whereas larger individuals mostly consume mysids and small fish (Nissling et al., 2007). In this study, several potential prey species including *M. balthica*, and *C. gibba*, exhibited high declines in Lammefjord between 1996-2025, whereas abundance of *M. arenaria* increased (table S1). However, a high abundance of juvenile *M. arenaria* might not compensate for the decline in other prey bivalves, in terms of quality and energy content, but could potentially have led to a necessary shift in food resources compared to *M. balthica*, and *C. gibba.* Another demersal species is the Flounder (*Platichthys flesus*) which adapts its feeding strategy according to habitat structure, consuming polychaetes, crustaceans, amphipods, and small fish depending on habitat type (Andersen et al., 2005). In vegetated habitats, juvenile polychaetes such as *H. diversicolor* and *P. elegans*, oligochaetes and crustaceans such as *M. gryllotalpa* were preferred, while in sandy areas, amphipods such as *Corophium volutator*, mysids and polychaetes were preferred (Andersen et al., 2005). This study, only 7 individuals of *Corophium* sp. were observed in Lammefjord samples, while *M. Gryllotalpa* occurred in higher abundances (table S1). This shift in amphipod dominance could potentially function as a replacement for *Corophium* sp., as a food resource. In contrast, a higher

abundance and diversity of amphipods was observed in Holbæk Fjord (table S1; figure 5b) possibly due to potential refugees in the eelgrass beds. Reducing the distribution of eelgrass and macroalgae habitats by dredging could therefore further affect the diversity and prey availability for fish in the ecosystem, but in this study a high amount of juvenile polychaetes were also found in Lammefjord 2025, and therefore a general decline in prey availability remains inconclusive.

6.5.2. Methodology considerations

An important critical factor in this study was to distinguish whether the observed effects were due to short-or long-term effects of dredging, since the only comprehensive before data was from 1996. An important consideration is what previously has been defined as the shifting baseline syndrome where an undisturbed reference community can be difficult to find due to lack of historical data. The reference area may therefore already represent an altered system rather than an undisturbed condition (Pommer et al., 2016). Especially macrozoobenthic surveys are only dated back to the mid 80's and we know that dredging has happened for centuries, with the earliest registrations dating back in the late 1300s in Britan (Jarvis and Brennan, 2024). These limitations should be considered when interpreting the BACI design applied in this study. Despite significant differences were found between sampling years and fjords, the absence of a comprehensive timeseries makes it difficult to directly link the observed community shifts in Lammefjorden to mussel dredging itself. As empathized by Underwood (1992), natural temporal and spatial variability between stations can be misinterpreted as effects of anthropogenic pressures when temporal a spatial replication is limited. Therefore, the patterns observed in this study may reflect the combined influence of chronic dredging and other environmental changes as a synergy effect.

7. Conclusion

This study aimed to investigate the effects of short -and long-term mussel dredging on soft-bottom communities, in the Danish estuary, Lammefjorden, where the results showed temporal changes in the macrozoobenthic community between 1996 and 2025. Both Lammefjord and Holbæk Fjord exhibited declines in abundance and biodiversity over the study period, but statistical analysis revealed a significant difference between dredged and non-dredged areas in Lammefjorden. In contrast, no clear effect of dredging was observed in the biomass of both fjords, but this observation might have been due to limited data for comparison. A comparison with Isefjorden showed that the biomass of several important deposit-feeding species declined in both fjords, while other scavenger and suspension-feeding species became more dominant contributors to the community biomass,

suggesting that the changes documented in Lammefjord may reflect a broader reorganization of benthic communities within the Isefjord system. Finally, there was a significant difference in community structure and functional diversity between the intensively dredged Lammefjord and less intensively dredged Holbæk Fjord, with an increase in few dominating opportunistic species in Lammefjorden. Despite the observed decline in abundance in Lammefjorden, the trophic response in food availability for fish populations was difficult to determine, as several species described as important fish prey, were replaced by other potential food resources rather than being lost.

8. Management and future prospects

For future management, more consistent short term and long-term monitoring across dredged areas may help distinguish the differences between these two effects on soft-bottom ecosystems and improve our understanding of community recovery and resilience. It could also be interesting to combine benthic monitoring data with information on dredging intensity, oxygen conditions, eelgrass distributions and fish populations with hydrodynamic conditions, to explore a more holistic ecosystem response. Furthermore, the regulation and compliance of marine protected areas such as Natura-2000 and the new marine national parks (Tænketankenhav, 2025) needs to be better monitored and with more strict compliance.

Finally, continued engagement of local stakeholders and the public in monitoring and communicating the environmental conditions of the marine ecosystems may help with increasing public awareness and understanding of the importance in improving and protecting our marine ecosystems.

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10. Appendix

10.1 Tabel (S1). Species list and abundances in Lammefjord and Holbæk Fjord 1996-2025.

Lammefjord 1996		Lammefjord 2025		Holbæk Fjord 1996		Holbæk fjord 2025	
Species	(N)	Species	(N)	Species	(N)	Species	(N)
Alderia modesta	12	*Abra nitida*	1	*Alderia modesta*	1	*Abra nitida*	1
Alitta succinea	98	*Alitta succinea*	59	*Alitta grandis*	2	*Alitta succinea*	24
Alitta virens	1	*Ampharete sp.*	1	*Alitta succinea*	15	*Aoridae indet.*	4
Arenicola marina	3	*Annelida*	1	*Ampharete acutifrons*	1	*Apherusa bispinosa*	1
Ascidiacea indet.	3	*Aoridae indet.*	2	*Ampharete sp.*	1	*Arenicola marina*	7
Asterias rubens	1	*Arenicola marina*	7	*Anobothrus gracilis*	2	*Ascidiacea indet.*	40
Bylgides sarsi	10	*Asterias rubens*	3	*Arenicola marina*	1	*Asterias rubens*	1
Campanulariidae indet.	1	*Balanus improvisus*	62	*Asterias rubens*	2	*Bittium reticulatum*	62
Capitella capitata	846	*Bittium reticulatum*	12	*Bylgides sarsi*	3	*Botryllus schlosseri*	1
Cerastoderma glaucum	1	*Bivalvia*	2	*Campanulariidae indet.*	1	*Bryozoa indet.*	1
Chironomus aprilinus	2	*Capitella capitata*	26	*Capitella capitata*	280	*Capitella capitata*	8
Chironomus salinarius	955	*Capitellidae indet.*	2	*Cerastoderma edule*	1	*Capitellidae indet.*	2
Clunio balticus	4	*Carcinus maenas*	1	*Cerastoderma glaucum*	1	*Carcinus maenas*	1
Corbula gibba	13	*Cerastoderma edule*	1	*Chironomus salinarius*	481	*Cerastoderma edule*	11
Monoorophium insidiosum	1459	*Chironomidae indet.*	3	*Clunio balticus*	53	*Chironomidae indet.*	24
Dipolydora quadrilobata	1	*Ciona intestinalis*	1	*Corbula gibba*	5	*Corophium sp.*	1
Ecrobia ventrosa	51	*Corbula gibba*	5	*Monocorophium insidiosum*	305	*Electra crustulenta*	76
Electra crustulenta	2	*Corophium sp.*	1	*Dendrodoa grossularia*	99	*Ericthonius brasiliensis*	74
Ephydridae indet.	1	*Ericthonius brasiliensis*	3	*Dexamine spinosa*	2	*Exogone naidina*	3
Eteone longa	4	*Eteone longa*	1	*Ecrobia ventrosa*	82	*Fabricia stellaris*	3
Fabriciola baltica	19	*Exogone naidina*	10	*Electra crustulenta*	11	*Gammarus locusta*	72
Gammarus inaequicauda	8	*Gammarus locusta*	5	*Eteone longa*	6	*Harmothoe imbricata*	23
Gammarus oceanicus	12	*Haminella solitaria*	1	*Exogone sp.*	4	*Hediste diversicolor*	1
Gammarus sp.	1	*Harmothoe imbricata*	60	*Gammarus duebeni*	1	*Heteromastus filiformis*	1

				Gammarus			
Gammarus zaddachi	4	*Hediste diversicolor*	1	*inaequicauda*	1	*Hydrozoa indet.*	6
Halacaridae indet.	10	*Heteromastus filiformis*	2	*Gammarus oceanicus*	3	*Hyrdrobia sp.*	2
Harmothoe imbricata	4	*Hydrozoa indet.*	32	*Halacaridae indet.*	1	*Idotea chelipes*	18
Harmothoe impar	12	*Kurtiella bidentata*	3	*Halocladius sp.*	7	*Kurtiella bidentata*	14
Harpacticoida indet.	1	*Littorina saxatilis*	1	*Harmothoe imbricata*	2	*Lagis koreni*	1
Hesionidae indet.	1	*Gattyana amondseni*	1	*Harmothoe impar*	23	*Littorina littorea*	1
Heteromastus filiformis	7	*Mediomastus fragilis*	1	*Hediste diversicolor*	2	*Littorina saxatilis*	1
						Microdeutopus	
Idotea balthica	26	*Microdeutopus gryllotalpa*	128	*Heteromastus filiformis*	13	*gryllotalpa*	187
		Monocorophium					
Jaera albifrons	4	*insidiosum*	9	*Hydrobia neglecta*	8	*Microdeutopus sp.*	1
						Monocorophium	
Kefersteinia cirrata	2	*Musculus discors*	2	*Hydrobia sp.*	1	*insidiosum*	131
Kurtiella bidentata	2	*Musculus subpictus*	62	*Idotea balthica*	66	*Musculus discors*	2
Lagis koreni	1	*Mya arenaria*	162	*Jaera albifrons*	1	*Musculus subpictus*	4
Littorina saxatilis	1	*Mytilus edulis*	134	*Kefersteinia cirrata*	1	*Mya arenaria*	3
Macoma balthica	7	*Nematoda indet.*	61	*Kurtiella bidentata*	1	*Mytilus edulis*	2
Macoma calcarea	1	*Nemertini indet.*	11	*Littorina littorea*	1	*Nematoda indet.*	8
Mediomastus fragilis	1	*Nephtys hombergi*	6	*Littorina saxatilis*	111	*Odostomia acuta*	12
Microdeutopus							
gryllotalpa	200	*Nephtys sp.*	1	*Macoma balthica*	30	*Oligochaeta indet.*	4
Molgula manhattensis	1	*Nucula nitidosa*	1	*Mediomastus fragilis*	5	*Parvicardium ovale*	1
				Microdeutopus			
Musculus discors	17	*Odostomia acuta*	26	*gryllotalpa*	86	*Peringia ulvae*	331
Mytilus edulis	320	*Peringia ulvae*	2462	*Musculus discors*	50	*Platynereis dumerilii*	5
Nematoda indet.	1750	*Platynereis dumerilii*	11	*Mya arenaria*	2	*Polydora ciliata*	1
Nemertini indet.	33	*Polydora ciliata*	5	*Mytilus edulis*	60	*Polydora cornuta*	24
Neomysis integer	2	*Polydora cornuta*	65	*Nematoda indet.*	1237	*Praunus inermis*	2
						Pseudopolydora	
Nephtys hombergii	2	*Pusillina sarsii*	12	*Nemertini indet.*	40	*antennata*	3
Notomastus latericeus	1	*Pygospio elegans*	218	*Nephtys hombergii*	2	*Pusillina sarsii*	48
Ophelia rathkei	1	*Retusa obtusa*	3	*Ophelia rathkei*	3	*Pygospio elegans*	60
Parvicardium							
pinnulatum	78	*Rissoa membranacea*	4	*Parvicardium hauniense*	2	*Rissoa membranacea*	26
				Parvicardium			
Peringia ulvae	210	*Scoloplos armiger*	27	*pinnulatum*	47	*Scoloplos armiger*	5
Philine aperta	5	*Spio filicornis*	7	*Peringia ulvae*	224	*Spirorbis corallinae*	101
Pholoe inornata	105	*Spionidae indet.*	2	*Pholoe inornata*	66	*Spirorbis spirorbis*	317
Platynereis dumerilii	55	*Stenothoe monoculoides*	1	*Platynereis dumerilii*	54	*Streblospio shrubsolii*	1
Polydora ciliata	13	*Streblospio shrubsolii*	5	*Polydora ciliata*	2	*Syllidae indet.*	1
Polydora cornuta	871	*Tritia reticulata*	42	*Polydora cornuta*	220	*Tritia reticulata*	12
Procladius sp.	1	*Tubificoides benedii*	5	*Procladius sp.*	1	*Tubificoides benedii*	27

Pusillina sarsii	2516		*Pusillina sarsii*	516	*Venerupis corrugata* 1
Pygospio elegans	65		*Pygospio elegans*	86	
Pyralidae indet.	1		*Rissoa membranacea*	17	
Retusa obtusa	9		*Scoloplos armiger*	154	
Scoloplos armiger	51		*Scrobicularia plana*	1	
Spio filicornis	1		*Syllidia armata*	100	
Spionidae indet.	1		*Tricladida indet.*	1	
Syllidia armata	49		*Tubificoides benedii*	373	
Tubificoides benedii	433		*Turbellaria indet.*	1	
Tubificoides sp.	1				
Tunicata indet.	2				
Total (n) of individuals	10387	3783		4982	1805

10.2 Tabel (S2). Change in community structure in Lammefjord and Holbæk Fjord 1996-2025, showing lost, new and shared species between fjords and within the same fjord on a special and temporal scale.

Fjord	1996-2025	Species list
Lammefjord	Lost	*Alderia modesta*
Lammefjord	Lost	*Alitta virens*
Lammefjord	Lost	*Ascidiacea indet.*
Lammefjord	Lost	*Bylgides sarsi*
Lammefjord	Lost	*Campanulariidae indet.*
Lammefjord	Lost	*Cerastoderma glaucum*
Lammefjord	Lost	*Chironomus aprilinus*
Lammefjord	Lost	*Chironomus salinarius*
Lammefjord	Lost	*Clunio balticus*
Lammefjord	Lost	*Dipolydora quadrilobata*
Lammefjord	Lost	*Ecrobia ventrosa*
Lammefjord	Lost	*Electra crustulenta*
Lammefjord	Lost	*Ephydridae indet.*
Lammefjord	Lost	*Fabriciola baltica*
Lammefjord	Lost	*Gammarus inaequicauda*
Lammefjord	Lost	*Gammarus oceanicus*
Lammefjord	Lost	*Gammarus sp.*
Lammefjord	Lost	*Gammarus zaddachi*
Lammefjord	Lost	*Halacaridae indet.*
Lammefjord	Lost	*Harmothoe impar*
Lammefjord	Lost	*Harpacticoida indet.*
Lammefjord	Lost	*Hesionidae indet.*

Lammefjord	Lost	*Idotea balthica*
Lammefjord	Lost	*Jaera albifrons*
Lammefjord	Lost	*Kefersteinia cirrata*
Lammefjord	Lost	*Lagis koreni*
Lammefjord	Lost	*Macoma balthica*
Lammefjord	Lost	*Macoma calcarea*
Lammefjord	Lost	*Molgula manhattensis*
Lammefjord	Lost	*Neomysis integer*
Lammefjord	Lost	*Notomastus latericeus*
Lammefjord	Lost	*Ophelia rathkei*
Lammefjord	Lost	*Parvicardium pinnulatum*
Lammefjord	Lost	*Philine aperta*
Lammefjord	Lost	*Pholoe inornata*
Lammefjord	Lost	*Procladius sp.*
Lammefjord	Lost	*Pyralidae indet.*
Lammefjord	Lost	*Syllidia armata*
Lammefjord	Lost	*Tubificoides sp.*
Lammefjord	Lost	*Tunicata indet.*
Lammefjord	Lost	*Turbellaria indet.*
Total	41	
Holbæk Fjord	Lost	*Alderia modesta*
Holbæk Fjord	Lost	*Alitta grandis*
Holbæk Fjord	Lost	*Ampharete acutifrons*
Holbæk Fjord	Lost	*Ampharete sp.*
Holbæk Fjord	Lost	*Anobothrus gracilis*
Holbæk Fjord	Lost	*Bylgides sarsi*
Holbæk Fjord	Lost	*Campanulariidae indet.*
Holbæk Fjord	Lost	*Cerastoderma edule*
Holbæk Fjord	Lost	*Chironomus salinarius*
Holbæk Fjord	Lost	*Clunio balticus*
Holbæk Fjord	Lost	*Corbula gibba*
Holbæk Fjord	Lost	*Dendrodoa grossularia*
Holbæk Fjord	Lost	*Dexamine spinosa*
Holbæk Fjord	Lost	*Ecrobia ventrosa*
Holbæk Fjord	Lost	*Eteone longa*
Holbæk Fjord	Lost	*Exogone sp.*
Holbæk Fjord	Lost	*Gammarus duebeni*
Holbæk Fjord	Lost	*Gammarus inaequicauda*
Holbæk Fjord	Lost	*Gammarus oceanicus*
Holbæk Fjord	Lost	*Halacaridae indet.*
Holbæk Fjord	Lost	*Halocladius sp.*

Holbæk Fjord	Lost	*Harmothoe impar*
Holbæk Fjord	Lost	*Hydrobia neglecta*
Holbæk Fjord	Lost	*Idotea balthica*
Holbæk Fjord	Lost	*Jaera albifrons*
Holbæk Fjord	Lost	*Kefersteinia cirrata*
Holbæk Fjord	Lost	*Macoma balthica*
Holbæk Fjord	Lost	*Mediomastus fragilis*
Holbæk Fjord	Lost	*Nemertini indet.*
Holbæk Fjord	Lost	*Nephtys hombergii*
Holbæk Fjord	Lost	*Ophelia rathkei*
Holbæk Fjord	Lost	*Parvicardium hauniense*
Holbæk Fjord	Lost	*Parvicardium pinnulatum*
Holbæk Fjord	Lost	*Pholoe inornata*
Holbæk Fjord	Lost	*Procladius sp.*
Holbæk Fjord	Lost	*Scrobicularia plana*
Holbæk Fjord	Lost	*Syllidia armata*
Holbæk Fjord	Lost	*Tricladida indet.*
Holbæk Fjord	Lost	*Turbellaria indet.*
Total	40	
Lammefjord	New	*Abra nitida*
Lammefjord	New	*Ampharete sp.*
Lammefjord	New	*Annelida*
Lammefjord	New	*Aoridae indet.*
Lammefjord	New	*Balanus improvisus*
Lammefjord	New	*Bittium reticulatum*
Lammefjord	New	*Bivalvia*
Lammefjord	New	*Capitellidae indet.*
Lammefjord	New	*Carcinus maenas*
Lammefjord	New	*Cerastoderma glaucun*
Lammefjord	New	*Chironomidae indet.*
Lammefjord	New	*Ciona intestinalis*
Lammefjord	New	*Corophium sp.*
Lammefjord	New	*Ericthonius brasiliensis*
Lammefjord	New	*Exogone naidina*
Lammefjord	New	*Gammarus locusta*
Lammefjord	New	*Gattyana amondseni*
Lammefjord	New	*Haminella solitaria*
Lammefjord	New	*Hediste diversicolor*
Lammefjord	New	*Hydrozoa indet.*
Lammefjord	New	*Musculus subpictus*
Lammefjord	New	*Mya arenaria*

Lammefjord	New	*Nephtys sp.*
Lammefjord	New	*Nucula nitidosa*
Lammefjord	New	*Odostomia acuta*
Lammefjord	New	*Rissoa membranacea*
Lammefjord	New	*Stenothoe monoculoides*
Lammefjord	New	*Streblospio shrubsolii*
Lammefjord	New	*Tritia reticulata*
Total	29	
Holbæk Fjord	New	*Abra nitida*
Holbæk Fjord	New	*Aoridae indet.*
Holbæk Fjord	New	*Apherusa bispinosa*
Holbæk Fjord	New	*Ascidiacea indet.*
Holbæk Fjord	New	*Bittium reticulatum*
Holbæk Fjord	New	*Botryllus schlosseri*
Holbæk Fjord	New	*Bryozoa*
Holbæk Fjord	New	*Capitellidae indet.*
Holbæk Fjord	New	*Carcinus maenas*
Holbæk Fjord	New	*Chironomidae indet.*
Holbæk Fjord	New	*Corophium sp.*
Holbæk Fjord	New	*Ericthonius brasiliensis*
Holbæk Fjord	New	*Exogone naidina*
Holbæk Fjord	New	*Fabricia stellaris*
Holbæk Fjord	New	*Gammarus locusta*
Holbæk Fjord	New	*Hydrozoa indet.*
Holbæk Fjord	New	*Idotea chelipes*
Holbæk Fjord	New	*Lagis koreni*
Holbæk Fjord	New	*Microdeutopus sp.*
Holbæk Fjord	New	*Musculus subpictus*
Holbæk Fjord	New	*Odostomia acuta*
Holbæk Fjord	New	*Oligochaeta indet.*
Holbæk Fjord	New	*Parvicardium ovale*
Holbæk Fjord	New	*Praunus inermis*
Holbæk Fjord	New	*Pseudopolydora antennata*
Holbæk Fjord	New	*Spirorbis corallinae*
Holbæk Fjord	New	*Spirorbis spirorbis*
Holbæk Fjord	New	*Streblospio shrubsolii*
Holbæk Fjord	New	*Syllidae indet.*
Holbæk Fjord	New	*Tritia reticulata*
Holbæk Fjord	New	*Venerupis corrugata*
Total	32	

Lammefjord	Both years	*Alitta succinea*
Lammefjord	Both years	*Arenicola marina*
Lammefjord	Both years	*Asterias rubens*
Lammefjord	Both years	*Capitella capitata*
Lammefjord	Both years	*Corbula gibba*
Lammefjord	Both years	*Eteone longa*
Lammefjord	Both years	*Harmothoe imbricata*
Lammefjord	Both years	*Heteromastus filiformis*
Lammefjord	Both years	*Kurtiella bidentata*
Lammefjord	Both years	*Littorina saxatilis*
Lammefjord	Both years	*Mediomastus fragilis*
Lammefjord	Both years	*Microdeutopus gryllotalpa*
Lammefjord	Both years	*Monocorophium insidiosum*
Lammefjord	Both years	*Musculus discors*
Lammefjord	Both years	*Mytilus edulis*
Lammefjord	Both years	*Nematoda indet.*
Lammefjord	Both years	*Nemertini indet.*
Lammefjord	Both years	*Nephtys hombergii*
Lammefjord	Both years	*Peringia ulvae*
Lammefjord	Both years	*Platynereis dumerilii*
Lammefjord	Both years	*Polydora ciliata*
Lammefjord	Both years	*Polydora cornuta*
Lammefjord	Both years	*Pusillina sarsii*
Lammefjord	Both years	*Pygospio elegans*
Lammefjord	Both years	*Retusa obtusa*
Lammefjord	Both years	*Scoloplos armiger*
Lammefjord	Both years	*Spio filicornis*
Lammefjord	Both years	*Spionidae indet.*
Lammefjord	Both years	*Tubificoides benedii*
Total	29	
Holbæk Fjord	Both years	*Alitta succinea*
Holbæk Fjord	Both years	*Arenicola marina*
Holbæk Fjord	Both years	*Asterias rubens*
Holbæk Fjord	Both years	*Capitella capitata*
Holbæk Fjord	Both years	*Cerastoderma glaucum*
Holbæk Fjord	Both years	*Electra crustulenta*
Holbæk Fjord	Both years	*Harmothoe imbricata*
Holbæk Fjord	Both years	*Hediste diversicolor*
Holbæk Fjord	Both years	*Heteromastus filiformis*
Holbæk Fjord	Both years	*Hydrobia sp.*

Holbæk Fjord	Both years	*Kurtiella bidentata*
Holbæk Fjord	Both years	*Littorina littorea*
Holbæk Fjord	Both years	*Littorina saxatilis*
Holbæk Fjord	Both years	*Microdeutopus gryllotalpa*
Holbæk Fjord	Both years	*Monocorophium insidiosum*
Holbæk Fjord	Both years	*Musculus discors*
Holbæk Fjord	Both years	*Mya arenaria*
Holbæk Fjord	Both years	*Mytilus edulis*
Holbæk Fjord	Both years	*Nematoda indet.*
Holbæk Fjord	Both years	*Peringia ulvae*
Holbæk Fjord	Both years	*Platynereis dumerilii*
Holbæk Fjord	Both years	*Polydora ciliata*
Holbæk Fjord	Both years	*Polydora cornuta*
Holbæk Fjord	Both years	*Pusillina sarsii*
Holbæk Fjord	Both years	*Pygospio elegans*
Holbæk Fjord	Both years	*Rissoa membranacea*
Holbæk Fjord	Both years	*Scoloplos armiger*
Holbæk Fjord	Both years	*Tubificoides benedii*
Total	29	
Both fjords	2025	*Abra nitida*
Both fjords	2025	*Alitta succinea*
Both fjords	2025	*Aoridae indet.*
Both fjords	2025	*Arenicola marina*
Both fjords	2025	*Asterias rubens*
Both fjords	2025	*Bittium reticulatum*
Both fjords	2025	*Capitella capitata*
Both fjords	2025	*Capitellidae indet.*
Both fjords	2025	*Carcinus maenas*
Both fjords	2025	*Chironomidae indet.*
Both fjords	2025	*Corophium sp.*
Both fjords	2025	*Ericthonius brasiliensis*
Both fjords	2025	*Exogone naidina*
Both fjords	2025	*Gammarus locusta*
Both fjords	2025	*Harmothoe imbricata*
Both fjords	2025	*Hediste diversicolor*
Both fjords	2025	*Heteromastus filiformis*
Both fjords	2025	*Hydrozoa indet.*
Both fjords	2025	*Kurtiella bidentata*
Both fjords	2025	*Littorina saxatilis*
Both fjords	2025	*Microdeutopus gryllotalpa*
Both fjords	2025	*Monocorophium insidiosum*

Both fjords	2025	*Musculus discors*
Both fjords	2025	*Musculus subpictus*
Both fjords	2025	*Mya arenaria*
Both fjords	2025	*Mytilus edulis*
Both fjords	2025	*Nematoda indet.*
Both fjords	2025	*Odostomia acuta*
Both fjords	2025	*Peringia ulvae*
Both fjords	2025	*Platynereis dumerilii*
Both fjords	2025	*Polydora ciliata*
Both fjords	2025	*Polydora cornuta*
Both fjords	2025	*Pusillina sarsii*
Both fjords	2025	*Pygospio elegans*
Both fjords	2025	*Rissoa membranacea*
Both fjords	2025	*Scoloplos armiger*
Both fjords	2025	*Streblospio shrubsolii*
Both fjords	2025	*Tritia reticulata*
Both fjords	2025	*Tubificoides benedii*
Total	40	
Both fjords	1996	*Alderia modesta*
Both fjords	1996	*Alitta succinea*
Both fjords	1996	*Arenicola marina*
Both fjords	1996	*Asterias rubens*
Both fjords	1996	*Bylgides sarsi*
Both fjords	1996	*Campanulariidae indet.*
Both fjords	1996	*Capitella capitata*
Both fjords	1996	*Cerastoderma glaucum*
Both fjords	1996	*Chironomus salinarius*
Both fjords	1996	*Clunio balticus*
Both fjords	1996	*Corbula gibba*
Both fjords	1996	*Ecrobia ventrosa*
Both fjords	1996	*Electra crustulenta*
Both fjords	1996	*Eteone longa*
Both fjords	1996	*Gammarus inaequicauda*
Both fjords	1996	*Gammarus oceanicus*
Both fjords	1996	*Halacaridae indet.*
Both fjords	1996	*Harmothoe imbricata*
Both fjords	1996	*Harmothoe impar*
Both fjords	1996	*Heteromastus filiformis*
Both fjords	1996	*Idotea balthica*
Both fjords	1996	*Jaera albifrons*
Both fjords	1996	*Kefersteinia cirrata*

Both fjords	1996	*Kurtiella bidentata*
Both fjords	1996	*Littorina saxatilis*
Both fjords	1996	*Macoma balthica*
Both fjords	1996	*Mediomastus fragilis*
Both fjords	1996	*Microdeutopus gryllotalpa*
Both fjords	1996	*Monocorophium insidiosum*
Both fjords	1996	*Musculus discors*
Both fjords	1996	*Mytilus edulis*
Both fjords	1996	*Nematoda indet.*
Both fjords	1996	*Nemertini indet.*
Both fjords	1996	*Nephtys hombergii*
Both fjords	1996	*Ophelia rathkei*
Both fjords	1996	*Parvicardium pinnulatum*
Both fjords	1996	*Peringia ulvae*
Both fjords	1996	*Pholoe inornata*
Both fjords	1996	*Platynereis dumerilii*
Both fjords	1996	*Polydora ciliata*
Both fjords	1996	*Polydora cornuta*
Both fjords	1996	*Procladius sp.*
Both fjords	1996	*Pusillina sarsii*
Both fjords	1996	*Pygospio elegans*
Both fjords	1996	*Scoloplos armiger*
Both fjords	1996	*Syllidia armata*
Both fjords	1996	*Tubificoides benedii*
Both fjords	1996	*Turbellaria indet.*
Total	48	