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Deep Fjords Are Excellent Natural Infrastructure for Climate Impact Studies

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ABSTRACT

Fjords provide valuable research opportunities for marine scientists. They are excellent natural infrastructure for climate impact studies associated with hypoxic episodes and consequences for mesopelagic and deep-sea ecosystems involving oceanographic circulation processes and basin water renewals. Repeated sampling from the same populations is possible, making fjords excellent systems for developing time series of data for climate impact studies. We provide an overview of the 14 years of data from Norwegian West Coast fjords, focusing on Masfjorden, and report major findings from Oslofjorden in Eastern Norway, exhibiting recurrent hypoxia in the basin waters. We document that the oxygen levels in Masfjorden decreased rapidly by over 60% at 450 m depth in < 8 years, which is much faster than the average rate of deoxygenation in the global ocean. We also discuss the increase in the deep-sea and low-light-adapted coronate jellyfish *Periphylla periphylla* in view of altered optical conditions of the basin water potentially related to deoxygenation. We argue that fjords like Masfjorden and Oslofjorden are not only macrocosms for ecological processes but also are likely an accelerated version of deep oceans with respect to climate impacts.

1 | Introduction

Landscapes above the sea surface make fjords attractive tourist destinations, sheltered locations allow fish farming, while fjord habitat conditions below the sea surface are often less known but provide valuable research opportunities for marine scientists. Fjords are glacial landforms common in temperate and polar regions including Norway, Alaska, Canada, Greenland, Iceland and Scotland in the northern hemisphere, and Argentina, Chile, New Zealand, and Antarctica, in the southern hemisphere. Natural

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Etymology of Ghoti: George Bernard Shaw (1856–1950), polymath, playwright, Nobel prize winner, and the most prolific letter writer in history, was an advocate of English spelling reform. He was reportedly fond of pointing out its absurdities by proving that 'fish' could be spelt 'ghoti'. That is: 'gh' as in 'rough', 'o' as in 'women' and 'ti' as in palatial.

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history studies of fjords have been going on for centuries (see overview for Norwegian waters in Brattegard et al. 2011). Recent climate impact studies have begun to investigate consequences of water column darkening (i.e., reduced light penetration) for mesopelagic regime shifts (Aksnes et al. 2009) and deoxygenation of the basin water of shallow-sill fjords (Aksnes et al. 2019; Darelius 2020; Johnsen, Loeng, and Myksvoll 2024).

Sill fjords are sites where deoxygenation linked to ocean warming is particularly common (Pitcher et al. 2021). Signals of oxygen loss are apparent in the benthic deep macrofauna, where typical opportunistic species characteristic of areas of hypoxia and sediments rich in organic matter occur (Levin et al. 2009; Johansen et al. 2018). Pelagic fishes and zooplankton monitored acoustically in shallow fjords appear adapted to variations in the oxygen conditions and change their behaviours to cope with varying oxygen concentrations both in the Pacific and Atlantic regions (Parker-Stetter, Horne, and Langness 2009; Solberg, Røstad, and Kaartvedt 2015). How mesopelagic and deep-sea ecosystems within deep fjord basins cope with oxygen loss and variations in oxygen concentrations is less known. Mesopelagic fishes are the largest unexploited vertebrate groups on earth (Gjøsæter and Kawaguchi 1980; Irigoien et al. 2014) and are abundant in West Norwegian fjords (Giske et al. 1990; Kaartvedt, Staby, and Aksnes 2012). Such fjord populations are close to the ideal units for studies of growth, mortality, life span and succession of generations as they often constitute semi-isolated components of oceanic species with limited connection to other populations (Bagøien et al. 2001; Brattegard et al. 2011). Time-series of data from such fjord populations may thus be valuable for studies of biological processes relevant for the open ocean, where repeated sampling from the same populations is difficult.

Fjords vary in morphometry and environmental conditions. Many are wide and/or shallow, whereas others are narrow and long, with steep sides and deep inlets carved out by glaciers. They were filled with seawater after the Younger Dryas ice sheet advance that reached its maximum around 11,600 years ago. Masfjorden, a fjord near Bergen (Figure 1A), was deglaciated 11,300 years ago (Mangerud et al. 2019). Many Norwegian west coast fjords are deep enough to support mesopelagic fish, crustaceans, deep-water jellyfishes like *Periphylla periphylla*, and deep-sea benthic communities. At the entrance of deep fjords there is typically a topographic barrier made by a sill. The sill isolates the deep-basin waters from waters outside the fjord (Inall and Gillibrand 2010; Aksnes et al. 2019; Figure 1B). As respiration continues below the euphotic zone and below shallow sills, oxygen losses can be notable in the basin water if the renewal rate decreases or if organic inputs increase through urbanisation, fish farming or other human-related activities.

Deoxygenation has become a big concern worldwide (Diaz and Rosenberg 2008; Keeling, Körtzinger, and Gruber 2010; Breitburg et al. 2018; Levin 2018). Open ocean as well as coastal waters have lost oxygen over the past 50 years (Keeling, Körtzinger, and Gruber 2010; Gilbert 2017; Schmidtko, Stramma, and Visbeck 2017; Oschlies et al. 2017) and the loss is particularly prevalent along continental margins and in enclosed seas and fjords (Pitcher et al. 2021). Works suggest that deoxygenation and coastal hypoxic events are linked to shifts in atmospheric circulation, rising greenhouse gas emissions, oceanic warming, and increased stratification (Straneo et al. 2016; Pérez-Santos et al. 2018; Aksnes et al. 2019; Jackson et al. 2021; Linford et al. 2023). In fjords with shallow sills such changes lead to lower renewal frequency of the basin water below sill depth (Aksnes et al. 2019; Darelius 2020) compared to deep-silled fjords which are more directly connected to coastal water masses (Hannah et al. 2024). The renewal frequency in sill-fjords is also sensitive to changes in seawater density, and reduced density of the upper water column linked to ocean warming makes deoxygenation more rapid in such fjords. The mechanisms underlying naturally hypoxic sub-tropical eastern boundary upwelling ecosystems, such as in the Pacific and Southern Atlantic, are well known (Bograd et al. 2008; Moffitt et al. 2014; Pitcher et al. 2021). When, how, and why hypoxic events occur in temperate and Arctic coastal areas and fjords of the North Atlantic and their ecosystem consequences are not equally well known. *Fjords that are easily accessible represent natural infrastructure for climate impact studies where the effects of deoxygenation on ecosystems can be investigated.*

In addition to deoxygenation, studies suggest that climate change can make fjords prone to water darkening (i.e., reduced

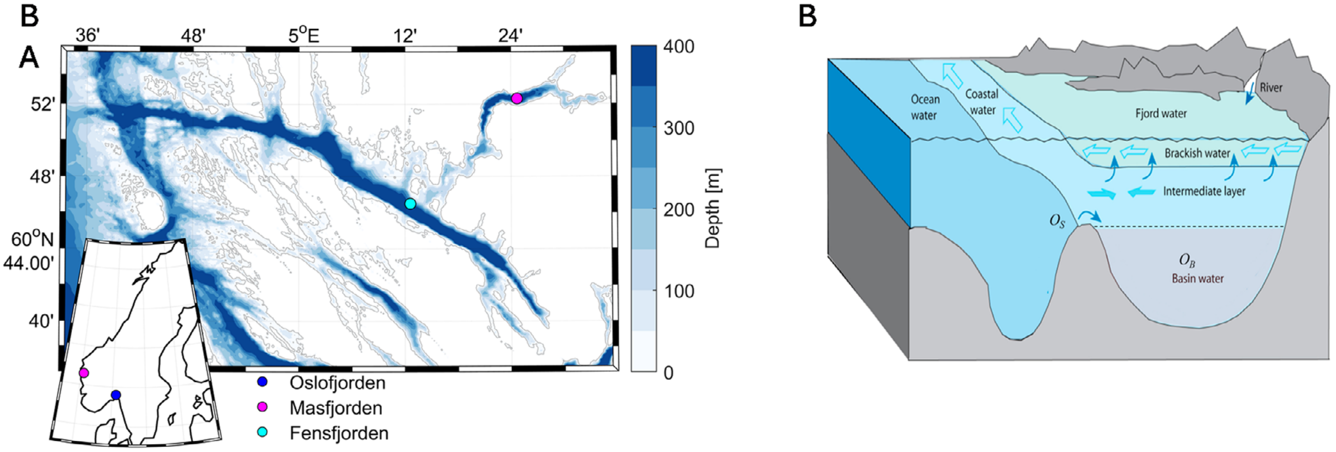

FIGURE 1 | (A) Map showing the location of study fjords; (B) A simplified illustration of fjord topography with three layers: a thin brackish layer at the top, a dynamic intermediate layer which extends down to the sill depth, and the basin water below the sill depth. O_B refers to dissolved oxygen of basin water and O_S to dissolved oxygen of the oceanic water (open access under the CCBY licence: Aksnes et al. 2019).

light penetration) (Aksnes et al. 2009; Frigstad et al. 2013; Opdal et al. 2023). Water darkening can alter competitive relationships and thereby ecosystem structure. For example, visual zooplanktivorous fishes have poor feeding success in dark water while the feeding success of tactile zooplanktivores such as jellyfish is unaffected by light availability (Sørnes and Aksnes 2004). One environmental driver linked to climate change and coastal water darkening is increased supplies of Coloured Dissolved Organic Matter (CDOM) of terrestrial origin (t-CDOM) transported to sea with rivers and run-off water (Aksnes et al. 2009; Larsen, Andersen, and Hessen 2011; Frigstad et al. 2013; Opdal et al. 2023). t-CDOM leads to darkening of the entire water column, including the mesopelagic habitat (Aksnes et al. 2009). Additional darkening can occur through locally produced CDOM (l-CDOM), produced below the depths mainly influenced by t-CDOM (Solås, Salvanes, and Aksnes 2024). l-CDOM production is likely associated with microbial degradation of organic matter—a process consuming oxygen, as is also suggested for parts of the mesopelagic ocean through the correlation between CDOM and apparent oxygen utilisation (Nelson and Siegel 2013). Stagnant basin waters with low oxygen concentrations might therefore have elevated l-CDOM concentrations. Solås, Salvanes, and Aksnes (2024) measured downwelling irradiance and the associated light attenuation in hypoxic and anoxic water in the 125 m deep Haugsværfjorden, a fjord that branches off from Masfjorden, and compared the measurements with the well-oxygenated upper 125 m in Masfjorden. These data showed increased light attenuation in the hypoxic and anoxic water (see Figure S1), likely due to elevated concentrations of CDOM produced locally in these layers (Solås, Salvanes, and Aksnes 2024). Water darkening, either associated with local deoxygenation (l-CDOM) or with terrestrial origin (t-CDOM) or both, can alter ecosystems from being dominated by fish to favour jellyfish. The abundance of visual planktivorous fishes and the mesopelagic food web structure of Norwegian fjords appear to be strongly affected by the optical qualities of the water column (Eiane et al. 1999; Aksnes et al. 2004). Compared to the open ocean, deep fjords represent a unique and inexpensive alternative to study the impacts of darkening and deoxygenation on the mesopelagic and deep-sea ecosystems.

Mesopelagic fishes carry out extensive diel vertical migrations (DVM) driven by light, and these pronounced vertical migrations bring organic material from the productive upper layer down into the mesopelagic zone, thus contributing to carbon sequestration (Davison et al. 2013; Bianchi et al. 2013; Irigoien et al. 2014; Saba et al. 2021; Aksnes et al. 2023). Together with invertebrates, these fishes are often visible on sonar as deep sound-scattering layers (SSLs). Daytime depths of SSLs are reported as being shallower in hypoxic water (Bianchi et al. 2013; Netburn and Koslow 2015; Klevjer et al. 2016), but are also observed deep into hypoxic water in the Pacific (Klevjer et al. 2016) and the Red Sea (Aksnes et al. 2023). Is shallowing occurring due to avoidance of hypoxia, or seeking better light conditions for visual feeding? According to the results of Aksnes et al. (2017), the depth positioning appears to be primarily regulated by light even in the hypoxic oceanic areas. In these areas, reduced light penetration and darker water appear to be associated with hypoxic water, which also Solås, Salvanes, and Aksnes (2024) report for fjords. Hence, fjords are suitable study sites for gaining major insights into how the depth distribution of DVM and mesopelagic fishes are affected by darkening and oxygen loss.

We have assessed the effects of hypoxia in moderately hypoxic fjords in western Norway, and in a periodically severely hypoxic and even anoxic basin water of the shallower inner Oslofjorden in eastern Norway. Our research group based at the University of Bergen (UiB) has benefited greatly from the short travel distance—only a few hours steaming by research ships—to our nearby fjord study sites. For 14 years, graduate students of the UiB Ocean Science field course have been sent out on the research vessel G.O. Sars and other ships; they visited Masfjorden, to collect paired biological and physical data. This data time-series allows for examination of how mesopelagic fish, crustaceans, and jellyfish responded to a period of oxygen loss, and a subsequent basin water renewal in this fjord. In eastern Norway, monitoring of a shallow fjord close to Oslo has provided valuable knowledge on the consequences of seasonal variability in oxygen and responses by krill, zooplankton and fish. Our data series includes full biological, acoustic and environmental sampling, and we have just begun analysing the material. Below we provide a few glimpses of pronounced changes in oxygen concentrations, abundance of jellyfish and predator–prey relationships.

2 | Basin Water Deoxygenation and Reoxygenation

Our environmental data set documents rapid oxygen loss rates in the deep basin of Masfjorden. These rates largely exceed what the general peer-reviewed literature reports on oxygen loss in the ocean (Figure 2). Global average oxygen loss was 2% over 50 years (Schmidtko, Stramma, and Visbeck 2017). At 300 m depth off California, a 20%–30% decline was measured over 23 years (1984–2006; Bograd et al. 2008). In < 8 years (between 2011 and 2018), the dissolved oxygen in Masfjorden, decreased rapidly with > 60% at 450 m depth (Figure 2), before a renewal event of the basin water occurred in April 2021. This event was followed by a new rapid deoxygenation that is still ongoing, with basin conditions likely to become hypoxic in 2026 if current rates of oxygen loss continue and no deepwater renewal event occurs.

3 | Deep-Water Jellyfish *Periphylla periphylla* Established

Our time series of trawl catch data from Masfjorden shows a change in the ecosystem from being dominated by mesopelagic fish, shrimps and krill to now also including high densities of the light-sensitive deepwater jellyfish *Periphylla periphylla* (Figure 3). This is an oceanic, mesopelagic species well adapted to the dark environment of the deep sea (Sørnes et al. 2007), and appears to establish in fjords dominated by water from the Norwegian Coastal Current, depending on optically conditioned retention related to fjord topography, light attenuation and photosensitivity (Sørnes et al. 2007; Bozman et al. 2017; Bozman, Aksnes, and Eiane 2018). Eiane et al. (1999) compared light levels and food web structures in two fjords (Masfjorden and Lurefjorden) back in the 1990s. Lurefjorden was (and still is) a fjord with high densities of *P. periphylla*. They found severely lower light flux in Lurefjorden compared to Masfjorden, where

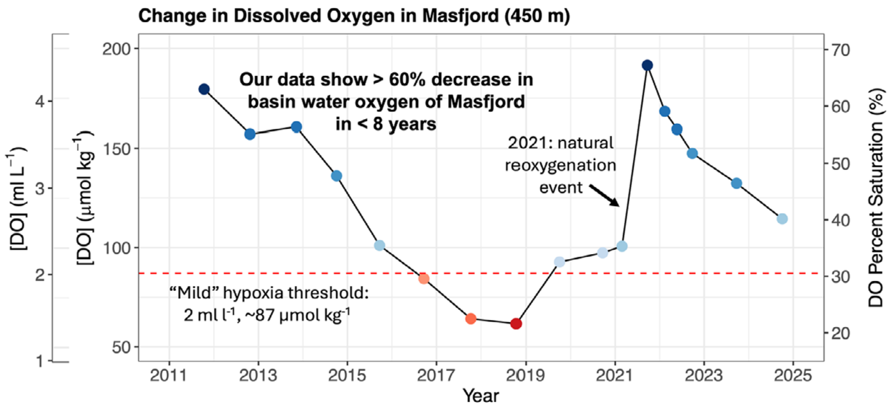

FIGURE 2 | Changes in dissolved oxygen in Masfjorden at 450 m depth from 2011 to 2024. Oxygen concentration was measured by CTD and converted to % saturation using temperature, salinity, and pressure conditions at 450 m. The threshold for mild hypoxia follows the definition of Hoffmann et al. (2011).

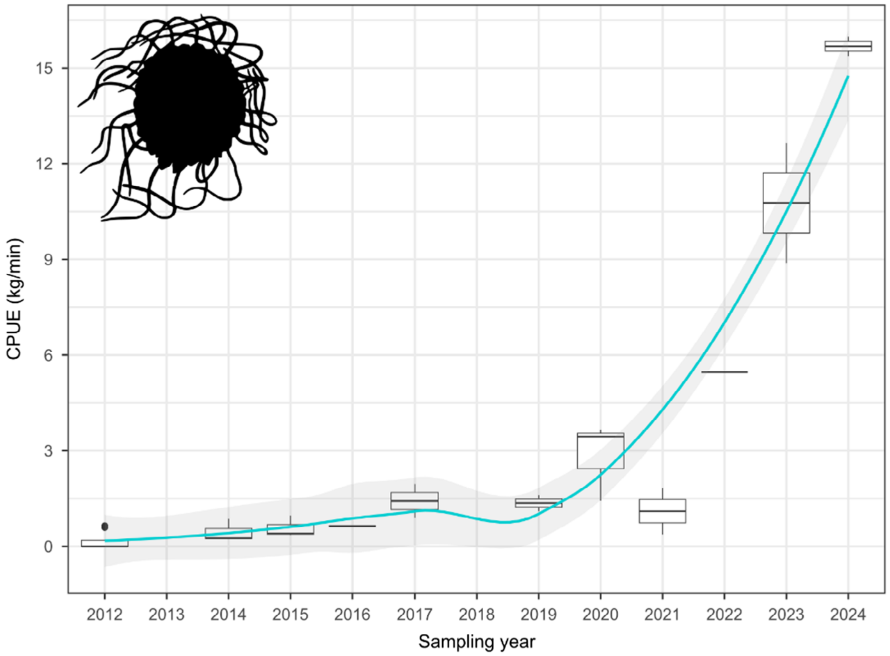

FIGURE 3 | Change in abundance measured as catch per unit of effort (kg of the jellyfish) *P. periphylla* caught per minute in Masfjorden from 2012 to 2024. The sampling was done at 450–350 m depth. The fitted line is a loess curve with 95% confidence intervals (shaded area).

P. periphylla was nearly absent at that time. It is not yet fully understood why *P. periphylla* in Norwegian waters occur in massive densities in some fjords and not in others, but our data on approximated light penetration from a light attenuation model indicate reduced light in deep waters where oxygen levels were low (Solås, Salvanes, and Aksnes 2024). Newly acquired data from the student cruise in 2023 suggest that *P. periphylla* now reproduces in Masfjorden based on the high abundance of reproductive adults captured in midwater tows, and early life stages captured in plankton tows.

4 | Hypoxia Affects the Individual Species as Well as Predator–Prey Relationships

The 150 m deep inner Oslofjord sustains populations of the krill *Meganyictiphanes norvegica* and overwintering *Calanus* spp., which occupy mesopelagic depths in clearer oceanic waters. Sprat (*Sprattus sprattus*) is a main predator of the copepods while gadoid fishes like cod (*Gadus morhua*) and whiting (*Merlangius merlangus*) prey on krill and sprat. Minimum oxygen tolerance of diapausing *Calanus* is 0.2–0.3 mL O_2 L^{-1}, while krill and sprat tolerate oxygen levels down to ~0.5 mL O_2 L^{-1} at 7°C–8°C (Kaartvedt, Røstad, and Klevjer 2009; Kaartvedt, Røstad, and Titelman 2021; Figure 4). The gadoids avoid waters with oxygen contents below ~15%–20% O_2 (<2 mL O_2 L^{-1}), so that krill and sprat have a potential refuge from their predators defined by relative oxygen tolerances.

Mortality is very low for *Calanus* in the lowest tolerable oxygen environment. However, as they move upwards with the progression of hypoxia, they come into the reach of short-term feeding excursions of sprat, with copepod mortality increasing (Solberg and Kaartvedt 2017; Kaartvedt, Røstad, and Titelman 2021).

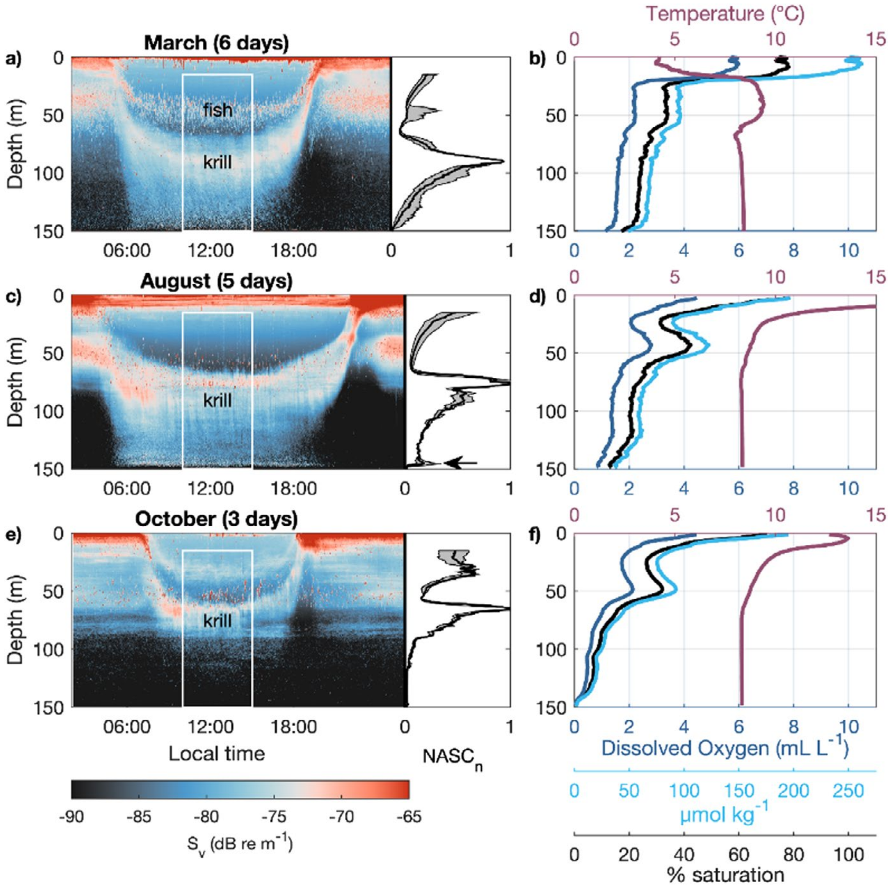

FIGURE 4 | Time series of backscatter, dissolved oxygen and temperature in the Oslofjord in 2020 showing a decrease in deep water oxygen concentration and corresponding upwards shift in krill scattering layers. (a, d, e) Averaged diel echograms and daytime (indicated by boxes) normalised integrated backscatter (NASC$_n$; grey shading: Interquartiles, black line: Median) based on several days of recording in March, August and October. The arrow in (c) indicates a peak in backscatter above the thin oxygen-poor bottom layer devoid of backscatter. (b, d, f) Dissolved oxygen and temperature profiles based on single CTD profiles around the acoustic recordings. Backscatter was recorded with a surface-facing 200 kHz WBAT (EK80 Wideband autonomous transceiver, Kongsberg) deployed on the bottom and mostly represents scattering layers of krill and fish. For details on the WBAT and CTD measurements see Appendix S1 and Christiansen et al. (2024).

5 | Benefits From Time-Series of Data

There is a lack of systematic sampling of entire water columns and time series of data from fjords. Long-term monitoring of environmental variables has occurred at coastal stations in Norwegian waters (Sætre, Aure, and Gade 2010). With these observations warming and oxygen loss have both been detected over the last 30 years. Such data were used to model the density distribution of the water masses on the coast and in a fjord, and the data suggest reduced frequency of basin water renewal (Aksnes et al. 2019; Darelius 2020).

While the CALCOFI program (California Cooperative Oceanic Fisheries Investigations) has sampled dissolved oxygen of the California Current System, including coastal basins, since 1950 (e.g., Gallo et al. 2019), the Norwegian Ministry of Fisheries only recently began full-depth monitoring for oxygen levels in selected west Norwegian fjords (since 2019). The longer monitoring series at coastal stations (Sætre, Aure, and Gade 2010) include only the basic oceanographic variables like salinity and temperature. There is no tradition for generating extensive time series and standardised sampling of biological data from the coast and the fjords. To our knowledge, the 14-year-long time series from Masfjorden is the first comprehensive biological/ecological time-series of data available from a fjord, and that includes sampling the mesopelagic habitat.

Commercial fish stocks are managed based on time series of data, but in the North Atlantic, these are used to manage fisheries in the open seas where oxygen loss is not a problem. In the Baltic Sea which is naturally prone to hypoxia (and where deoxygenation is exacerbated by human activity), monitoring also involves oxygen as this severely influences ecosystem function and fish production (Limburg and Casini 2018; Carstensen and Conley 2019). Since the oxygen loss is particularly high along continental margins and in enclosed seas and fjords (e.g., Pitcher et al. 2021), it is now time to focus more on coastal and fjord studies and climate impacts.

The overall objective of our work is to provide new knowledge on the effects of oxygen loss and reduced light on life histories, distribution, behaviour and trophic interactions of mesopelagic and demersal communities, utilising Norwegian fjords as natural infrastructure. While each fjord is different, they offer opportunity for replicating studies of processes (e.g., response to deoxygenation and reduced light) in a single geographical region. Our 14-year dataset, which is constantly extended with additional field campaigns, is proving to be extremely valuable to investigate the effects of deoxygenation and coastal water darkening on populations of mesopelagic fish and jellyfish, as well as ecosystem structure, functioning, variation, and change. We can compare across fjords that differ in basin water oxygen levels and in water clarity. For Masfjorden, our data allow us to study changes in a well-documented ecosystem before, during and after the fjord turned hypoxic and changes following basin water reoxygenation—including a recent massive increase in the abundance of *P. periphylla*. Our secondary objectives are to study the effects of the environmental drivers on vertical migration behaviours of mesopelagic fish species, their visual pelagic predators and demersal fish, as well as recruitment variability and population vital rates of the understudied mesopelagic fish.

6 | Conclusions

The unique 'natural infrastructure' we have in fjords allows for generating time series of data for basic ecological and climate change impact studies of biological processes that are relevant for open ocean species where repeated sampling from the same populations are difficult. Deep Norwegian West Coast fjords contains an ecosystem with physical and biological processes like those of large oceanic ecosystems, including hosting large populations of mesopelagic fishes. As the environmental and ecological changes appear faster in fjords than in the open ocean, fjords like Masfjorden and Oslofjorden may not only be considered as macrocosms for ecological processes, but might also be considered as accelerated versions of deep oceans with respect to climate impacts similar to Reusch et al. (2018) arguing for the Baltic Sea to be viewed as a 'time machine for the future coastal ocean'.

Additionally, deep fjords are useful study sites for mesopelagic fishes, which globally represent a huge marine biomass that is considered for future harvesting but for which vital rates and the effects of abiotic and biotic stressors on recruitment, growth, and survival are not yet known (St. John et al. 2016; Standal and Grimaldo 2020). Compared to the open ocean, mesopelagic fish populations contained in fjords represent an easily accessible, inexpensive opportunity for gaining knowledge of recruitment, mortality, growth, and DVM behaviour. Such knowledge is valuable also for a deeper understanding of the open ocean where repeated sampling from the same population is challenging and expensive. Hypoxic/anoxic deep waters might moreover open the avenue for novel process studies. Røstad and Kaartvedt (2013) assessed the seasonal and diel patterns in the sedimentary flux of krill faecal pellets. Even individual sinking pellets were recorded acoustically since the low-oxygen water below the krill habitat excluded targets with the ability to swamp the weak acoustic signals from the pellets. Any deeper fjords offering corresponding opportunities for studies of mesopelagic fish might be an asset in unveiling the passive and active role of mesopelagic fishes for vertical carbon flux (cf. Saba et al. 2021). Fjords represent a valuable tool to assess the impacts of environmental drivers on populations and ecosystems.

Acknowledgements

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The physical data are available in the repository of the Norwegian Marine Data Center: Darelius E, Salvanes AGV, Folkvord A, Daae K, Asplin L 2023. Physical, biogeochemical and biological data from Masfjorden, Lurefjorden and neighbouring fjords in Vestland, Norway https://doi.org/10.21335/NMDC-92774636. The biological data will be available upon request to the corresponding author.

References

Aksnes, D. L., J. Aure, P. O. Johansen, G. H. Johnsen, and A. G. Vea Salvanes. 2019. "Multi-Decadal Warming of Atlantic Water and Associated Decline of Dissolved Oxygen in a Deep Fjord." *Estuarine, Coastal and Shelf Science* 228: 106392. https://doi.org/10.1016/j.ecss.2019.106392.

Aksnes, D. L., N. Dupont, A. Staby, Ø. Fiksen, S. Kaartvedt, and J. Aure. 2009. "Coastal Water Darkening and Implications for Mesopelagic Regime Shifts in Norwegian Fjords." *Marine Ecology Progress Series* 387: 39–49.

Aksnes, D. L., A. S. Løtvedt, C. Lindemann, et al. 2023. "Effects of Migrating Mesopelagic Fishes on the Biological Carbon Pump." *Marine Ecology Progress Series* 717: 107–126. https://doi.org/10.3354/meps14373.

Aksnes, D. L., J. Nejstgaard, E. Sædberg, and T. Sørnes. 2004. "Optical Control of Fish and Zooplankton Populations." *Limnology and Oceanography* 49: 233–238.

Aksnes, D. L., A. Røstad, S. Kaartvedt, U. Martinez, C. M. Duarte, and X. Irigoien. 2017. "Light Penetration Structures the Deep Acoustic Scattering Layers in the Global Ocean." *Science Advances* 3: e1602468.

Bagøien, E., S. Kaartvedt, D. L. Aksnes, and K. Eiane. 2001. "Vertical Distribution and Mortality of Overwintering Calanus." *Limnology and Oceanography* 46: 1494–1510.

Bianchi, D., E. D. Galbraith, D. A. Carozza, K. A. S. Mislan, and C. A. Stock. 2013. "Intensification of Open-Ocean Oxygen Depletion by Vertically Migrating Animals." *Nature Geoscience Letters* 6: 545–548. https://doi.org/10.1038/NGEO1837.

Bograd, S. J., C. G. Castro, E. di Lorenzo, et al. 2008. "Oxygen Declines and the Shoaling of the Hypoxic Boundary in the California Current." *Geophysical Research Letters* 35: L12607. https://doi.org/10.1029/2008GL034185.

Bozman, A., D. L. Aksnes, and K. Eiane. 2018. "First Reports of a Mass Mortality Event Across Multiple Life Stages in a Mesopelagic Jellyfish in High Latitude Coastal Waters." *Marine Ecology* 39, no. 2: e12498.

Bozman, A., J. Titelman, S. Kaartvedt, K. Eiane, and D. L. Aksnes. 2017. "Jellyfish Distribute Vertically According to Irradiance." *Journal of Plankton Research* 39, no. 2: 280–289.

Brattegard, T., T. Høisæter, K. Sjøtun, T. Fenchel, and F. Uiblein. 2011. "Norwegian Fjords: From Natural History to Ecosystem Ecology and

Beyond." *Marine Biology Research* 7: 421–424. https://doi.org/10.1080/17451000.2011.561355.

Breitburg, D., L. A. Levin, A. Oschlies, et al. 2018. "Ocean Deoxygenation – Causes and Consequences in a Changing World." *Science* 359, no. 6371: eaam7240.

Carstensen, J., and D. J. Conley. 2019. "Baltic Sea Hypoxia Takes Many Shapes and Sizes." *Limnology and Oceanography Bulletin* 28: 125–129. https://doi.org/10.1002/lob.10350.

Christiansen, S., M. P. Bråthen, F. L. Moksnes, et al. 2024. "Extensive avoidance behaviour of krill from predators and nets." *ICES Journal of Marine Science* 81, no. 9: 1764–1773. https://doi.org/10.1093/icesjms/fsae123.

Darelius, E. M. K. 2020. "On the Effect of Climate Trends in Coastal Density on Deep Water Renewal Frequency in Sill Fjords – A Statistical Approach." *Estuarine, Coastal and Shelf Science* 243: 106904. https://doi.org/10.1016/j.ecss.2020.106904.

Davison, P. C., D. M. Checkley Jr., J. A. Koslow, and J. Barlow. 2013. "Carbon Export Mediated by Mesopelagic Fishes in the Northeast Pacific Ocean." *Progress in Oceanography* 116: 14–30.

Diaz, R. J., and R. Rosenberg. 2008. "Spreading Dead Zones and Consequences for Marine Ecosystems." *Science* 321: 926–929.

Eiane, K., D. L. Aksnes, E. BagØien, and S. Kaartvedt. 1999. "Fish or Jellies—A Question of Visibility?" *Limnology and Oceanography* 44: 1352–1357.

Frigstad, H., T. Andersen, D. O. Hessen, et al. 2013. "Long-Term Trends in Carbon, Nutrients and Stoichiometry in Norwegian Coastal Waters: Evidence of a Regime Shift." *Progress in Oceanography* 111: 113–124. https://doi.org/10.1016/j.pocean.2013.01.006.

Gallo, N. D., E. Drenkard, A. R. Thompson, et al. 2019. "Bridging From Monitoring to Solutions-Based Thinking: Lessons From CalCOFI for Understanding and Adapting to Marine Climate Change Impacts." *Frontiers in Marine Science* 6: 695. https://doi.org/10.3389/fmars.2019.00695.

Gilbert, D. 2017. "Oceans Loose Oxygen." *Nature* 542: 303–304.

Giske, J., D. L. Aksnes, B. M. Baliño, et al. 1990. "Vertical Distribution and Trophic Interactions of Zooplankton and Fish in Masfjorden, Norway." *Sarsia* 75: 65–81.

Gjøsæter, J., and K. Kawaguchi. 1980. A Review of the World Resources of Mesopelagic Fish. FAQ Fish Tech Pap No. 193.

Hannah, C. G., S. C. Johannessen, C. A. Wright, and S. J. Page. 2024. "Oxygen Dynamics in a Deep-Silled Fjord: Tight Coupling to the Open Shelf." *Limnology and Oceanography* 69: 652–666. https://doi.org/10.1002/lno.12522.

Hoffmann, A. F., E. T. Peltzer, P. M. Walz, and P. G. Brewer. 2011. "Hypoxia by Degrees: Establishing Definitions for a Changing Ocean." *Deep Sea Research* 158: 1212–1226.

Inall, M. E., and P. A. Gillibrand. 2010. "The Physics of Mid-Latitude Fjords: A Review." In *Fjord Systems and Archives*, edited by J. A. Howe, W. E. N. Austin, M. Forwick, and M. Paetzel, 17–33. London, UK: Geological Society. Special Publications.

Irigoien, X., T. A. Klevjer, A. Røstad, et al. 2014. "Large Mesopelagic Fishes Biomass and Trophic Efficiency in the Open Ocean." *Nature Communications* 5: 3271.

Jackson, J. M., L. Bianucci, C. G. Hannah, E. C. Carmack, and J. Barrette. 2021. "Deep Waters in British Columbia Mainland Fjords Show Rapid Warming and Deoxygenation From 1951 to 2020." *Geophysical Research Letters* 48: e2020GL091094.

Johansen, P.-O., T. E. Isaksen, E. Bye-Ingebrigtsen, et al. 2018. "Temporal Changes in Benthic Macrofauna on the West Coast of Norway Resulting From Human Activities." *Marine Pollution Bulletin* 128: 483–495.

Johnsen, I. A., H. Loeng, and M. S. Myksvoll. 2024. "Coastal Alterations Influence Deep Water Renewal in Norwegian Sill Fjords." *Estuarine, Coastal and Shelf Science* 297: 108604. https://doi.org/10.1016/j.ecss.2023.108604.

Kaartvedt, S., A. Røstad, and T. A. Klevjer. 2009. "Small Clupeid Fishes (*Sprattus sprattus*) can Exploit Low Oxygen Waters for Overwintering." *Marine Ecology Progress Series* 390: 237–249.

Kaartvedt, S., A. Røstad, and J. Titelman. 2021. "Sleep-Walking Copepods? Calanus Diapausing in Hypoxic Waters Adjust Their Vertical Position During Winter." *Journal of Plankton Research* 43: 199–208. https://doi.org/10.1093/plankt/fbab004.

Kaartvedt, S., A. Staby, and D. L. Aksnes. 2012. "Efficient Trawl Avoidance by Mesopelagic Fishes Causes Large Underestimation of Their Biomass." *Marine Ecology Progress Series* 456: 1–6.

Keeling, R. F., A. Körtzinger, and N. Gruber. 2010. "Ocean Deoxygenation in a Warming World." *Annual Review of Marine Science* 2: 199–229.

Klevjer, T. A., X. Irigoien, A. Røstad, E. Fraile-Nuez, V. M. Benítez-Barrios, and S. Kaartvedt. 2016. "Large Scale Patterns in Vertical Distribution and Behaviour of Mesopelagic Scattering Layers." *Scientific Reports* 6: 19873.

Larsen, S., T. Andersen, and D. O. Hessen. 2011. "Climate Change Predicted to Cause Severe Increase of Organic Carbon in Lakes." *Global Change Biology* 17: 1186–1192.

Levin, L. 2018. "Manifestation, Drivers and Emergence of Open Ocean Deoxygenation." *Annual Review of Marine Science* 10: 229–260.

Levin, L., W. Ekau, A. J. Gooday, et al. 2009. "Effects of Natural and Human-Induced Hypoxia on Coastal Benthos." *Biogeosciences* 6: 2063–2098.

Limburg, K., and M. Casini. 2018. "Effect of Marine Hypoxia on Baltic Sea Cod *Gadus morhua*: Evidence From Otolith Chemical Proxies." *Frontiers in Marine Science* 5: 482. https://doi.org/10.3389/fmars.2018.00482.

Linford, P., I. Pérez-Santos, I. Montes, et al. 2023. "Recent Deoxygenation of Patagonian Fjord Subsurface Waters Connected to the Peru–Chile Undercurrent and Equatorial Subsurface Water Variability." *Global Biogeochemical Cycles* 37: e2022GB007688.

Mangerud, J., A. L. C. Hughes, T. H. Sæle, and J. I. Svendsen. 2019. "Ice-Flow Patterns and Precise Timing of Ice Sheet Retreat Across a Dissected Fjord Landscape in Western Norway." *Quaternary Science Reviews* 214: 139–163. https://doi.org/10.1016/j.quascirev.2019.04.032.

Moffitt, S. E., T. M. Hill, K. Ohkushi, J. P. Kennett, and R. J. Behl. 2014. "Vertical Oxygen Minimum Zone Oscillations Since 20 Ka in Santa Barbara Basin: A Benthic Foraminiferal Community Perspective." *Paleoceanography* 29: 44–57. https://doi.org/10.1002/2013PA002483.

Nelson, N. B., and D. A. Siegel. 2013. "The Global Distribution and Dynamics of Chromophoric Dissolved Organic Matter." *Annual Review of Marine Science* 5: 447–476.

Netburn, A. N., and A. J. Koslow. 2015. "Dissolved Oxygen as a Constraint on Daytime Deep Scattering Layer Depth in the Southern California Current Ecosystem." *Deep Sea Research Part I: Oceanographic Research Papers* 104: 149–158.

Opdal, A. F., T. Andersen, D. O. Hessen, C. Lindemann, and D. L. Aksnes. 2023. "Tracking Freshwater Browning and Coastal Water Darkening From Boreal Forests to the Arctic Ocean." *Limnology and Oceanography* 8: 611–619. https://doi.org/10.1002/lol2.10320.

Oschlies, A., O. Duteil, J. Getzlaff, W. Koeve, A. Landolfi, and S. Schmidtko. 2017. "Patterns of Deoxygenation: Sensitivity to Natural and Anthropogenic Drivers." *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* 375: 20160325. https://doi.org/10.1098/rsta.2016.0325.

Parker-Stetter, S. L., J. K. Horne, and M. M. Langness. 2009. "The Influence of Midwater Hypoxia on Necton Vertical Migration." *ICES Journal of Marine Science* 66: 1296–1302.

Pérez-Santos, I., L. Castro, L. Ross, et al. 2018. "Turbulence and Hypoxia Contribute to Dense Biological Scattering Layers in Patagonian Fjord System." *Ocean Science* 14: 1185–1206.

Pitcher, G., A. Aguirre-Velarde, D. Breitburg, et al. 2021. "System Controls of Coastal and Open Ocean Oxygen Depletion." *Progress in Oceanography* 197: 102613. https://doi.org/10.1016/j.pocean.2021.102613.

Reusch, T. B. H., J. Dierking, H. C. Andersson, et al. 2018. "The Baltic Sea as a Time Machine for the Future Coastal Ocean." *Science Advances* 4: eaar8195.

Røstad, A., and S. Kaartvedt. 2013. "Seasonal and Diel Patterns in Sedimentary Flux of Krill Fecal Pellets Recorded by an Echosounder." *Limnology and Oceanography* 58: 1985–1997.

Saba, G. K., A. B. Burd, J. P. Dunne, et al. 2021. "Toward a Better Understanding of Fish-Based Contribution to Ocean Carbon Flux." *Limnology and Oceanography* 66: 1639–1664.

Sætre, R., J. Aure, and H. G. Gade. 2010. "Oseanografi Og Klima." In *Bergensfjordene – Natur Og Bruk*, edited by P. Johannessen, R. Sætre, H. Kryvi, and H. Hjelle, 33–55. Bergen Kommune: Havforskningsinstituttet, Uni Research, Universitetet I Bergen.

Schmidtko, S., L. Stramma, and M. Visbeck. 2017. "Decline in Global Oceanic Oxygen Content During the Past Five Decades." *Nature* 542: 335–339.

Solås, M. R., A. G. V. Salvanes, and D. L. Aksnes. 2024. "Association Between Water Darkening and Hypoxia in a Norwegian Fjord." *Estuarine, Coastal and Shelf Science* 310: 108988. https://doi.org/10.1016/j.ecss.2024.108988.

Solberg, I., and S. Kaartvedt. 2017. "The Diel Vertical Migration Patterns and Individual Swimming Behavior of Overwintering Sprat *Sprattus sprattus*." *Progress in Oceanography* 151: 49–61.

Solberg, I., A. Røstad, and S. Kaartvedt. 2015. "Ecology of Overwintering Sprat (*Sprattus sprattus*)." *Progress in Oceanography* 138: 116–135.

Sørnes, T. A., and D. L. Aksnes. 2004. "Predation Efficiency in Visual and Tactile Zooplanktivores." *Limnology and Oceanography* 49: 69–75.

Sørnes, T. A., D. L. Aksnes, U. Båmstedt, and M. J. Youngbluth. 2007. "Causes for Mass Occurrence of the Jellyfish *Periphylla periphylla*: A Hypothesis That Involves Optically Conditioned Retention." *Journal of Plankton Research* 29: 157–167.

St. John, M. A., Á. Borja, G. Chust, et al. 2016. "A Dark Hole in Our Understanding of Marine Ecosystems and Their Services: Perspectives From the Mesopelagic Community." *Frontiers in Marine Science* 3: 31. https://doi.org/10.3389/fmars.2016.00031.

Standal, D., and E. Grimaldo. 2020. "Institutional Nuts and Bolts for a Mesopelagic Fishery in Norway." *Marine Policy* 119: 104043. https://doi.org/10.1016/j.marpol.2020.104043.

Straneo, F., G. S. Hamilton, L. A. Stearns, and D. A. Sutherland. 2016. "Connecting the Greenland Ice Sheet and the Ocean: A Case Study of Helheim Glacier and Sermilik Fjord." *Oceanography* 29, no. 4: 34–45. https://doi.org/10.5670/oceanog.2016.97.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.