

Abstract

The aim of this study was to test the hypothesis that, under low-temperature conditions, ectothermic megafauna plays a significant role in the functioning of marine ecosystems. In warm environments, short life cycles and rapid biomass turnover promote the dominance of small-bodied organisms with limited spatial influence. In Arctic ecosystems, however, processes occurring at the pelagic–benthic interface become particularly important. Consequently, special attention was given to mechanisms of pelagic–benthic coupling, as the traditional distinction between planktonic and benthic organisms does not adequately reflect the functional roles of many taxa in these environments.

The coastal waters of Svalbard, including fjords, bays, and adjacent shelf areas under direct terrestrial influence, represent some of the most dynamic marine environments in the European Arctic. The intensive inflow of Atlantic waters, the retreat of tidewater glaciers, seasonal salinity fluctuations, and the highly variable input of glacial derived mineral suspended sediment create ecosystems functioning under conditions of pronounced environmental disturbance. In such systems, the classical approach to benthic research—based primarily on quantitative sediment samples collected with grabs or corers—provides detailed knowledge of small benthic fauna, but does not adequately capture the ecological significance of large, mobile organisms and processes operating at spatial scales exceeding a single sampling station.

Arctic megabenthos has been studied for more than a century, and its classical zoogeographic framework was formulated, among others, in the works of Robert Blacker, who proposed a division of the North Atlantic and the Arctic into species-indicator zones based on bottom trawl material. Subsequent studies, conducted since the late twentieth century using photographic and video documentation (including systems such as OFOS and similar observational platforms), have substantially expanded knowledge of megafauna in deep ocean basins and open shelf areas. However, these efforts have only marginally included coastal zones and Arctic fjords.

In parallel, large-scale seabed mapping programs—such as the Norwegian MAREANO programme—were developed, in which visual observations became a primary tool for habitat identification, assessment of megafauna distribution, and the interpretation of

processes occurring at the sediment surface. Although these programs provided valuable data from shelf and open areas, their spatial coverage within the inner basins of Arctic fjords has remained limited.

Consequently, fjord systems—characterized by strong environmental variability, high rates of mineral sedimentation, and dynamic pelagic–benthic coupling—remain relatively poorly recognized with respect to processes occurring at the sediment surface and to the ecological role of mobile megafauna. The observations and in situ data analyses presented in this dissertation constitute the first comprehensive, long-term video-based dataset from Svalbard fjords explicitly designed for process-oriented analysis, focusing on fjord environments that have so far been underrepresented in large-scale seabed and benthic habitat mapping programmes. Particular emphasis was placed on assessing the role of large, mobile organisms—both benthic and formally pelagic—in the redistribution of organic matter and in modifying the sediment surface in the near-bottom zone.

This approach allows organisms traditionally classified as plankton, including krill, as well as episodically sinking discarded appendicularian houses, to be treated as significant components of benthic ecosystem functioning through their contribution to the transport of matter and energy to the seafloor, particularly during periods of increased primary production.

The analyses were based on integrated in situ observations conducted using various research methods, encompassing both classical sampling of benthic faunal assemblages and seabed imaging with underwater camera systems, including a drop camera, and in selected cases, time-lapse recording systems. This approach enabled the documentation of processes and organismal behaviour in their actual spatial context, which remains inaccessible to classical sampling methods based solely on point sediment sampling. The research was carried out primarily aboard the research vessel R/V *Oceania* at depths ranging from approximately 15–394 m, across different seabed types in fjords and on the shelf of the Svalbard archipelago. Between 2015 and 2021, 253 video sequences were recorded, corresponding to approximately 170 hours of footage obtained directly above the seafloor. Additionally, selected analyses incorporated recordings from the drop-camera system descent phase, covering the entire water column from the surface to the bottom, which allowed the assessment of pelagic organism occurrence along the vertical profile.

The scale of the collected material constitutes one of the largest datasets of in situ megafaunal observations from Arctic fjords. All recordings were accompanied by spatial and temporal metadata and archived in the database at the Institute of Oceanology of the Polish Academy of Sciences. Taxonomic identification was conducted through the comparison of recorded imagery with specimens collected from the same regions using fishing gear, based on literature data and consultations with specialists representing particular taxonomic groups. In some cases, identification was possible only to the genus level due to limitations in image resolution and visibility conditions. Detailed results concerning the distribution, species structure, and ecological characteristics of echinoderms were presented in the first publication included in this dissertation (“Recent distribution of Echinodermata species in Spitsbergen coastal waters”, *Polish Polar Research*, 2016). This study analysed the distribution of benthic megafauna based on an extensive dataset comprising more than 460 stations sampled between 1996 and 2014, demonstrating a clear blurring of classical zoogeographic patterns in the coastal waters of Svalbard. Species previously regarded as indicators of distinct distributional zones now co-occur within the same fjords and coastal regions, and the boundaries of their ranges are weakly defined or entirely indistinct.

This is particularly evident in echinoderms, which do not form clearly defined species assemblages either along the depth gradient or in relation to the distance from sources of glacial sedimentation or substrate type. Multivariate analyses revealed no distinct faunal groupings, and species distributions exhibited a continuous pattern corresponding rather to gradual environmental gradients than to discrete ecological zones. The composition of benthic megafauna in the coastal waters of Svalbard proved to be largely a subset of the fauna of northern Norway and the eastern Atlantic, with no endemic forms recorded. The overwhelming majority consists of species with a wide boreal–Arctic distribution, while strictly Arctic forms are limited in representation.

These findings indicate a strong faunal linkage between the coastal waters of Svalbard and the Atlantic region, as well as an ongoing process of borealisation of the European Arctic. At the same time, the results suggest a high degree of ecological plasticity in the dominant megafaunal species, capable of functioning under conditions of considerable variability in temperature, salinity, and intensive mineral sedimentation. The absence of distinct, stable faunal assemblages and the blurring of zoogeographic boundaries indicate that, in dynamic fjord environments, functional processes become of primary importance

relative to the mere presence of particular species. In this context, the first paper provides the starting point for the further analyses presented in this dissertation, focusing on the role of large and mobile organisms—both benthic and pelagic—and on pelagic–benthic coupling processes, such as near-bottom krill concentrations or the episodic deposition of discarded appendicularian houses. This approach allows a shift from a classical zoogeographic description of fauna towards a process-based interpretation of benthic ecosystem functioning.

An important component of this dissertation was the analysis of the functional role of megazooplankton in the utilisation of organic matter resources available in the near-bottom zone of Spitsbergen fjords. This phenomenon was described in detail in the second paper included in the dissertation (“Plankton or benthos: where krill belongs in Spitsbergen fjords? (Svalbard Archipelago, Arctic)”, *Polar Biology*, 2019), based on video material collected at 107 stations and parallel plankton net sampling conducted in fjords of western Spitsbergen. Considering that a substantial proportion of primary production in this region is not consumed in the water column and sinks to the seafloor, this study aimed to determine whether the majority of krill biomass is functionally associated with the pelagic realm or with the near-bottom zone, and to what extent these organisms participate in the secondary utilisation of organic matter deposited on the seabed.

Particular attention was given to krill, traditionally treated as a pelagic component, yet potentially playing an important role at the sediment–water interface. Analysis of video material recorded using near-bottom camera systems revealed numerous krill aggregations occurring in the immediate vicinity of the seafloor, where individuals frequently exhibited behaviors associated with feeding within the upper sediment layer. Documented behaviors included shallow insertions into the sediment surface (“nose diving”) and disturbance of its uppermost layer, which may have enabled the uptake of organic matter settled from the water column during feeding in the near-bottom zone.

Comparison of near-bottom observations with simultaneous sampling conducted in the water column showed that krill densities near the seafloor were approximately an order of magnitude higher than those in the pelagic realm. During the summer season, krill concentrations in the near-bottom layer exceeded 700 individuals m^{-3} , whereas densities recorded in the water column were roughly an order of magnitude lower. These

comparisons concerned the same locations and study periods, which limits the possibility of interpreting the differences as an effect of spatial or seasonal variability. Quantitative analyses further indicate that, in summer, a substantial proportion of the population—at least half of the individuals—remains in the immediate vicinity of the seafloor.

It was demonstrated that three krill species (*Thysanoessa inermis*, *T. raschii*, and *T. longicaudata*), despite their pelagic mode of life, regularly form aggregations in the near-bottom zone and participate in processes occurring at the sediment surface. Since near-bottom krill concentrations were observed in multiple fjords and in more than one study season, this phenomenon does not appear to be purely incidental. The results indicate that krill functionally participates in the cycling of matter and energy at the pelagic–benthic interface, contributing to the redistribution of organic matter and to the modification of sediment surface properties. From a functional perspective, krill constitutes a significant component of benthic communities in Svalbard fjords.

Similar krill behaviour has previously been described in deep oceanic regions of Antarctica and the North Atlantic, as well as locally in Arctic fjords. The results of the present study expand these observations by documenting the scale, frequency, and functional significance of near-bottom krill aggregations in coastal fjords of Spitsbergen and emphasise the complementarity of in situ imaging methods relative to classical plankton sampling techniques.

Another component of the dissertation expanding knowledge on megafaunal functioning in Spitsbergen fjords concerned observations of the distribution and behaviour of feather stars of the order Comatulida (*Heliometra glacialis*) in the inner fjord basins, strongly affected by mineral sediment input. This part of the study was based on continuous in situ time-lapse recording of the decomposition process of bait consisting of Atlantic cod (*Gadus morhua*), with an exposure time of 16 hours and 45 minutes. During this sequence, in addition to numerous scavenging and opportunistic organisms (mainly amphipods), three individuals of *Heliometra glacialis*—mobile suspension-feeding crinoids—were recorded.

Two of them were observed attached to the carapace of crabs of the genus *Hyas* while the crabs were feeding on the bait. Complementary to these observations was the analysis of video material from 202 locations recorded using a drop-camera system between 2015

and 2020, which confirmed the presence of *Heliometra glacialis* in the inner fjord regions, although no analogous interactions with crabs were documented.

These results indicate that the occurrence of feather stars in environments characterized by high sediment dynamics is unlikely to be incidental. The episode of individuals attached to crabs should be interpreted as a rare yet potentially adaptive behaviour, enabling the temporary functioning of suspension feeders above the sediment surface of soft, unstable seabed under conditions of intensive mineral sedimentation. Considering the very limited number of in situ observations concerning the order Comatulida in Arctic fjords, these findings significantly expand current knowledge of the habitat and behavioural plasticity of this group at high latitudes.

A detailed description of these observations and their interpretation is presented in the third publication included in this dissertation (“New strategies for the new environment in Spitsbergen fjords (Arctic). Scattering of the feather star *Heliometra glacialis* (Echinodermata, unstalked crinoid) clinging to a crab”, *Polar Biology*, 2023).

Another important line of research concerned the recognition of the significance of mass occurrences of gelatinous pelagic organisms as an episodic yet potentially important source of organic matter reaching the seafloor in Spitsbergen fjords. This phenomenon was described in detail in the fourth paper included in this dissertation (“Observation of discarded appendicularian houses in the benthic and pelagic zones of Spitsbergen fjords using drop-camera imagery”, *Marine Ecology Progress Series*, 2025), based on the analysis of 253 video stations recorded in fjords of western Spitsbergen. This study fits within the broader concept of pulsating plankton dynamics, according to which short-lived and irregular occurrences of pelagic organisms, particularly gelatinous forms, may play a key role in marine ecosystem functioning, despite being rarely recorded by classical research methods (Boero et al. 2008).

Analysis of video material recorded using a drop-camera system revealed the presence of extensive seabed areas covered with gelatinous structures, which were identified during the course of the study as discarded appendicularian houses of the genus *Oikopleura*. During these observations, the density of discarded appendicularian houses on the sediment surface ranged from single structures to more than 900 objects m⁻². In extreme cases, the houses almost completely covered the observed sediment surface. Parallel recordings conducted in the water column indicated a mass occurrence of organisms in

the same areas, suggesting a direct relationship between intensive pelagic population development and the observed “spent structures” on the seafloor.

Such a mechanism corresponds to the role described in the literature of gelatinous filter feeders as organisms capable of rapidly capturing energy from low trophic levels and directly transferring it to the benthos, thereby bypassing part of the classical intermediate links (“short-circuiting” of food webs; Boero et al. 2008). Based on literature data concerning the organic carbon content of individual houses of *Oikopleura vanhoeffeni*, it was possible to estimate the potential organic carbon flux to the sediment during such episodes, which ranged from approximately 1-60 mg C m⁻². These estimates are necessarily approximate and do not include direct measurements of carbon content in the material deposited during the observed events. The observed events were clearly episodic in nature and were recorded only in a single study season, indicating a pulsed rather than continuous character of this matter transfer mechanism. However, literature reports confirm the occurrence of similar phenomena in the past and suggest that this process may constitute an important, though difficult to detect, component of fjord ecosystem functioning. As emphasised in the literature (Boero et al. 2008), short-term episodes of this type represent an integral element of marine ecosystem dynamics, even though they are often underestimated in studies based on classical observational methods.

In contrast to slowly sinking detrital fractions, discarded *Oikopleura* houses, due to the presence of mineral ballast derived from glacial suspension, sink relatively rapidly, thereby promoting efficient transfer of organic matter from the water column to the benthic zone. These observations provide direct evidence of strong, though episodic, pelagic–benthic coupling, in which macroscopic pelagic organisms—traditionally not included in benthic studies—participate both in modifying the sediment surface and in supplying readily available organic matter to the seafloor.

This phenomenon fits within the broader context of research on rapid carbon transport in the oceans (including “jelly falls” and “blue carbon”) and highlights the importance of in situ imaging methods in documenting ecological processes that remain largely invisible to classical sampling techniques.

The fifth publication included in the dissertation (“Surface lebensspuren and their tracemakers in Arctic fjords of Spitsbergen: Patterns, diversity, and environmental controls”, *Polish Polar Research*, 2025) is based on video material collected at 206

stations, of which 57% contained clear examples of lebensspuren. In the course of the study, a total of 19 morphological trace types were distinguished for the first time in Spitsbergen fjords, including eight forms not previously described in the literature. For 18 types, their tracemakers could be identified, and for ten, assignment to a particular species or genus was possible, representing a level of taxonomic resolution rarely achieved in neoichnological studies of marine environments.

A key element of this work was the direct linkage of traces with the organisms producing them, made possible by long-term, high-resolution video recordings documenting both the presence of the trace and the behaviour of the organism during its formation. As emphasised in the literature, identification of a tracemaker in marine environments is exceptionally difficult and usually requires the analysis of hundreds of hours of recordings; in most previous studies, traces and organisms have been analysed separately. The method applied in this series of studies allowed the simultaneous analysis of trace morphology, organism behavior, and the environmental context of their occurrence, thereby providing an extensive dataset for Arctic environments.

The analysis showed that echinoderms constituted the dominant group of tracemakers, responsible for more than half of all recorded lebensspuren, with a particularly important role played by the sea star *Urasterias lincki*, whose locomotion and resting traces were the most frequently observed types of biogenic structures. Decapod crustaceans (mainly hermit crabs), gastropods, and—to a lesser extent—polychaetes and demersal fish also contributed significantly. The distribution and diversity of traces exhibited clear relationships with environmental factors, particularly the distance from glacier fronts, near-bottom suspended matter levels, and sediment characteristics.

These results clearly indicate the importance of so-called horizontal bioturbation, understood as the cumulative impact of mobile megafauna on the sediment surface at a spatial scale exceeding its momentary presence recorded in a single video frame. In this context, lebensspuren constitute an integrated record of benthic ecosystem functioning, accumulating the effects of organism activity over time and enabling assessment of their influence on sediment surface structure even under conditions of low faunal abundance.

The significance of these findings extends beyond the ecology of contemporary Arctic ecosystems. The identified trace types, together with their assigned tracemakers and

environmental context, provide valuable reference material for the interpretation of fossil trace assemblages and the reconstruction of past sedimentary environments where organisms are rarely preserved and biogenic structures constitute the only evidence of their presence. Thus, these studies integrate ecological approaches with neoichnology and paleoichnology, contributing to modern, interdisciplinary research on seafloor functioning.

Taken together, the results presented in this dissertation demonstrate that megabenthos in the coastal waters of Svalbard plays a significant role in benthic ecosystem functioning, both as a component coupling pelagic and benthic processes and as a factor modifying the seafloor surface at the scale of the benthic “landscape.” Under conditions of low temperatures and extended life cycles, large mobile organisms influence the environment in a cumulative manner, combining the redistribution of organic matter with persistent modification of the sediment surface. Their impact therefore exceeds the scale of their instantaneous presence captured in individual observations.

The demonstrated links with plankton and the nearly ubiquitous presence of megafauna across the seabed confirm the initial hypothesis regarding the importance of this group of organisms in polar fjords. These results suggest that the traditional view of benthos requires supplementation with in situ observations and analyses of processes operating at temporal and spatial scales exceeding those represented by a single sampling station.