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Benthic megafauna, the record of its activity
(lebensspuren), and pelago-benthic processes in Svalbard
fjord ecosystems

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Ph. D. Thesis

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Megafauna bentosowa, zapis jej aktywności
(lebensspuren) i procesy pelagiczno-bentosowe w
ekosystemach fiordów Svalbardu

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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.

Streszczenie

Celem badań było zweryfikowanie hipotezy, że w warunkach niskich temperatur megafauna zmiennocieplna odgrywa istotną rolę w funkcjonowaniu ekosystemów morskich. W środowiskach ciepłych krótkie cykle życiowe i szybka rotacja biomasy sprzyjają dominacji drobnych form o ograniczonym zasięgu oddziaływania. W ekosystemach arktycznych większego znaczenia nabierają natomiast procesy zachodzące na styku pelagialu i bentosu. Z tego względu szczególną uwagę poświęcono mechanizmom sprzężenia pelagiczno-dennego (benthic-pelagic coupling), gdyż klasyczne rozgraniczenie organizmów planktonowych i bentosowych nie oddaje rzeczywistej funkcjonalnej roli wielu taksonów w tych środowiskach. Wody przybrzeżne Svalbardu, obejmujące fiordy, zatoki oraz przyległe obszary szelfowe, pozostające pod bezpośrednim wpływem lądu, należą do najbardziej dynamicznych środowisk morskich europejskiej Arktyki. Intensywny dopływ wód atlantyckich, cofanie się lodowców uchodzących bezpośrednio do morza, sezonowe zmiany zasolenia oraz wysoka zmienność dopływu zawiesiny mineralnej powodują, że ekosystemy te funkcjonują w warunkach silnych zaburzeń środowiskowych. W takich systemach klasyczne ujęcie bentosu, oparte głównie na ilościowych próbkach osadu pobieranych czerpakami dna lub sondami rdzeniowymi, dostarcza szczegółowej wiedzy o drobnej faunie dennej, lecz jedynie w ograniczonym stopniu pozwala uchwycić znaczenie dużych, mobilnych organizmów oraz procesów zachodzących w skali przestrzennej większej niż pojedyncze stanowisko. Megabentos Arktyki był przedmiotem badań od ponad stu lat, a jego klasyczne ujęcie zoogeograficzne zostało sformułowane m.in. w pracach Roberta Blackera, który na podstawie materiału z połowów dennych zaproponował podział północnego Atlantyku i Arktyki na strefy występowania gatunków wskaźnikowych. Późniejsze badania, prowadzone od końca XX wieku z wykorzystaniem rejestracji fotograficznej i wideo (m.in. systemów takich jak OFOS i podobnych platform obserwacyjnych), znacząco poszerzyły wiedzę o megafaunie głębokich basenów oceanicznych i otwartego szelfu, jednak obejmowały strefy przybrzeżne oraz fiordy arktyczne jedynie w ograniczonym stopniu. Równolegle rozwijane były wielkoskalowe programy kartowania dna, takie jak norweski program MAREANO, w których obserwacje wizualne stały się podstawowym narzędziem identyfikacji siedlisk, oceny rozmieszczenia megafauny oraz interpretacji procesów zachodzących na powierzchni osadu. Programy te dostarczyły cennych danych dotyczących obszarów szelfowych i

otwartych, jednak ich zasięg w wewnętrznych częściach fiordów arktycznych pozostawał i nadal pozostaje ograniczony. W konsekwencji fiordy, charakteryzujące się silną zmiennością środowiskową, wysoką sedymentacją mineralną oraz dynamicznym sprzężeniem procesów pelagicznych i dennych, są relatywnie słabo rozpoznane pod względem procesów zachodzących na powierzchni osadu oraz pod względem roli mobilnej megafauny. Zebrane w niniejszej rozprawie obserwacje i analizy danych *in situ* stanowią pierwszy tak obszerny zestaw długoterminowych rejestracji wideo z fiordów Svalbardu ukierunkowany na analizę procesową i koncentrujący się na środowiskach fiordowych dotychczas słabo reprezentowanych w wielkoskalowych programach kartowania dna i siedlisk przydennych.

Szczególne nacisk położono na ocenę roli dużych, mobilnych organizmów – zarówno dennych, jak i formalnie pelagicznych – w redystrybucji materii organicznej oraz w modyfikacji powierzchni osadu w strefie naddennej. Takie ujęcie pozwala traktować organizmy tradycyjnie klasyfikowane jako plankton, w tym kryla, a także epizodycznie opadające porzucone domki ogonic (*Appendicularia*), jako istotne elementy funkcjonowania ekosystemów bentosowych poprzez ich udział w transporcie materii i energii do dna, szczególnie w okresach zwiększonej produkcji pierwotnej.

Podstawą analiz były zintegrowane obserwacje *in situ* prowadzone z wykorzystaniem różnych metod badawczych, obejmujących zarówno klasyczne próbkowanie dennych zespołów faunistycznych, jak i obrazowanie dna przy użyciu systemów kamer podwodnych, w tym kamery opuszczanej (*drop camera*) oraz, w wybranych przypadkach, systemów rejestracji poklatkowej. Takie podejście umożliwiło uchwycenie procesów i zachowań organizmów w ich rzeczywistym układzie przestrzennym, który pozostaje niedostępny dla klasycznych metod próbkowania opartych wyłącznie na punktowych poborach osadu. Badania realizowano głównie z pokładu statku badawczego *r/v Oceania* w zakresie głębokości od około 15-394 m, na różnych typach dna morskiego w fiordach oraz na szelfie archipelagu Svalbard. W latach 2015–2021 zarejestrowano 253 sekwencje wideo, odpowiadające około 170 godzinom materiału filmowego zarejestrowanego bezpośrednio nad dnem morskim. Dodatkowo w wybranych analizach wykorzystywano nagrania z fazy opuszczania podwodnej kamery, obejmujące całą kolumnę wody od powierzchni do dna, co umożliwiło ocenę występowania organizmów pelagicznych w profilu pionowym. Skala zgromadzonego materiału stanowi jeden z największych zestawów obserwacji *in situ* megafauny w arktycznych fiordach. Wszystkie nagrania były

opatrzone metadanymi przestrzennymi i czasowymi oraz archiwizowane w bazie danych Instytutu Oceanologii Polskiej Akademii Nauk. Identyfikacja organizmów była prowadzona poprzez porównanie zarejestrowanych obrazów z okazami pozyskanymi z tych samych rejonów przy użyciu narzędzi połowowych, w oparciu o dane literaturowe oraz konsultacje ze specjalistami zajmującymi się poszczególnymi grupami taksonomicznymi; w części przypadków możliwa była jedynie identyfikacja do poziomu rodzaju ze względu na ograniczenia w rozdzielczości obrazu oraz warunki widzialności. Szczegółowe wyniki dotyczące rozmieszczenia, struktury gatunkowej i charakterystyki ekologicznej szkarłupni przedstawiono w pierwszej publikacji wchodzącej w skład niniejszej rozprawy („Recent distribution of Echinodermata species in Spitsbergen coastal waters”, *Polish Polar Research*, 2016). W ramach tej publikacji przeprowadzono analizę rozmieszczenia megafauny dennej na podstawie obszernego materiału obejmującego ponad 460 stanowisk próbkowania z lat 1996–2014, co wykazało wyraźne zatarcie klasycznych wzorców zoogeograficznych w wodach przybrzeżnych Svalbardu. Gatunki uznawane w przeszłości za wskaźniki odrębnych stref występowania obecnie współwystępują w tych samych rejonach fiordów i obszarów przybrzeżnych, a granice ich zasięgów są słabo zaznaczone lub całkowicie nieczytelne. W szczególności dotyczy to szkarłupni, które nie tworzą wyraźnych zespołów gatunkowych ani wzdłuż gradientu głębokości, ani w odniesieniu do odległości od źródeł sedymentacji glacialnej czy typu podłoża. Analizy wielowymiarowe wykazały brak jednoznacznych grup faunistycznych, a rozmieszczenie gatunków miało charakter ciągły, odpowiadający raczej płynnym gradientom środowiskowym niż dyskretnym strefom ekologicznym. Skład megafauny dennej w wodach przybrzeżnych Svalbardu okazał się w dużej mierze podzbiorem fauny północnej Norwegii i wschodniego Atlantyku, bez obecności form endemicznych. Zdecydowaną większość stanowią gatunki o szerokim zasięgu borealno-arktycznym, przy czym udział form ściśle arktycznych jest ograniczony. Wskazuje to na silne faunistyczne powiązanie wód przybrzeżnych Svalbardu z obszarem atlantyckim oraz na postępujący proces borealizacji europejskiej Arktyki. Jednocześnie wyniki te sugerują wysoki stopień plastyczności ekologiczną dominujących gatunków megafauny, zdolnych do funkcjonowania w warunkach znacznej zmienności temperatury, zasolenia oraz intensywnej sedymentacji mineralnej. Brak wyraźnych, stabilnych zespołów faunistycznych oraz rozmycie granic zoogeograficznych wskazują, że w dynamicznych środowiskach fiordowych kluczowego znaczenia nabierają procesy funkcjonalne, względem samej obecności określonych gatunków. W tym kontekście pierwsza praca

stanowi punkt wyjścia dla dalszych analiz przedstawionych w rozprawie, koncentrujących się na roli dużych i mobilnych organizmów – zarówno dennych, jak i pelagicznych – oraz na procesach sprzężenia pelagialu i bentosu, takich jak naddenne koncentracje kryla czy epizodyczne opady porzuconych domków ogonic. Podejście to pozwala przejść od klasycznego, zoogeograficznego opisu fauny do interpretacji funkcjonowania ekosystemu dennego w ujęciu procesowym.

Istotnym elementem rozprawy była analiza funkcjonalnej roli megazooplanktonu w wykorzystaniu zasobów materii organicznej dostępnych w strefie przydennej fiordów Spitsbergenu. Zjawisko to zostało szczegółowo opisane w drugiej pracy wchodzącej w skład niniejszej rozprawy („Plankton or benthos: where krill belongs in Spitsbergen fjords? (Svalbard Archipelago, Arctic)”, *Polar Biology*, 2019), opartej na analizie materiału wideo z 107 stacji oraz równoległych połowów planktonowych prowadzonych w fiordach zachodniego Spitsbergenu. Uwzględniając fakt, że znaczna część produkcji pierwotnej w tym regionie nie jest konsumowana w toni wodnej i opada na dno, w pracy tej podjęto próbę określenia, czy zasadnicza część biomasy kryla jest funkcjonalnie związana z pelagiałem, czy ze strefą naddenną oraz w jakim stopniu organizmy te uczestniczą w wtórnym wykorzystaniu materii organicznej zdeponowanej na dnie. W szczególności skoncentrowano się na krylu, tradycyjnie traktowanym jako komponent pelagialu, lecz potencjalnie odgrywającym istotną rolę na styku osad–woda. Analiza materiału wideo zarejestrowanego przy użyciu systemów kamer przydennych ujawniła liczne koncentracje kryla w bezpośrednim sąsiedztwie dna, gdzie osobniki wykazywały zachowania związane z żerowaniem w górnej warstwie osadu. Udokumentowane zachowania obejmowały płytkie zanurzenia w powierzchni osadu („nose diving”) oraz naruszanie jego wierzchniej warstwy, co mogło umożliwiać pobór materii organicznej opadłej z toni wodnej podczas żerowania w strefie naddennej. Porównanie obserwacji przydennych z równoczesnymi połowami prowadzonymi w toni wodnej wykazało, że zagęszczenia kryla przy dnie były o rząd wielkości wyższe niż w pelagialu. W sezonie letnim koncentracje kryla w warstwie przydennej osiągały wartości przekraczające 700 osobników na m^{-3} , podczas gdy zagęszczenia rejestrowane w toni wodnej były o rząd wielkości niższe. Porównania te dotyczyły tych samych lokalizacji i okresów badawczych, co ogranicza możliwość interpretacji różnic jako efektu zmienności przestrzennej lub sezonowej. Analizy ilościowe wskazują ponadto, że latem znaczna część populacji – co najmniej połowa osobników – przebywa w bezpośrednim

sąsiedztwie dna. Wykazano, że trzy gatunki kryła (*Thysanoessa inermis*, *T. raschii* oraz *T. longicaudata*), mimo pelagicznego trybu życia, regularnie tworzą koncentracje w strefie naddennej i uczestniczą w procesach zachodzących na powierzchni osadu. Ponieważ naddenne koncentracje kryła obserwowano w wielu fiordach oraz w więcej niż jednym sezonie badawczym, zjawisko to nie wydaje się mieć charakteru wyłącznie incydentalnego. Wyniki wskazują, że krył funkcjonalnie uczestniczy w obiegu materii i energii na styku pelagialu i bentosu, przyczyniając się do redystrybucji materii organicznej oraz do modyfikacji właściwości powierzchni osadu. W ujęciu funkcjonalnym krył stanowi istotny element biocenozy bentosowych fiordów Svalbardu. Podobne zachowania kryła opisywano wcześniej w głębokich obszarach oceanicznych Antarktyki oraz północnego Atlantyku, a także lokalnie w arktycznych fiordach. Wyniki niniejszej pracy rozszerzają te obserwacje, dokumentując skalę, częstotliwość oraz funkcjonalne znaczenie naddennych koncentracji kryła w przybrzeżnych fiordach Spitsbergenu i podkreślają komplementarność metod obrazowych *in situ* względem klasycznych metod próbkowania planktonu.

Kolejnym elementem rozprawy poszerzającym wiedzę o funkcjonowaniu megafauny w fiordach Spitsbergenu były obserwacje rozmieszczenia i zachowań liliowców z rzędu Comatulida (*Heliometra glacialis*) w wewnętrznych częściach fiordów, silnie obciążonych dopływem zawiesiny mineralnej. Podstawą tej części badań była długotrwała rejestracja poklatkowa *in situ* procesu dekompozycji przynęty mięsnej z dorsza atlantyckiego (*Gadus morhua*), o czasie ekspozycji wynoszącym 16 godzin i 45 minut. W trakcie tej sekwencji, obok licznych organizmów padlinożernych i oportunistycznych (głównie obunogów), zarejestrowano obecność trzech osobników *Heliometra glacialis* – mobilnych liliowców filtrujących – z których dwa obserwowano jako osobniki przyczepione do karapaksu krabów z rodzaju *Hyas* w trakcie żerowania krabów na przynęcie. Uzupełnieniem tych obserwacji była analiza materiału wideo z 202 lokalizacji zarejestrowanych przy użyciu kamery opuszczanej (drop camera) w latach 2015–2020, która potwierdziła obecność *Heliometra glacialis* w wewnętrznych rejonach fiordów, jednak bez rejestracji analogicznych interakcji z krabami. Wyniki te wskazują, że występowanie liliowców w środowiskach o wysokiej dynamice osadu nie ma charakteru incydentalnego. Epizod obecności osobników przyczepionych do krabów należy interpretować jako rzadkie, lecz potencjalnie adaptacyjne zachowanie, umożliwiające czasowe funkcjonowanie filtratorów ponad powierzchnią miękkiego,

niestabilnego dna w warunkach intensywnej sedymentacji mineralnej. Biorąc pod uwagę bardzo ograniczoną liczbę obserwacji in situ dotyczących rzędu Comatulida w arktycznych fiordach, wyniki te istotnie poszerzają wiedzę o plastyczności siedliskowej i behawioralnej tej grupy w wysokich szerokościach geograficznych. Szczegółowy opis tych obserwacji oraz ich interpretację przedstawiono w trzeciej publikacji wchodzącej w skład niniejszej rozprawy („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).

Kolejnym istotnym wątkiem badań było rozpoznanie znaczenia masowego pojawienia się galaretowatych organizmów pelagicznych jako epizodycznego, lecz potencjalnie istotnego źródła materii organicznej docierającej do dna morskiego w fiordach Spitsbergenu. Zjawisko to zostało szczegółowo opisane w czwartej pracy wchodzącej w skład niniejszej rozprawy („Observation of discarded appendicularian houses in the benthic and pelagic zones of Spitsbergen fjords using drop-camera imagery”, *Marine Ecology Progress Series*, 2025), opartej na analizie 253 stacji wideo zarejestrowanych w fiordach zachodniego Spitsbergenu. Wpisuje się w szerszą koncepcję pulsacyjnej dynamiki planktonu, zgodnie z którą krótkotrwałe i nieregularne pojawy organizmów pelagicznych, w szczególności form galaretowatych, mogą odgrywać kluczową rolę w funkcjonowaniu ekosystemów morskich, mimo że są rzadko rejestrowane przez klasyczne metody badawcze (Boero et al. 2008). Analiza materiału wideo zarejestrowanego przy użyciu kamery opuszczanej ujawniła występowanie rozległych obszarów dna pokrytych galaretowatymi strukturami, które w toku badań zostały zidentyfikowane jako porzucone domki ogonic (*Appendicularia*) z rodzaju *Oikopleura*. W trakcie tych obserwacji stwierdzono, że zagęszczenie porzuconych domków ogonic na powierzchni dna wahało się od pojedynczych struktur do ponad 900 obiektów m⁻², przy czym w skrajnych przypadkach domki te niemal całkowicie pokrywały obserwowaną powierzchnię osadu. Równoległe rejestracje prowadzone w toni wodnej wskazywały na masowe występowanie organizmów w kolumnie wody w tych samych rejonach, co sugeruje bezpośredni związek pomiędzy intensywnym rozwojem populacji pelagicznych a obserwowanymi „wyeksploatowanymi strukturami” na powierzchni dna morskiego. Taki mechanizm odpowiada opisaney w literaturze roli galaretowatych filtratorów jako organizmów zdolnych do szybkiego przechwytywania energii z niskich poziomów sieci troficznej i jej bezpośredniego transferu do bentosu, z pominięciem części klasycznych

ogniów pośrednich („short-circuiting” sieci troficznych; Boero et al. 2008). Na podstawie danych literaturowych dotyczących zawartości węgla organicznego w pojedynczych domkach *Oikopleura vanhoeffeni* możliwe było oszacowanie potencjalnego dopływu węgla organicznego do osadu w trakcie takich epizodów, który mieścił się w zakresie od około 1-60 mg C m⁻². Szacunki te mają charakter przybliżony i nie obejmują bezpośrednich pomiarów zawartości węgla w materiale zdeponowanym w trakcie obserwowanych epizodów. Zaobserwowane zdarzenia miały charakter wyraźnie epizodyczny i zostały zarejestrowane jedynie w jednym sezonie badawczym, co wskazuje na pulsacyjny, a nie stały charakter tego mechanizmu transferu materii. Doniesienia literaturowe potwierdzają jednak występowanie podobnych zjawisk w przeszłości oraz sugerują, że proces ten może stanowić istotny, choć trudny do uchwycenia, element funkcjonowania ekosystemów fiordowych. Jak wskazuje literatura (Boero et al. 2008), krótkotrwałe epizody tego typu stanowią integralny element dynamiki ekosystemów morskich, mimo że często pozostają niedoszacowane w badaniach opartych na klasycznych metodach obserwacyjnych. W przeciwieństwie do wolno opadających frakcji detrytus, porzucone domki *Oikopleura* dzięki obecności balastu mineralnego pochodzącego z zawiesiny glacialnej opadają stosunkowo szybko, co sprzyja efektywnemu transferowi materii organicznej z toni wodnej do strefy dennej. Obserwacje te dostarczają bezpośrednich dowodów na istnienie silnego, choć epizodycznego sprzężenia pelagiczno-dennego, w którym makroskopowe organizmy pelagiczne – tradycyjnie nieuwzględniane w badaniach bentosu – uczestniczą zarówno w modyfikacji powierzchni osadu, jak i w dopływie łatwo dostępnej materii organicznej do dna. Zjawisko to wpisuje się w szerszy kontekst badań nad szybkim transportem węgla w oceanach (m.in. „jelly falls”, „blue carbon”) i podkreśla znaczenie metod obrazowych *in situ* w dokumentowaniu procesów ekologicznych, które pozostają w dużej mierze niewidoczne dla klasycznych technik próbkowania.

Piąta publikacja wchodząca w skład rozprawy („Surface lebensspuren and their tracemakers in Arctic fjords of Spitsbergen: Patterns, diversity, and environmental controls”, *Polish Polar Research*, 2025) opiera się na materiale wideo zebrany na 206 stacjach, z których na 57% zarejestrowano jednoznaczne przykłady lebensspuren. W toku badań po raz pierwszy w fiordach Spitsbergenu wyróżniono łącznie 19 morfologicznych typów śladów, w tym osiem form nieopisanych wcześniej w literaturze. Dla 18 typów możliwe było wskazanie ich twórców, a dla dziesięciu – przypisanie do konkretnego

gatunku lub rodzaju, co stanowi rzadko osiągnięty poziom rozpoznania taksonomicznego w badaniach neoichnologicznych środowisk morskich. Kluczowym elementem tej pracy było bezpośrednie powiązanie śladów z organizmami je wytwarzającymi, możliwe dzięki długotrwałej, wysokorozdzielczej rejestracji wideo dokumentującej zarówno obecność śladu, jak i zachowanie organizmu w trakcie jego powstawania. Jak podkreśla literatura, identyfikacja wytwórcy śladu w środowisku morskim jest wyjątkowo trudna i zwykle wymaga analizy setek godzin nagrań, przy czym w większości dotychczasowych badań ślady i organizmy analizowane są rozdzielnie. Zastosowana w niniejszym cyklu prac metoda pozwoliła na jednoczesną analizę morfologii śladów, zachowania organizmów oraz kontekstu środowiskowego ich występowania, dostarczając obszernego zestawu danych dla środowisk arktycznych.

Analiza wykazała, że dominującą grupą wytwórców śladów były szkarłupnie, odpowiedzialne za ponad połowę wszystkich zarejestrowanych lebensspuren, przy szczególnie istotnej roli rozgwiżdzy *Urasterias lincki*, której ślady lokomocyjne i spoczynkowe były najczęściej obserwowanym typami struktur biogenicznych. Istotny udział miały również skorupiaki dziesięcionogie (głównie kraby pustelniki), ślimaki oraz – w mniejszym stopniu – wieloszczety i ryby denne. Rozmieszczenie i różnorodność śladów wykazywały wyraźne związki z czynnikami środowiskowymi, w szczególności z odległością od czoła lodowców, poziomem zawiesiny przydennej oraz charakterem osadu.

Wyniki te jednoznacznie wskazują na znaczenie tzw. poziomej bioturbacji (horizontal bioturbation), rozumianej jako kumulatywny wpływ mobilnej megafauny na powierzchnię osadu w skali większej niż jej chwilowa obecność rejestrowana na pojedynczym obrazie wideo. Lebensspuren stanowią w tym ujęciu zintegrowany zapis funkcjonowania ekosystemu dennego, kumulujący efekty aktywności organizmów w czasie i umożliwiający ocenę ich wpływu na strukturę powierzchni osadu nawet w warunkach niskiej liczebności fauny.

Znaczenie tych wyników wykracza poza ekologię współczesnych ekosystemów arktycznych. Zidentyfikowane typy śladów, wraz z przypisanymi im wytwórcami i kontekstem środowiskowym, stanowią cenny materiał referencyjny dla interpretacji kopalnych zespołów śladów oraz rekonstrukcji dawnych środowisk sedymentacyjnych, w których organizmy rzadko zachowują się w zapisie kopalnym, a jedynym śladem ich

obecności są struktury biogeniczne. Tym samym badania te łączą podejście ekologiczne z neoichnologią i paleoichnologią, wpisując się w nowoczesne, interdyscyplinarne badania funkcjonowania dna morskiego.

Podsumowując, rozprawa wykazuje, że megabentos wód przybrzeżnych Svalbardu odgrywa istotną rolę w funkcjonowaniu ekosystemów dennych, zarówno jako element sprzęgający procesy pelagiczne i denne, jak i jako czynnik modyfikujący powierzchnię dna w skali „krajobrazu” bentosowego. Uzyskane wyniki wskazują ponadto, że w warunkach niskich temperatur i wydłużonych cykli życiowych duże, mobilne organizmy oddziałują na środowisko w sposób kumulatywny, łącząc redystrybucję materii organicznej z trwałą modyfikacją powierzchni osadu. Tym samym ich wpływ przekracza skalę chwilowej obecności obserwowanej w pojedynczym momencie. Powiązania z planktonem oraz niemal powszechna obecność megafauny na całym obszarze dna potwierdza wstępną hipotezę o znaczeniu tej grupy organizmów w polarnych fiordach. Wyniki te sugerują, iż tradycyjne ujęcie bentosu wymaga uzupełnienia o obserwacje *in situ* oraz analizy procesów zachodzących w skali czasowo-przestrzennej większej niż pojedyncze stanowisko.

List of research papers:

1. **Deja K.**, Węśławski J. M., Borszcz T., Włodarska-Kowalczyk M., Kuklinski P., Bałazy P., Kwiatkowska P., 2016. *Recent distribution of Echinodermata species in Spitsbergen coastal waters* Polish Polar Research, 37, pp. 511-526.
2. **Deja K.**, Ormańczyk M., Dragańska-Deja K., 2019. *Plankton or benthos: where krill belongs in Spitsbergen fjords? (Svalbard Archipelago, Arctic)* Polar Biology, 42, pp. 1415-1430.
3. **Deja K.**, Dragańska-Deja K., Węśławski J.M., 2023. *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, 46, pp. 1137-1143.
4. **Deja K.**, 2025. *Observation of discarded appendicularian houses in the benthic and pelagic zones of Spitsbergen fjords using drop-camera imagery* Marine Ecology Progress Series, 771, pp. 71-88.
5. **Deja K.**, Uchman A., 2025. *Surface lebensspuren and their tracemakers in Arctic fjords of Spitsbergen: Patterns, diversity, and environmental controls* Polish Polar Research, 46, pp. 147-165.

Research paper no 1

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Recent distribution of Echinodermata species in Spitsbergen coastal waters

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Abstract: Thirty-two species of echinoderms from epibenthic sledges, dredges, scuba diving, and other samples (in total: 467 samples and *c.* 20 000 specimens) from fjords and coastal waters off Spitsbergen were analysed between 1996 and 2014. The most numerous group of echinoderms in the coastal waters off Spitsbergen is brittle stars (78% of the total individuals). The echinoderms do not form any clear assemblages according to depth or distance from glacial sedimentation and substrate. Some species prefer hard bottom (*Strongylocentrotus droebachiensis*) or water free from glacial suspensions (*Ophiopholis aculeata*). In contrast to the species listed above, we also found opportunistic species such as the starfish *Urasterias lincki* and the brittle star *Ophiocten sericeum*. These two species are distributed quite uniformly, regardless of the environmental factors. The majority of the species prefer a soft bottom below 200 m.

Key words: Arctic, fjords, Echinodermata, climate change, species distribution, megabenthos.

Introduction

Most echinoderms are megafauna, which are animals larger than a few centimeters that live as epifauna and are visible in underwater images. These large, long-living animals form an important element of the macroscopic food web and often serve as indicators of environmental change (*e.g.* Blacker 1957; Hoey *et al.* 2010). Because the European Arctic is considered the area most

impacted by ongoing climate change (ACIA 2005), identifying the distribution patterns of key species is also of great interest for general environmental knowledge and fisheries; this knowledge is expressed in large-scale mapping initiatives (Anisimova *et al.* 2010). Echinoderms in the Northern Atlantic belong to well-known taxa; *i.e.*, no major problems exist with species identification, and the expected number of unknown taxa is very low (Piepenburg and Schmidt 1996; Piepenburg 2000; Appeltans *et al.* 2011).

Due to its accessibility, the Svalbard archipelago was an area of early faunistic studies during the Arctic expeditions at the end of the 19th century, which collected data on Decapoda, Echinodermata, Amphipoda, Gastropoda, fish and macroalgae (see the review in Palerud *et al.* 2004). Recently, some of the old sampling stations were revisited and revealed a surprising stability of some animal taxa such as Decapoda (Berge *et al.* 2009) and the benthos in general (Renaud *et al.* 2007; Kędra *et al.* 2011). Large-scale fishery research in the Barents and Norwegian seas led to the use of by-catch animals that may serve as indicators of hydrological and climatic variability (Blacker 1957; Dyer *et al.* 1984). These animals may follow major environmental driving forces in the area: fluctuations in Atlantic water inflow to the Svalbard shelf and the Fram Strait (Walczowski and Piechura 2006) and instability in pack ice and fast ice cover (ACIA 2005). Coastal water fauna have received much less attention in this respect (bioindicators) than have the shelf and offshore benthos (Piepenburg *et al.* 1996; Berge *et al.* 2005; Renaud *et al.* 2011; Włodarska-Kowalczyk *et al.* 2012). Nevertheless, in view of the massive change in the distribution of tidal glaciers (melting, discharge of sediment-laden freshwater, and the uncovering of new areas of the seabed), the fjords are interesting sites for studying the occurrence patterns of megafauna. Our study aims to document the recent (1996–2014) occurrence of echinoderm species in the coastal and fjord waters of Svalbard with special reference to Hornsund, Isfjorden and Kongsfjorden, which are the most visited and studied Arctic fjords (Hop *et al.* 2002; Svendsen *et al.* 2002; Kędra *et al.* 2010). We wanted to determine whether cold water species (based on the literature) had retreated to give space to the thermophilic newcomers. Coastal Echinodermata distribution analysis can be an indicator of the presence of a water mass and an increase in temperature.

Study area

The Svalbard archipelago is situated in the northern Atlantic Ocean on the zoogeographical border between the Subarctic and Arctic provinces (Bakus 1986). The division runs along the west coast of Spitsbergen Island and is usually reported as a border between the Barents Sea and the Norwegian Sea marine

fauna (Blacker 1957). The west coast is washed with the recently increasing inflow of Atlantic waters from the West Spitsbergen Current (Loeng 1991; Walczowski and Piechura 2006), whereas the eastern part of the archipelago is under the influence of the colder Barents Sea shelf waters and transformed local coastal waters of Atlantic origin. The difference between the particular water masses is not very sharp: salinity ranges from the lowest value of 33.5 in the Arctic waters to the highest value of 34.7 in the core Atlantic waters (Beszczyńska-Moller *et al.* 1997). Seasonal differences are important because the inner fjord basins and most of the eastern parts of the archipelago are covered with fast ice and ice pack between December and June (Pavlov *et al.* 2010). In the winter, the water column cools to an isothermic -1.5°C in the fjords and coastal waters (Węsławski *et al.* 1994). In the summer, the maximum temperatures did not exceed 8°C at the surface and 5°C in the near-bottom waters (Swerpel 1985; Drewnik *et al.* 2016a). Most of the sediments in fjordic and coastal waters are glaciomarine and occur from numerous tidal glaciers that discharge turbid freshwaters and cause heavy mineral sedimentation in the fjords (Elverhoi *et al.* 1983; Lydersen *et al.* 2014). Stony and rocky outcrops are common, both as ice-rafted debris (dropstones) and as bedrock washed by the near-bottom currents (Elverhoi and Solheim 1983; Hop *et al.* 2002). Productivity in the Svalbard fjords and coastal waters is high, up to $120\text{ g C/m}^2/\text{year}$ (Eilertsen *et al.* 1989). The entire Svalbard is within an area of intensive warming (ACIA 2005), and numerous studies were recently undertaken on its hydrography and related interannual changes (*e.g.*, Walczowski and Piechura 2006; Cotier *et al.* 2010).

Materials and methods

The present material was collected between 1996 and 2014 during summer cruises of the *r/v Oceania* and *r/v Helmer Hansen*, including a number of scuba diving trips and underwater photography sessions (Lander, drop camera) within the framework of various projects run by the Institute of Oceanology PAS (Polish Academy of Sciences) in cooperation with Norsk Polarinstitutt, the University Centre in Svalbard and AkvaplanNiva. The various gear and the numbers of samples obtained are listed in Table 1. All of the samples were georeferenced and labelled with the depth, date and basic environmental parameters (temperature, salinity, and sediment/bottom type) and are stored at the Institute of Oceanology of Polish Academy of Sciences in the data repository (<http://www.iopan.gda.pl/projects/Game/Data>). The taxonomy was adopted from WoRMS (<http://www.marinespecies.org/>). The organisms were preserved on board/in the field in a 4% buffered formaldehyde solution or industrial alcohol and were identified

Table 1

Set of the samples collected and examined in this study during the summer seasons from 1996–2014.

Type of gear	Number of samples	Depth range [m]	Remarks
Van Veen grab	8	0–30	mainly small organisms and sampling only the soft bottom
Van Veen grab	61	31–100	
Van Veen grab	44	101–200	
Van Veen grab	43	201–400	
Epibenthic sledge	7	0–30	small and large organisms and different types of bottom
Epibenthic sledge	31	31–100	
Epibenthic sledge	14	101–200	
Epibenthic sledge	57	201–400	
Triangle dredge	4	0–30	small and large organisms and different types of bottom
Triangle dredge	1	31–100	
Triangle dredge	1	201–400	
Drop camera, Landers	3	31–100	mostly larger organisms and different types of bottom
Drop camera, Landers	9	101–200	
Scuba diver	181	0–30	mostly larger organisms and mainly hard bottom
Scuba diver	3	31–100	
Total	467		

under a stereomicroscope in the lab either as dry or wet samples, depending on the specific group. Identification was attempted to the lowest taxonomic level possible using the keys by: Clark (1970) Anisimova (1989), Hayward and Ryland (1990) and Anisimova (1992) *et al.*, and the dedicated web page (<http://www.iopan.gda.pl/ekologia/borszcz-echino/bor77.htm>.) The number of species in the sample was used to create arrays as the basis for the multivariate analysis. The data were transformed by presence/absence with dominant and rare species considered equally important (0 = absent in a sample, 1 = present) (Clarke and Green 1988). The similarities between the pairs of samples were calculated using the Bray-Curtis index (Bray and Curtis 1957). This formula is recommended in these types of analyses due to its insensitivity to the effect of “common absent” species in the samples (Clarke and Warwick 1994). Bray-Curtis similarities between the samples are shown by the nMDS (non-metric multidimensional scaling) method. Dendrogram of similarities between the species was created

based on transformed presence/absence data and used clustering algorithm “group average”. The Chao2 estimator is based on the principle that rare and uncommon species carry information about the number of species that are missing in samples (Chao 2004). $Chao2 = S_{obs} + Q_1^2/2Q^2$, where Q_1 is number of species that occurred only in one sample (uniques) and Q^2 is the number of species that have occurred exactly in two samples (duplicates). The Michaelis-Menten (MM) estimator is one of the most commonly used methods to generate a curve for the accumulation of species (Magurran 2004). The MM asymptote estimation is used to estimate the total species richness. The data were computed using the STATISTICA and PRIMER (multivariate statistics for ecologist) software.

Results

We registered over 460 positive findings (samples containing Echinodermata) from over 1000 seabed samples (Fig. 1). The analysed material contained 19.830 individual echinoderms. The material was determined to represent 32 species, including 14 starfish, 10 brittle stars, 5 sea cucumbers, 2 crinoids, and one species of sea urchin (Table 2 and 3). The species accumulation curve increased along its entire length and approached a level asymptote. Chao2 provided an estimate of 38 species and 30 species after using the Michaelis-Menten estimator (MM) (Fig. 2). The most common species were the sea urchin *Strongylocentrotus droebachiensis* and the brittle stars *Ophiura robusta*, *Ophiosten sericeum*, *Ophiopholis aculeata*, and *Ophiura sarsii* (over 10% of the frequency in samples containing echinoderms). Three species were most abundant: *O. sericeum*, *O. robusta* and *S. droebachiensis* (6972, 4772 and 3672 individuals, respectively, Table 3). Singletons, which were single individuals in the whole collection, included two sea cucumbers (*Acanthotrochus mirabilis* and *Cucumaria frondosa*), one brittle star (*Gorgonocephalus eucnemis*) and four starfish (*Hippasteria phrygiana*, *Hymenaster pellucidus*, *Poraniomorpha tumida*, and *Pteraster obscurus*, Table 2). The majority of the species found have wide boreal-arctic distributions (75%), with only six species described as true Arctic cold water species (*Acanthotrochus mirabilis*, *A. sundevalli*, *Hymenaster pellucidus*, *Ophiopleura borealis*, *Poliometra proluxa* and *Poraniomorpha tumida*; Table 3), (Brattegard and Holthe 2001; Sirienko 2001; Fetzer and Arntz 2008). The dominant functional groups were deposit feeders (10 species) and carnivores (12 species, Table 3). Species found in the collected samples were analysed for their co-occurrence to reveal species assemblages; however, there is no well-defined grouping (associations among the species analysed are on the very low level of similarity) below 40% (Fig. 3). The depth is not a factor that separates the collected species; *i.e.*, among the samples collected in the four depth strata, very

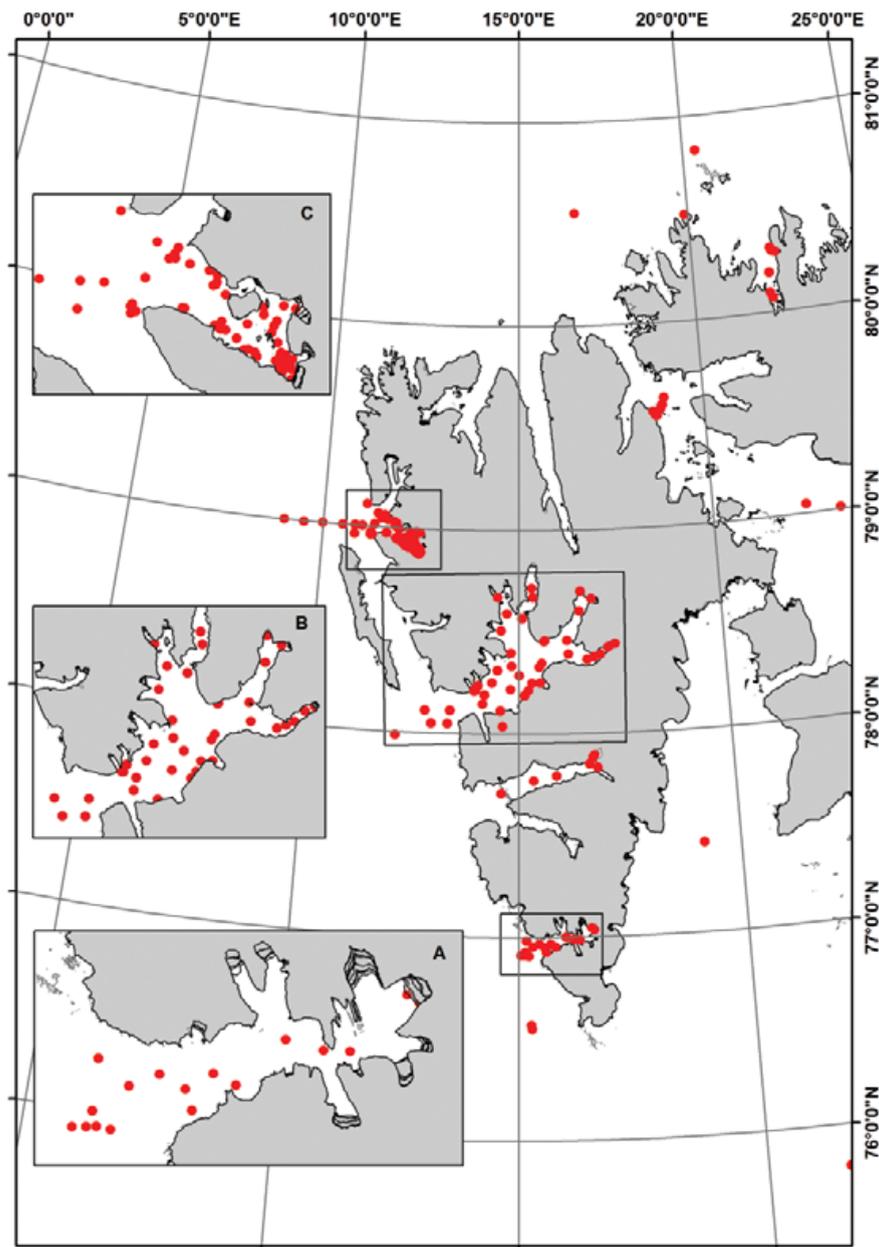


Fig. 1. Distribution of sampling stations in the Svalbard archipelago, with a focus on Hornsund (A), Isfjorden (B) and Kongsfjorden (C).

little difference in species composition was found (Fig. 4). The stations analysed for the spatial distribution pattern are spread nearly evenly on the nMDS plot (Fig. 4). Analysing the nMDS related to different sub-areas/fjords did not show any significant patterns. Depth, temperature, and other environmental variables were checked as the occurrence predictors, and the main relationship was between the shallow samples and the presence of *S. droebachiensis* (reportedly a sole herbivorous species feeding on kelp). Individual species distribution maps are available at the following web page: (www.ioPAN.gda.pl/projects/).

Table 2

Dominance-relative contribution (D%) and frequency of occurrence (F%) of species in three studied fjords combined with the entire research area (all data).

Fjord	Isfjord		Kongsfjord		Hornsund		All data	
	D%	F%	D%	F%	D%	F%	D%	F%
<i>Acanthotrochus mirabilis</i> Danielssen et Koren, 1881	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2
<i>Amphiura sundevalli</i> (Müller et Troschel, 1842)	1.8	11.6	0.4	4.4	4.1	28.1	0.9	12.4
<i>Asterias rubens</i> Linnaeus, 1758	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.6
<i>Crossaster papposus</i> (Linnaeus, 1767)	0.2	3.3	0.3	2.6	0.0	0.0	0.2	3.9
<i>Ctenodiscus crispatus</i> (Retzius, 1805)	0.7	6.6	0.0	0.0	0.4	3.1	0.7	4.5
<i>Cucumaria frondosa</i> (Gunnerus, 1767)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2
<i>Diplopteraster multipes</i> (M. Sars, 1866)	0.1	0.8	0.0	0.0	0.0	0.0	0.0	1.3
<i>Eupyrigus scaber</i> Lütken, 1857	0.4	2.9	1.9	8.8	0.2	4.7	0.3	4.7
<i>Gorgonocephalus eucnemis</i> (Müller et Troschel, 1842)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4
<i>Heliometra glacialis</i> (Owen, 1833 ex Leach MS)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6
<i>Henricia sanguinolenta</i> (O.F. Müller, 1776)	0.6	7.1	0.1	0.9	0.1	3.1	0.2	5.4
<i>Hippasteria phrygiana</i> (Parelius, 1768)	0.0	0.0	0.0	0.0	0.1	1.6	0.0	0.2
<i>Hymenaster pellucidus</i> Thomson, 1873	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2
<i>Marthasterias glacialis</i> (Linnaeus, 1758)	0.0	0.0	0.0	0.0	1.3	3.1	0.1	0.4
<i>Myriotrochus rinkii</i> Steenstrup, 1851	0.1	1.2	0.4	4.4	0.0	0.0	0.0	1.7
<i>Ophiacantha bidentata</i> (Bruzelius, 1805)	0.5	1.7	1.6	10.5	4.1	14.1	1.1	8.6
<i>Ophiocten sericeum</i> (Forbes, 1852)	9.8	10.8	22.5	22.8	45.7	40.6	35.2	20.2
<i>Ophiopholis aculeata</i> (Linnaeus, 1767)	2.0	15.4	9.6	12.3	14.4	10.9	3.9	16.5
<i>Ophiopleura borealis</i> Danielssen et Koren, 1877	0.1	0.4	0.0	0.0	0.0	0.0	0.1	0.4
<i>Ophioscolex glacialis</i> Müller et Troschel, 1842	0.0	0.4	0.1	0.9	0.0	0.0	0.0	0.6
<i>Ophiura robusta</i> (Ayres, 1854)	11.9	18.3	19.3	23.7	6.9	23.4	24.1	22.5
<i>Ophiura sarsii</i> Lütken, 1855	1.9	10.4	12.2	18.4	3.7	12.5	2.6	15.2
Ophiuroidea juv. non determined	4.6	13.7	6.9	15.8	1.0	7.8	8.9	13.3
<i>Poliometra proluxa</i> (Sladen, 1881)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4
<i>Pontaster tenuispinus</i> (Düben et Koren, 1846)	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.9
<i>Poraniomorpha tumida</i> (Stuxberg, 1878)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2
<i>Psolus squamatus</i> (O.F. Müller, 1776)	0.4	2.1	0.1	0.9	0.0	0.0	0.1	1.3
<i>Pteraster militaris</i> (O.F. Müller, 1776)	0.1	1.2	0.0	0.0	0.0	0.0	0.0	0.6
<i>Pteraster obscurus</i> (Perrier, 1891)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2
<i>Solaster endeca</i> (Linnaeus, 1771)	0.2	1.7	0.1	0.9	0.0	0.0	0.1	1.1
<i>Stegophiura nodosa</i> (Lütken, 1855)	4.3	10.0	0.0	0.0	0.0	0.0	1.2	5.4
<i>Strongylocentrotus droebachiensis</i> (O.F. Müller, 1776)	60.3	60.6	13.4	22.8	5.8	4.7	18.5	41.6
<i>Urasterias lincki</i> (Müller et Troschel, 1842)	0.1	1.2	11.0	11.4	12.0	20.3	1.7	7.5

Table 3

Species composition and basic characteristics including food guilds (sus – suspension feeders, df – deposit feeders, car – carnivores, omni – omnivorous, sca – scavengers, and herb – herbivorous), habitat (m – mud bottom, mg – muddy gravel, r – rocky bottom, s – sand, ms – mixed sediments, si/ssi – silt, sandy silt, sb – soft bottom, and vs – variety of substrates) and zoogeographic rank (A – arctic, B – boreal, BA – boreal-arctic, and C – circumboreal). The data were compiled from Connor *et al.* (1997), Piepenburg (2000), Fetzer and Arntz (2008), and web sources <http://www.marinespecies.org/>, <http://www.habitas.org.uk/marinelife/>, and <http://www.iopan.pl>.

N	Species	n	depth [m]	Food guild	Habitat	Zoogeography
1	<i>Acanthotrochus mirabilis</i>	1	201	df?	m/mg	A
2	<i>Amphiura sundevalli</i>	187	6–355	sus	m	A
3	<i>Asterias rubens</i>	3	19–67	car	r/s/m	B
4	<i>Crossaster papposus</i>	31	15–207	car/omni/sca	r	BA
5	<i>Ctenodiscus crispatus</i>	133	74–323	df	m/ms	BA
6	<i>Diplopteraster multipes</i>	7	18–178	car?	vs?	BA. C
7	<i>Eupyrigus scaber</i>	53	54–305	df?	m/ms/mg	BA
8	<i>Gorgonocephalus eucnemis</i>	2	80	car/sus	r	BA
9	<i>Helioметра glacialis</i>	3	56–207	sus	si/ssi	BA
10	<i>Henricia sanguinolenta</i>	44	10–120	sus	r	BA
11	<i>Hippasteria phrygiana</i>	2	147	car	ms	BA
12	<i>Hymenaster pellucidus</i>	1	207	df?	m	A
13	<i>Marthasterias glacialis</i>	19	50–100	car/omni/sca	hs	BA
14	<i>Myriotrochus rinkii</i>	9	10–308	df	mg/ms	BA
15	<i>Ophiacantha bidentata</i>	212	50–355	sus	ms	BA
16	<i>Ophiocten sericeum</i>	6972	10–323	df	sb	BA
17	<i>Ophiopholis aculeata</i>	782	6–390	sus	h	BA
18	<i>Ophiopleura borealis</i>	15	113–323	car/omni	sb/m	A
19	<i>Ophioscolex glacialis</i>	4	10–288	car	sb/m	BA
20	<i>Ophiura robusta</i>	4772	6–390	sus/car/omni/sca	vs	BA
21	<i>Ophiura sarsii</i>	509	2–288	car/omni/sca	sf	BA
22	Ophiuroidea juv	1768	4–300			
23	<i>Poliometra prolixa</i>	5	178–207	sus	si/ssi	A
24	<i>Pontaster tenuispinus</i>	11	178–323	df	sb/ms	BA
25	<i>Poraniomorpha (Poraniomorpha) tumida</i>	2	323			A
26	<i>Psolus squamatus</i>	22	120–240	df	mg/ms	BA
27	<i>Pteraster militaris</i>	4	15–20	df?	mg/ms	BA
28	<i>Pteraster obscurus</i>	1	60	df?	mg/ms	BA

N	Species	n	depth [m]	Food guild	Habitat	Zoogeography
29	<i>Solaster endeca</i>	12	12–100	car/omni	mg	BA
30	<i>Stegophiura nodosa</i>	231	6–240	car	s/mg	BA
31	<i>Strongylocentrotus droebachiensis</i>	3672	6–260	herb	r	BA
32	<i>Urasterias lincki</i>	340	15–323	car/omni/sca	ms	BA
33	<i>Cucumaria frondosa</i>	1	45	sus	mg/r	BA

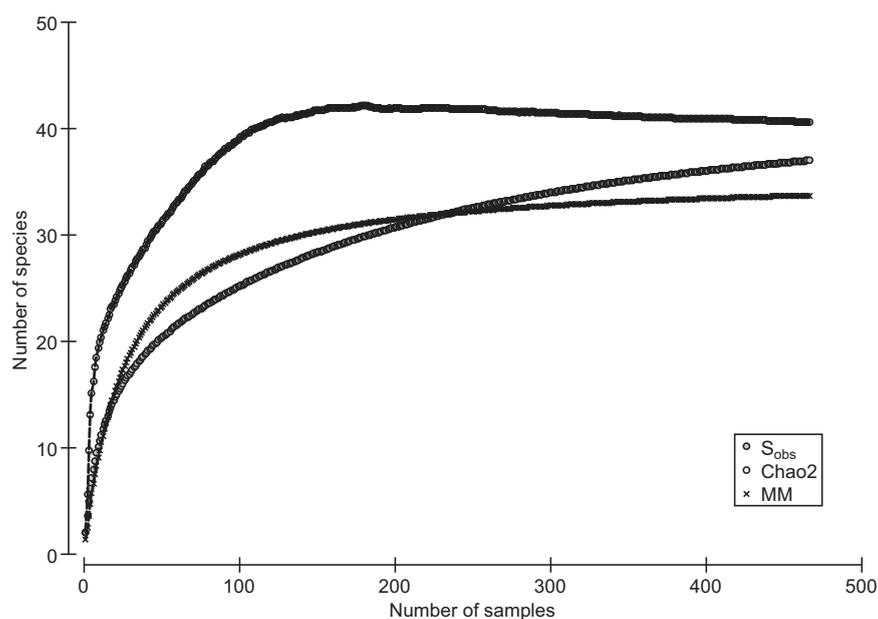


Fig. 2. Species accumulation curve representing the number of species (S_{obs}) and the number of species estimated by the Chao2 and Michaelis - Menten (MM) equations.

Discussion

The representativeness of the collected material was limited to the qualitative information regarding species presence/absence. The number of sampling points was high, although the samples were not distributed on a regular grid, as is recommended for species distribution modelling (Drewnik *et al.* 2016b). However, the set of species collected in the present study seems to be very complete, considering the obtained species accumulation curve (a similar result was obtained for other taxa collected in our projects; *e.g.*, Kędra *et al.* 2013). We found four new species for the area, including a single specimen of *Acantotrochus mirabilis*, which is a deep-water holothurian that has also been reported from Norwegian and Greenland seas below depths of 1000 m (Gebruk *et al.* 2014), but our record is a distinctly shallow one (250 m). Three other species (*Asterias rubens*, *Diplopteraster multipes*, and *Marthasterias glacialis*),

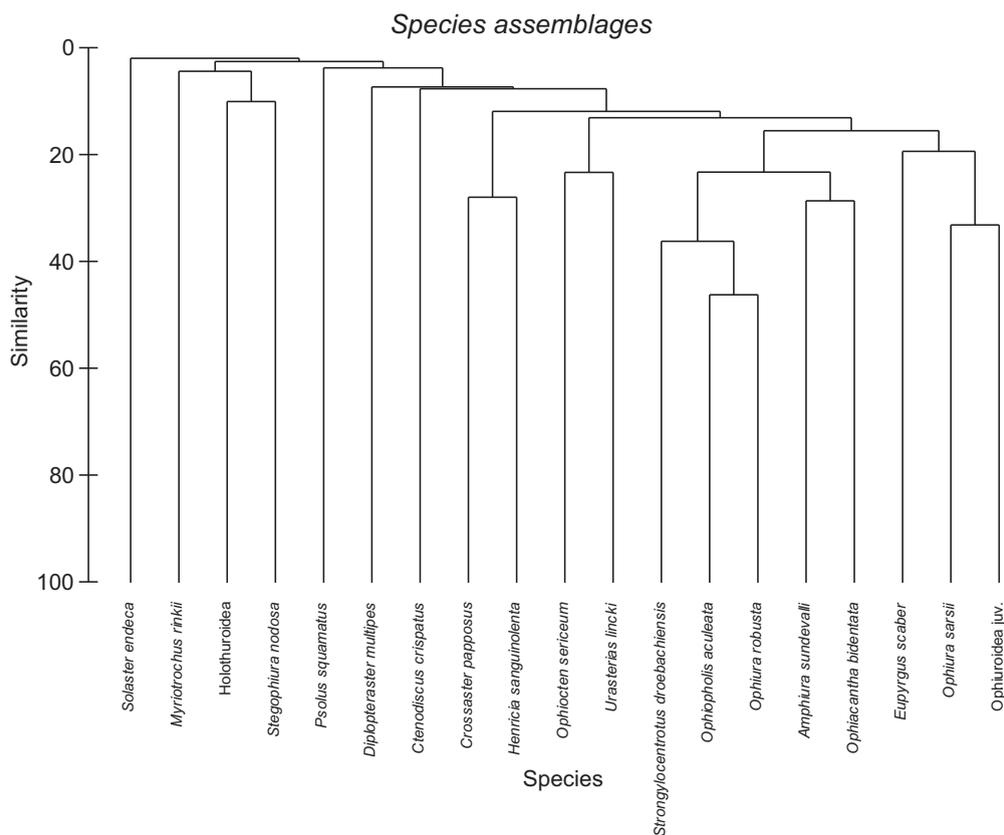


Fig. 3. Echinodermata species co-occurrence; data from the entire collection to reveal the species associations. Based on transformed presence/absence data; only species observed at five or more stations are included.

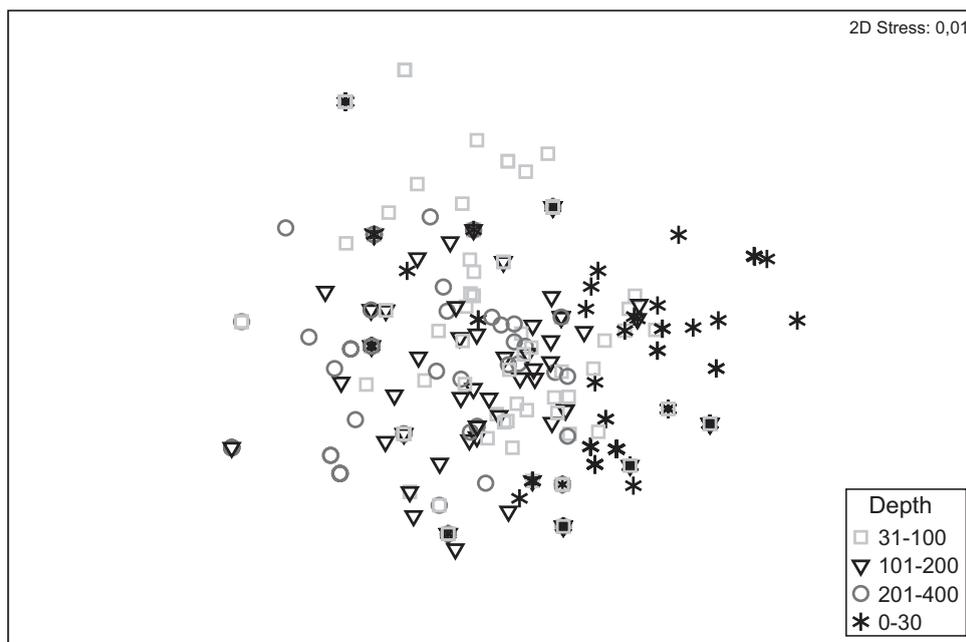


Fig. 4. Echinodermata species depth occurrence; the level of species similarity among the four depth intervals on the nMDS chart. The data were transformed as presence/absence.

all of wide boreal or circumpolar distributions, are known from Norway but had not been recorded so far north. We did not find the 30 species that had previously been recorded from Svalbard (Palerud *et al.* 2004), but some of these were rare echinoderms reported from deep water and the open shelf. The only exception was *Strongylocentrotus pallidus* (Voronkov *et al.* 2013), which might have been missed in our collection because it is very rare and almost indistinguishable from *Strongylocentrotus droebachiensis*. The set of echinoderm species observed at Svalbard might be treated as a subsample of the Norwegian Sea continental fauna, with the exception of only three species (*Stegophiura nodosa*, *Hymenaster pellucidus*, and *Ophiopleura borealis*); all three have been recorded from the Barents and Greenland Seas but have not been reported from coastal Norway (Piepenburg *et al.* 1996; Brattegard and Holthe 2001). All of the other echinoderm taxa collected on Svalbard have also been recorded in Norway, and the species number drops evenly from over 150 in western Norway to fewer than 60 in eastern Svalbard, along with the diminishing influence of Atlantic waters away from the Norwegian Sea (Fig. 5). This pattern of diminishing species number from the source (Atlantic) towards the Siberian shelf was presented for a number of taxa by Sirienko (2001).

The marine ecosystem of Svalbard is highly productive on the shelf (Wassmann *et al.* 2010) and in the fjords and coastal waters and in terms of habitats is no less diversified than that of continental Norway. The habitat heterogeneity is commonly considered a good predictor of species richness in the marine benthos (*e.g.*, Ellingsen and Gray 2002). Therefore, the reason

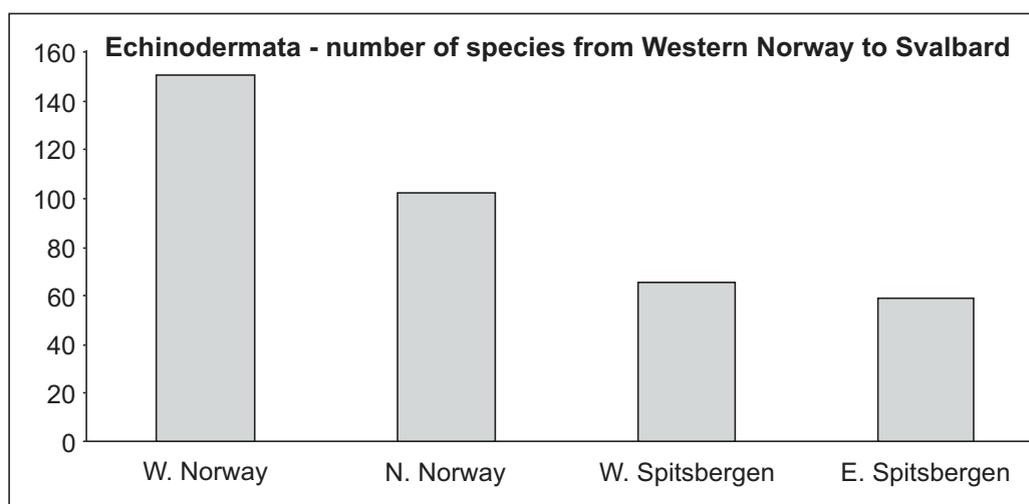


Fig. 5. Compilation of the distribution data from Norway (Brattegard & Holthe 2001) and Svalbard (Gulliksen *et al.* 1999). The number of valid species of Echinodermata recorded in the given regions including offshore shelf waters (Western Norway, Northern Norway, West Spitsbergen, and East Spitsbergen).

for the deficit in species richness in the Svalbard fjords is unclear. It might be evolutionary history following the deglaciations because the area is still recovering from the ice sheet (Ellingsen and Gray 2002); for the neritic, shallow water species, it could simply be the island effect (the distance from the mainland versus the size of the inhabited island; McArthur and Wilson 1964), which has been found as a strong predictor in European benthos distribution (Arvanitidis *et al.* 2009).

The wide occurrence of all of the observed species and the lack of clear distributional patterns in the study area confirms the observations of Dyer *et al.* (1985), who concluded that compared to the Blacker (1957) data, species are more widespread with fewer clear links to temperature-salinity patterns. This also follows a general observation by Thrush *et al.* (2006) regarding the homogenisation of habitats that follows global warming. Stability refers to the taxa presence in the fjords (Renaud *et al.* 2007; Berge *et al.* 2009), whereas homogeneity was recorded on the shelf (Dyer *et al.* 1984). Species having pelagic larvae, as is the case for most of our echinoderms, are expected to expand their occurrence ranges with the ongoing borealisation of the Svalbard area (Berge *et al.* 2005). West Spitsbergen fjords and coastal waters that were previously exposed to regular freezing and maintained local cold water pools are now often washed by Atlantic waters from the shelf and represent an ecotone type of area with mixed subarctic/boreal conditions (Drewnik *et al.* 2016a). This may explain the lack of zonation among the Echinodermata species found in this study.

Conclusions

The fjords of Spitsbergen, despite their diversity in physical factors such as water temperature, salinity and sedimentation, do not differ significantly from each other with respect to their Echinodermata fauna (Table 2). There was no depth zonation or other factor (water mass or sediment) that would clearly separate observed coastal and neritic species of echinoderms. Compared to historical records collected between 1900 and 1970 (Hofsten 1915; Clark 1970; Anisimova 1989; Gulliksen *et al.* 1999), the new thermophilic elements are sparse (three new records: *Acanthotrochus mirabilis*, *Diplopteraster multipes*, *Marthasterias glacialis* and eight species that were identified in older records were not present in our collection), and local cold water species are still in the same places in which they have been reported over the last 100 years. It is probable that the echinoderm fauna of Spitsbergen coastal waters is homogenous in terms of distribution and species associations. Reasons for the unexpected homogeneity could be the dominance of subpolar (Atlantic) species with a high physiological and ecological plasticity.

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Plankton or benthos: where krill belongs in Spitsbergen fjords? (Svalbard Archipelago, Arctic)

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Abstract

This study couples observations of krill (*Thysanoessa inermis*, *Thysanoessa longicaudata*, *Thysanoessa rashii*) from Tucker trawl nets and cameras, trying to test hypothesis that in the glaciated fjords of Svalbard most of the euphausiids biomass is located in near-bottom habitat and explains why in this region there are a substantial part of the krill population near the sea floor. Photographic material from the summers of 2013–2017 shows large numbers of near-bottom euphausiids (39% of the total krill biomass in Hornsund and 41% in Kongsfjorden), which reached a maximum density of 751 ± 224 indiv. m^{-3} in Kongsfjorden, 731 ± 198 indiv. m^{-3} in Hornsund, and 426 ± 124 indiv. m^{-3} in Adventfjorden. Regional distribution of near-bottom aggregations of krill seem to be associated with close proximity to the glacier front rather than with depth. The highest densities were located in the glacial bays. Where and why these aggregations occur is probably complicated and dependent on many environmental factors acting together. However, the dominant factors seem to be sedimentation and estuarine circulation. No krill aggregations were found during the winter cruise. The dominating species was *T. inermis* which made up 90% of the community. Other krill species—*T. rashii* and *T. longicaudata*, made up 6% and 4%, respectively. In the summer, aggregations of other macrozooplankton were also observed: amphipods of the genus *Themisto* and chaetognaths of the genera *Eukrohnia* and *Parasagitta*. Euphausiid densities in the water column (from Tucker trawl hauls) were an order of magnitude lower (0.33 indiv. m^{-3} for Kongsfjorden and 0.61 indiv. m^{-3} for Hornsund) than those of the near-bottom aggregations observed on cameras system. At most stations, the krill exhibited a behaviour, known as “nose diving” in the sediment, which is likely related to feeding. Observation of this phenomenon may indicate that krill (mostly *T. inermis*), found near the bottom of Spitsbergen fjords, is looking for food there. Near-bottom aggregations of zooplankton, mainly krill, are common in glacial bays and can be important in the function of the fjord ecosystem. Our research proves that the zooplankton biomass can be highly underestimated if only Tucker trawl sampling is done, due to neglecting the near-bottom layer in this type of method.

Keywords Arctic · Fjords · Spitsbergen · Plankton · Benthos · Krill

Introduction

Krill (the collective name of Euphausiacea species) is a key component of many marine ecosystems. Additionally, krill is an important link between microscopic algae

(microplankton) and large predators such as whales, sea-birds, and fish (Cleary et al. 2012). Globally, there are 86 species of krill (Everson 2000); in the fjords of Spitsbergen, there are five. The most common is *Thysanoessa inermis*, followed by also numerous *Thysanoessa rashii* and *Thysanoessa longicaudata*. In connection with the intensification of Atlantic water inflow, species *Meganctiphanes norvegica* and *Nematoscelis megalops* are increasingly noted in Arctic region (Buchholz and Buchholz 2010). Many species of krill are known to form dense pelagic swarms and schools in temperate and polar seas, mostly in the euphotic zone, and near the sea surface or close to the sea ice (Mauchline and Fisher 1969). There has been a recent increase in the number of publications on benthopelagic krill aggregations due to the

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development of new techniques that use underwater imagery and hydroacoustics (Hirche et al. 2016). Benthopelagic aggregations of krill were discovered in both the Northern Hemisphere (Greene et al. 1988; Gomez-Gutierrez and Robinson 2006; Laudien and Orchard 2012; Hirai and Jones 2012; Hirche et al. 2016) and the Southern Hemisphere (Gutt and Siegel 1994; Clarke and Tyler 2008; Nicol and Brierley 2010). Antarctic krill (*Euphausia superba*) were found near the seafloor at depths up to 3500 m (Clarke and Tyler 2008; Schmidt et al. 2011). A multitude of observations of krill near the bottom of the ocean, especially at great depths, indicate that these are not accidental observations of "ecological outliers" (Brierley 2008). Deep migration and feeding at the sea bottom is probably an important part of the ecology of krill, and this characteristic constitutes a link between the benthic and pelagic food webs. However, occasionally epizotic parasitoid infection cause large numbers of individuals descend to die, resulting in mass mortalities (Gómez-Gutiérrez et al. 2003). The depth data showing near-bottom concentrations of *M. norvegica* presented by Hirai and Jones (2012) suggest that these aggregations may be an important source of nutrients and carbon for the deep-living pelagic and benthic fauna in deep sea environment. Schmidt et al. (2011) showed that local differences in the vertical distribution (lower concentration of krill in surface waters) of Antarctic krill could indicate less efficient food acquisition or higher predator pressure in surface waters. Due to their frequent change of feeding location (from the seabed to the upper water column and back), krill can provide considerable amounts of labile iron to the surface waters of the Southern Ocean (Schmidt et al. 2011) and this process might also occur in the Spitsbergen fjords.

The observations of benthopelagic aggregations of euphausiids in Kongsfjorden (Hirche et al. 2016), Hornsund, and Adventfjorden (this study) support the hypothesis of the wider nature of this phenomenon, as well as the need for a new assessment of the impact of a benthopelagic community on the fjord ecosystem. Our aim was to determine which habitat retains most of the krill biomass in glacial fjords—the water column or the near-bottom waters and explain why in this region there are a substantial part of the krill population near the sea floor. A combination of two sampling approaches—Tucker trawl net and near-bottom inspection with camera, let us evaluate adequate methodologies for study densities of zooplankton in Spitsbergen fjords.

Study area

The study area in the West Spitsbergen fjords is at high latitude (above 77°N) but is considered sub-Arctic due to frequent exposure to warm North Atlantic water inflows (Cottier et al. 2005, 2016; Promińska et al. 2017). The examined fjords have different morphologies, Kongsfjorden

is a deep fjord (more than 300 m at the entrance) connected to the outer shelf and has easy advection of shelf waters, while Hornsund is shallower (<200 m at the entrance) and usually filled with colder coastal waters (Drewnik et al. 2016; Promińska et al. 2017). Isfjorden, on the other hand, is a large fjord system with several branches. One of the branches is Adventfjorden which is approximately 8 km long and 3.5 km wide. Both Isfjorden and Adventfjorden are exposed to Atlantic water advection because they have no sill in the fjord mouth. Glaciers are present in the innermost fjord basins and the meltwater discharge is responsible for the strong summer density stratification and resulting estuarine circulation (Promińska et al. 2017). The water exchange in these fjords might be very dynamic (Jakacki et al. 2017) due to the tidal currents, wind-driven advection from the shelf (Goszczko et al. 2018), and glacial outflow (Urbanski et al. 2017). The following water masses were separated on the basis of CTD data (IOPAN, unpublished data) collected during our study in the fjords: Atlantic Waters (salinity above 35, temperature above 2.5 °C), Local Coastal Waters (salinity around 34–35, temperature between 2.5 and 0 °C), Winter Cooled Waters (salinity above 35, temperature below 0 °C), and Surface Coastal Waters (salinity below 34 and temperature above 0 °C). Characteristics distinguishing individual water masses in the Arctic fjords have been taken from the literature noted above.

Material and methods

The data presented here were collected between 2013 and 2017 during summer cruises (daylight) each year on S/Y Oceania and one winter cruise (only darkness) in 2016 on R/V Helmer Hanssen. There were 107 photographic stations established in the fjords of western Spitsbergen, mainly in Hornsund and Kongsfjorden (Fig. 1, Online Resource 1), and there were a total of 52 horizontal stratified Tucker trawl hauls conducted in the summer seasons of 2014, 2015, and 2016 for both fjords combined (Fig. 1, Online Resource 2). Photographic data were collected with three different systems depending on what was available on each cruise. In 2013, photographic stations were sampled using a lander equipped with a DSLR camera. The lander took ten digital photos per station. Most photographic data (2014–2017) were collected using an underwater camera, referred to here as a drop camera. This consisted of an analogue camera with a resolution of 700 TV lines (TVL) for live view and a digital camera (Panasonic HX-A500) that recorded material at high resolution (1280 × 720 px) on a memory card. The device was towed for 10 min above the bottom at a speed of 0.1–0.2 knots (0.05–0.1 m/s). For both types of gear, a pair of lasers was used to determine scale in the images. At some stations in 2016, the film material was collected using

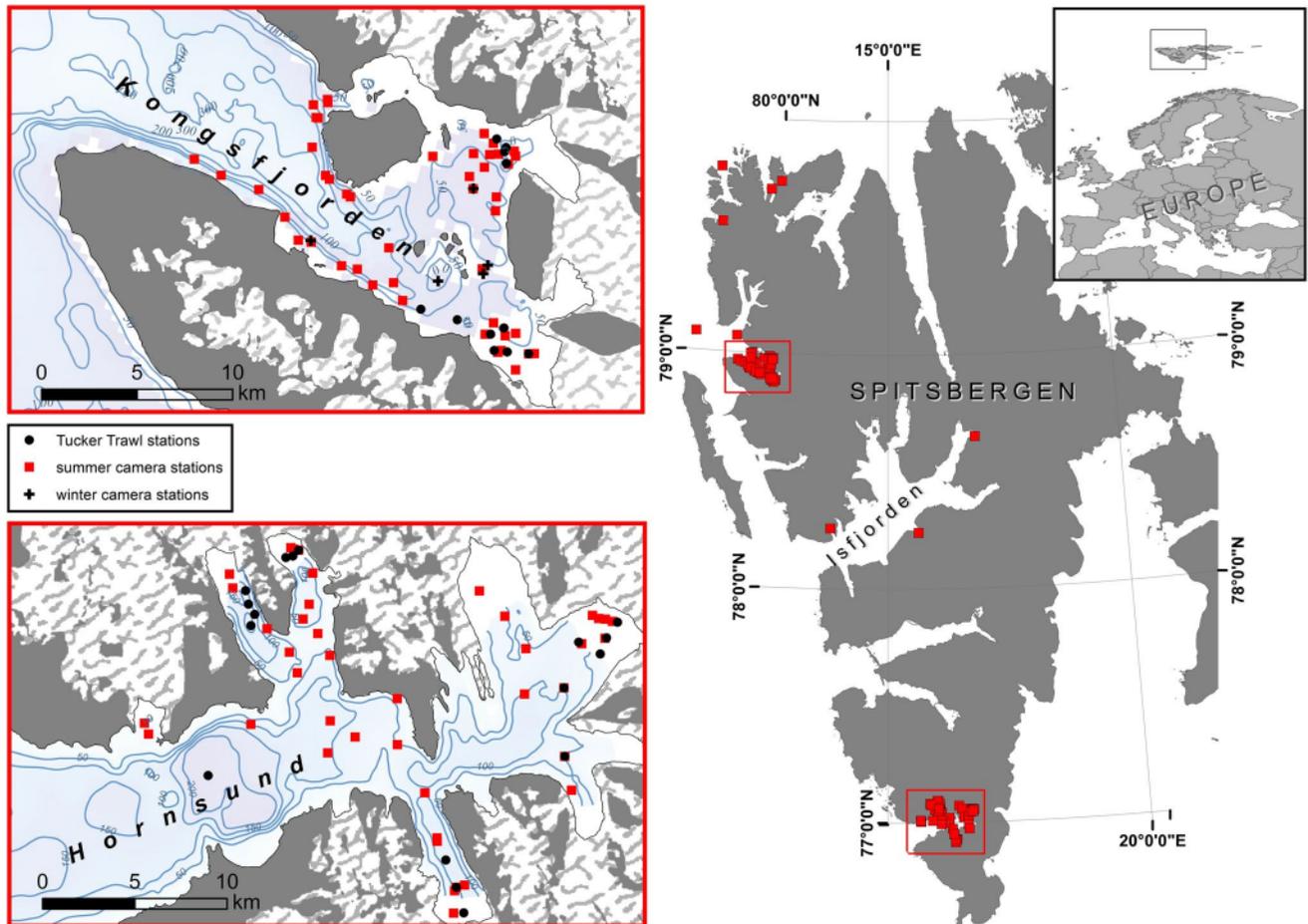


Fig. 1 Location of stations where seabed photos and Tucker trawl hauls were collected

a camera mounted on an epibenthic sledge (Online Resource 1). The camera used here is the same as in the case of drop cameras. None of the instruments were equipped with a pressure sensor. The camera on the lander was mounted one metre above a special weight, which released the trigger mechanism of the camera at the moment of contact with the bottom. This system worked well in hard bottom environments and in areas where the sediments were relatively well compacted. Soft, poorly compacted deposits, characteristic for glacier bays and the inner part of the fjord, mostly prevented the application of this method, because the process caused resuspension of the sediment and resulted in poor or null visibility. To minimize the chance of this happening with the drop camera, it was towed approximately 50 cm above the bottom. At stations located near the glacier front, this distance was 10–20 cm due to very poor visibility caused by high concentration of suspended particular matter from glacier discharge. Estimates of the height of the device over the bottom were supported by comparison with objects of known size in the images, e.g. sponges and sea anemones. Other researchers have used a similar method to assess

the height of the camera above the bottom (Gutt and Siegel 1994; Hirche et al. 2016). To calculate the number of individual krill at a station, five snapshots were selected from each video transect (drop camera) and five photos in the case of the lander. Snapshots and photos were selected from the beginning, middle, and end of the station recording and the average number of krill from all five counts was taken for further analysis. This method reduces the phototaxy effect, since the counts from the beginning of the recording, where krill did not have time to react, are also taken to the average. Following Gutt and Siegel (1994), the volume of water in which counts were made (number of individuals was expressed in m^3) was calculated using the known geometry of the camera lens and the distance to the bottom which is known. The density values from the video material are presented in six intervals: (0; 1–10; 11–50; 51–150; 151–350; and ≥ 350 indiv. m^{-3}).

The Tucker trawl had an opening of 1 m^2 and 1 mm mesh size. It was hauled horizontally for 10 min at an average speed of 1.5 knots (0.8 m/s). At each station, there was a surface haul (20–0 m) and a bottom haul (approximately

5 m above the bottom) (Fig. 1). The samples were preserved in 4% formaldehyde and analysed in the laboratory a few months later. All organisms from a subsample were counted, weighted, and identified, and these data were converted to the volume of the whole sample. All of the samples were georeferenced and labelled with the depth, date, and basic environmental parameters (e.g. temperature, salinity, and sediment/bottom type). The taxonomy nomenclature was adopted from WoRMS (<https://www.marinespecies.org/>).

CTD profiles were collected from the bottom to the surface on all cruises and the water mass types were classified based on the information in the literature (Promińska et al. 2017).

To visualize the area of interest and the distribution of the near-bottom krill aggregations, GIS analyses were performed using ArcGIS 10.4 software. Coastline and glacier were digitized from Landsat 8 satellite data from 2015. Near-bottom abundance estimations for whole fjords are based on the following assumptions: near-bottom aggregation of krill does not occur in areas shallower than 25 m and this krill aggregation occupies 1-m layers of water above the bottom. On the basis of bathymetric data (www.iopan.gda.pl/projects/Visual/index.html) for both fjords, areas with depths < 25 m were not taken into account in the analysis, and the unknown bathymetry near the glacier front was extrapolated using the inverse distance weighted (IDW) interpolation method. Near-bottom krill concentrations from measurement points were interpolated (kriging ordinary method) into the remaining area of the fjord (Fig. 4). After interpolation, data were divided into five density classes (polygons): 0, 1–10, 11–50, 51–150, and 150–300 (indiv. m⁻³). The water volume near the bottom (1 m layer) assigned to individual classes was calculated. To determine the krill density, the central value for each interval was selected (0, 5, 30, 100, and 200 (indiv. m⁻³), respectively), and the krill density was calculated for the individual polygons. The biomass for the studied area was calculated using a wet weight of 79.5 mg for individual krill. This weight was calculated as weighted arithmetic mean of the wet mass obtained for each Tucker trawl stations for each species separately. A weight to each species corresponding to its percentage was assigned: *Thysanoessa inermis*—0.9, *Thysanoessa longicaudata*—0.04, *Thysanoessa rashii*—0.06. The results from all examined polygons were summed to obtain an estimated krill biomass in the entire fjord near-bottom area for depths > 25 m. The krill concentration in the water column was calculated based on the average krill density obtained from the Tucker trawl data and the calculated volume of each fjord. GIS analyses were performed according to methods described in the ArcGIS Help Library (<https://resources.arcgis.com/>).

Results

Photographic material was examined from 107 photo stations (Fig. 1). Krill densities exceeding 100 indiv. m⁻³ were recorded at ten stations, with the largest numbers at the KGF9 station (751 ± 224 indiv. m⁻³) and at the HSD10 station (731 ± 198 indiv. m⁻³) (Fig. 2). Krill aggregations with > 100 individuals m⁻³ were recorded at five stations in Kongsfjorden (KGF 2, KGF 34, KGF 44, KGF 46, KGF 9), four stations in Hornsund (HSD 1, HSD 1', HSD 10, HSD 7), and at one station in Isfjorden (ISF 1) which should be interpreted as "cohesive swarms", i.e. swarms that are several dozen metres in diameter and contain several tons of biomass (Kalinowski and Witek 1980; Miller and Hampton 1990). The most abundant species dominating euphausiid community was *T. inermis* which made up 90% of it. Other krill species—*T. rashii* and *T. longicaudata* made up 6% and 4% of total krill abundance, respectively. In our study, an aggregation of chaetognaths (> 50 indiv. m⁻³) from the genera *Eukrohnia* and *Parasagitta* (Fig. 3a) (289 indiv. m⁻³) was recorded at one station (KGF 51), and dense aggregations (119–530 indiv. m⁻³) of hyperiid amphipods from the genus *Themisto* (most likely *Themisto libellula*) were recorded at three locations (KGF 2S, KGF 44, KGF 9) (Table 1; Fig. 3b). It is worth noting that the amphipods occurred together with krill, while the chaetognaths were a monotypic aggregation. In addition, copepods co-occurred with krill in considerable numbers at two stations—at one station in Isfjorden (ISF 1) and one station in Hornsund (HSD 10). Due to the very small size of the copepods, it was not possible to determine their number based on the recordings from the available camera systems. Pteropods, one of the most important components of the macroplankton in the fjords of Spitsbergen (Węśławski et al. 2000; Walkusz et al. 2009), were not found at any bottom location. Krill were completely absent at 46 stations. Results grouped by location and density classes are presented in Table 1. Zooplankton aggregations were not observed in the winter season, but individual zooplankton were present at station KGF28 (1 indiv. m⁻³) and at the ISF2 and ISF3 stations (5 and 1 indiv. m⁻³, respectively). Nine out of eleven observations of the largest benthic aggregations of krill (> 50 indiv. m⁻³) were in the depth range between 60 and 100 m, and four of them were in Atlantic type water (AW). There were no significant correlations between the formation of aggregations of zooplankton and the type and depth of the water masses (Fig. 4).

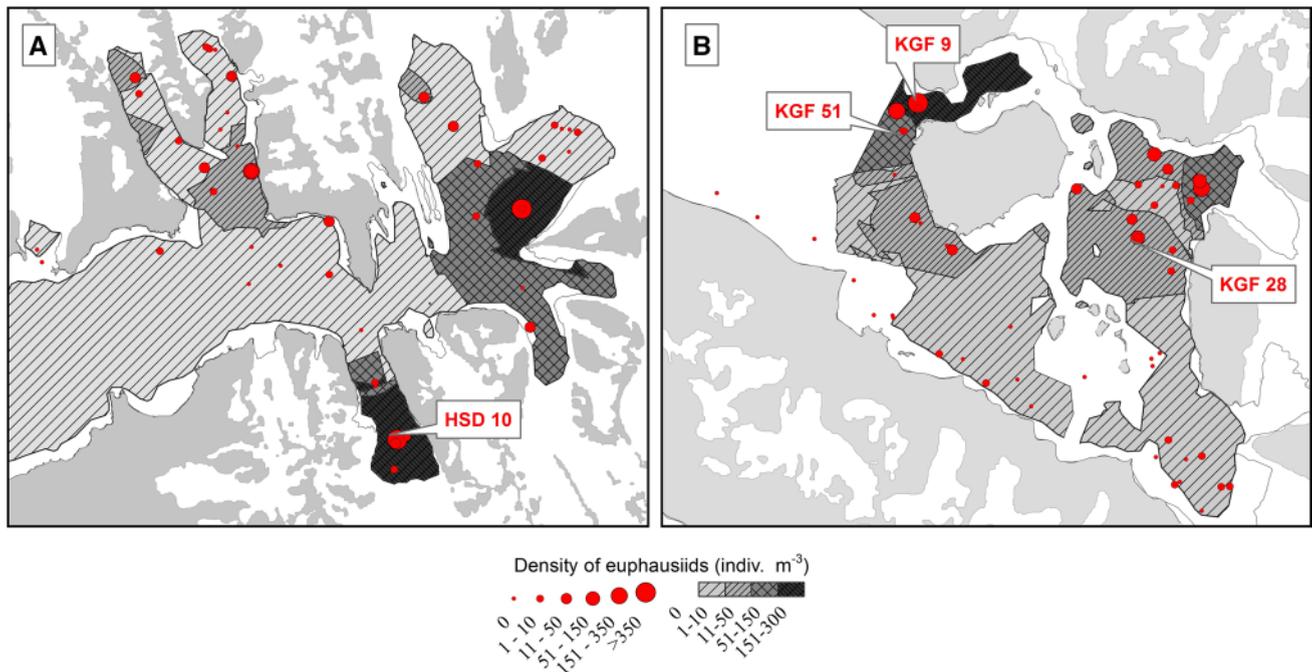


Fig. 2 Visualization of where zooplankton aggregations are most likely to form in both fjords **a** Hornsund, **b** Kongsfjorden in the summer season. The area of designated polygons is heavily dependent on the environmental factors described in the text and should be treated as indicative

Assessment of the importance of benthic aggregation

Based on the localized areas in which near-bottom krill aggregations may occur, the estimated volumes of near-bottom water layers in the present study were 0.25 km³ in Hornsund and 0.14 km³ in Kongsfjorden (Fig. 2). The biomass values (wet weight) in this volume were estimated to be 711 tons in Hornsund and 203 tons in Kongsfjorden. The krill present in the water column in Hornsund was 1130 tons (for a volume of 23.7 km³ and an average density of 0.6 indiv. m⁻³) and in Kongsfjorden there were 296 tons (12.4 km³ with 0.3 indiv. m⁻³). However, the percentage of the biomass in both fjords being associated with near-bottom habitats (39% in Hornsund and 41% in Kongsfjorden) is similar in the two fjords, despite the fact that Hornsund is estimated to host twice as much krill as Kongsfjorden. Predators (such as the Atlantic cod) in Kongsfjorden were twice as numerous as predators in Hornsund (Szcucka et al. 2017), and this difference may partially explain the difference in krill biomass between these locations.

Data obtained from 52 Tucker trawl stations showed no statistically significant differences between the densities of krill in the surface and bottom layers in both fjords (Fig. 5) and between them. However, it is worth mentioning that consistently in the lower layer there were more krill individuals. The dominant species of krill in both fjords was *T. inermis*,

but *T. rashii* and *T. longicaudata* were also registered. In Hornsund, *T. inermis* constituted up to 92% of total krill abundance in this fjord, *T. rashii* 5% and *T. longicaudata* 3%. In Kongsfjorden, *T. inermis*, *T. rashii* and *T. longicaudata* constituted, respectively, 78%, 11%, and 11% but there were also recorded *Meganyctiphanes norvegica* (three individuals) associated with the influx of Atlantic water masses (Wesławski et al. 2017). Regarding the size of the individuals, it can be concluded that *T. inermis* population in Hornsund is mainly composed of adults (body size > 21 mm), whereas in Kongsfjorden the population structure is more even (Fig. 6). There were also statistically significant differences in the numbers between upper and lower water layers for *Themisto* and chaetognaths in Kongsfjorden. *Themisto* abundance was significantly greater in Kongsfjorden. Photographic material confirmed this observations—all three *Themisto* aggregations were located in Kongsfjorden.

Discussion

The study of benthopelagic communities is inherently problematic (e.g. unintentional equipment contact with the sediment) and often requires modification of existing tools and the design and construction of new ones (Christiansen et al. 1999; Hirche et al. 2006, 2016). The results presented here show that traditional sampling, such as the Tucker trawl, and recently developed imaging techniques, such as the

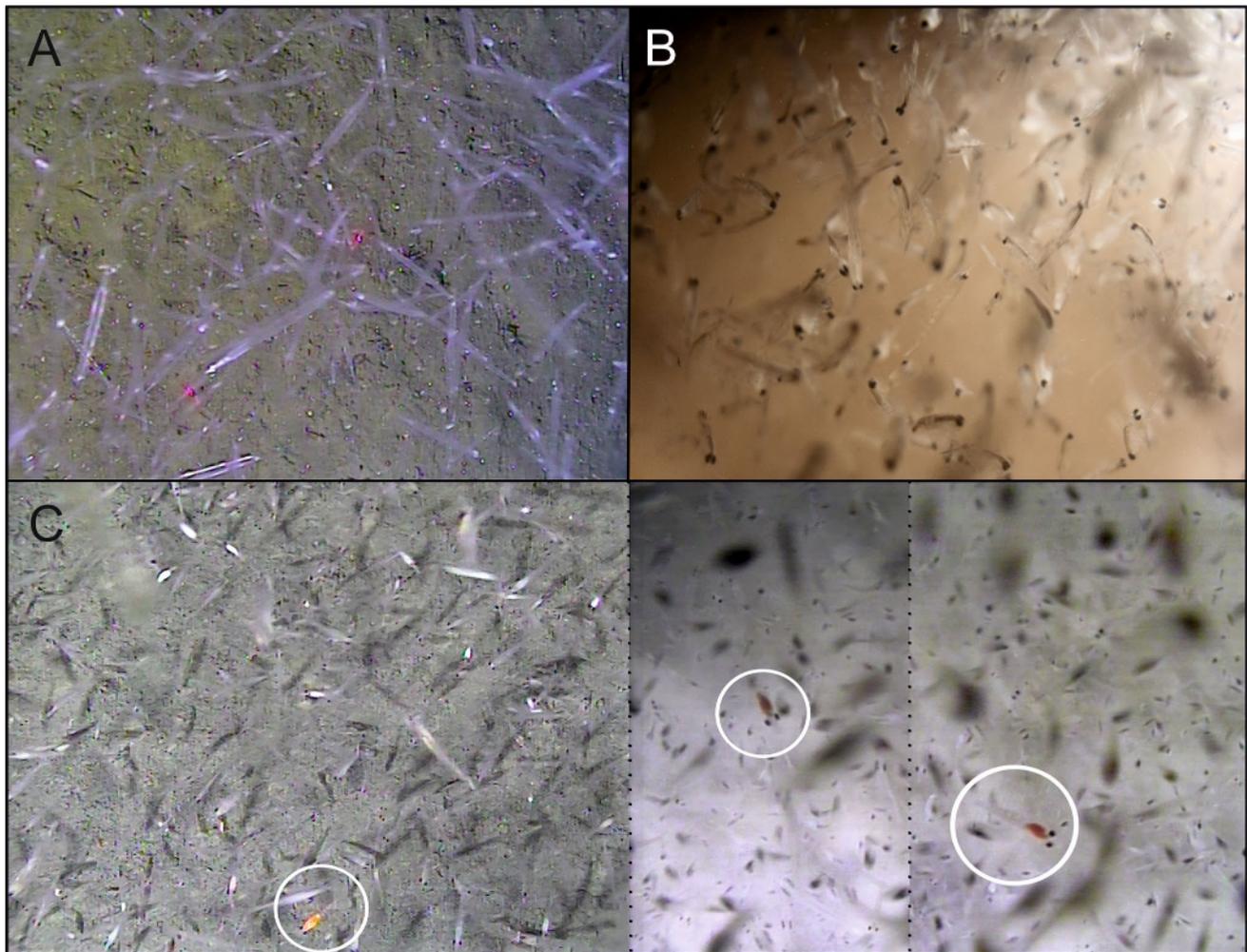


Fig. 3 **a** The registered aggregation of the chaetognaths, **b** hyperiid amphipods. In **c**, aggregations of krill with marked white circles of distinctly different individuals are shown. These individuals have a

clearly orange body which may suggest the last stage of infection of the parasitoid *Pseudocollinia ciliate* as described by Gómez-Gutiérrez et al. (2003) and Cleary et al. (2019)

drop camera, photographic landers, and epibenthic sledge-mounted camera, can be combined to yield a wider understanding than is possible from data obtained using any of these techniques separately.

Benthic aggregations of plankton

The drop camera allowed us to sample in places that were inaccessible to both the Tucker trawl (the area just above the bottom) and the epibenthic sledge (where sediments were too muddy). There are relatively few papers dealing with bottom benthopelagic zooplankton communities. Dense clusters of zooplankton were previously reported in the Antarctic (*Euphausia superba*) (Gutt and Siegel 1994; Clarke and Tyler 2008; Nicol and Brierley 2010; Fuentes et al. 2016), in the Faroe-Shetland Channel area (Hirai and Jones 2012), and in the Spitsbergen area (Laudien and Orchard 2012; Hirche

et al. 2016). It is considered that the biomass of benthopelagic communities decreases exponentially with depth. At 1000 m, the biomass is 1% that of the surface zooplankton, and at 5000 m, this value is approximately 0.1% (Wishner 1980). However, the results presented in this paper and in the other work (Gutt and Siegel 1994) show that the average numbers of krill obtained using imaging methods are much higher than the average numbers obtained from trawls. The numbers of krill found during this study are consistent with values from the literature, e.g. 596 ± 261 indiv. m^{-3} of *Meganyctiphanes norvegica* recorded at 480 m at the bottom of the Faroe-Shetland Channel (Hirai and Jones 2012). Such large numbers have the potential to impact the amount of carbon supplied to the bottom of the ocean. In most works, sinking zooplankton is treated as an artefact rather than as a significant process (Michaels et al. 1990; Wakeham et al. 1993). The importance of dead krill as a source of organic

Table 1 Macrozooplankton near the bottom; frequency of observations of the different density classes; data from 107 photo stations (see Fig. 1)

Fjord	Number of stations	0	1–10	11–50	51–150	151–350	≥ 350
Abundance of Euphausiids m⁻³							
Hornsund	44	15	17	8	1	1	2
Isfjorden	3	0	2	0	0	0	1
Kongsfjorden	52	24	17	5	3	2	1
Other	8	7	1	0	0	0	0
Summary	107	46	37	13	4	3	4
Abundance of Chaetognaths (<i>Eukrohnia</i> and <i>Parasagitta</i> combined) m⁻³							
Hornsund	44	38	5	1	0	0	0
Isfjorden	3	2	1	0	0	0	0
Kongsfjorden	52	43	5	3	0	1	0
Other	8	6	2	0	0	0	0
Summary	107	89	13	4	0	1	0
Abundance of <i>Themisto</i> m⁻³							
Hornsund	44	39	3	2	0	0	0
Isfjorden	3	2	1	0	0	0	0
Kongsfjorden	52	37	7	5	0	2	1
Other	8	8	0	0	0	0	0
Summary	107	86	11	7	0	2	1

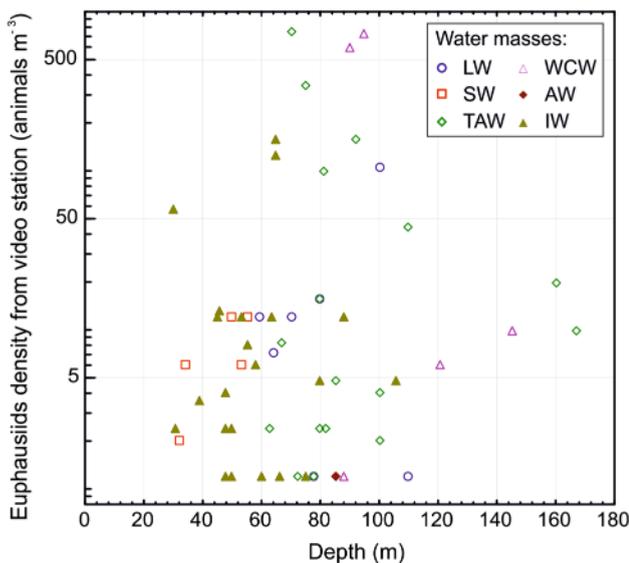


Fig. 4 Summary of all positive krill observations recorded by the drop camera with the depth and water mass type associated with each observation

matter for benthic organisms has been previously documented (Sokolova 1994).

Krill food sources include items filtered out of the water column (sponge spicules, diatoms, dinoflagellates, silicoflagellates, foraminiferans, crustacean exuviae, tintinnid ciliates), other zooplankton, and detritus from sediments (Ritz et al. 1990; Dilling et al. 1998; Nakagawa, 2004). Krill with access to the ocean bottom utilize several methods to obtain

food from the sediments (Fig. 7). One method is to swim at a high angle (almost vertical) to the bottom to create a strong water current with their pleopods. This disturbs the top layer of sediment, which the animal then feeds on by filtering. In the second method, the individual swims slowly very close to the bottom and uses its antennae to plough up the surface layers of the sediment, also disturbing it and making it available for filtering. The third method is called “nose diving” (Mauchline and Fisher 1969; Clarke and Tyler 2008), where Antarctic krill (*Euphausia superba*) swim headfirst into the surface layer of the sediments and feed on the disturbed sediment. The nose diving method of feeding was very often observed in our research (additional video are given in Online Resource 3) in drop camera images from Hornsund, Kongsfjorden, and Adventfjorden (Fig. 7, Online Resource 3). The resuspension of sea floor sediment structure by krill activity was so effective that, after a short time, they had resuspended so much material that the reduced visibility prevented further observations.

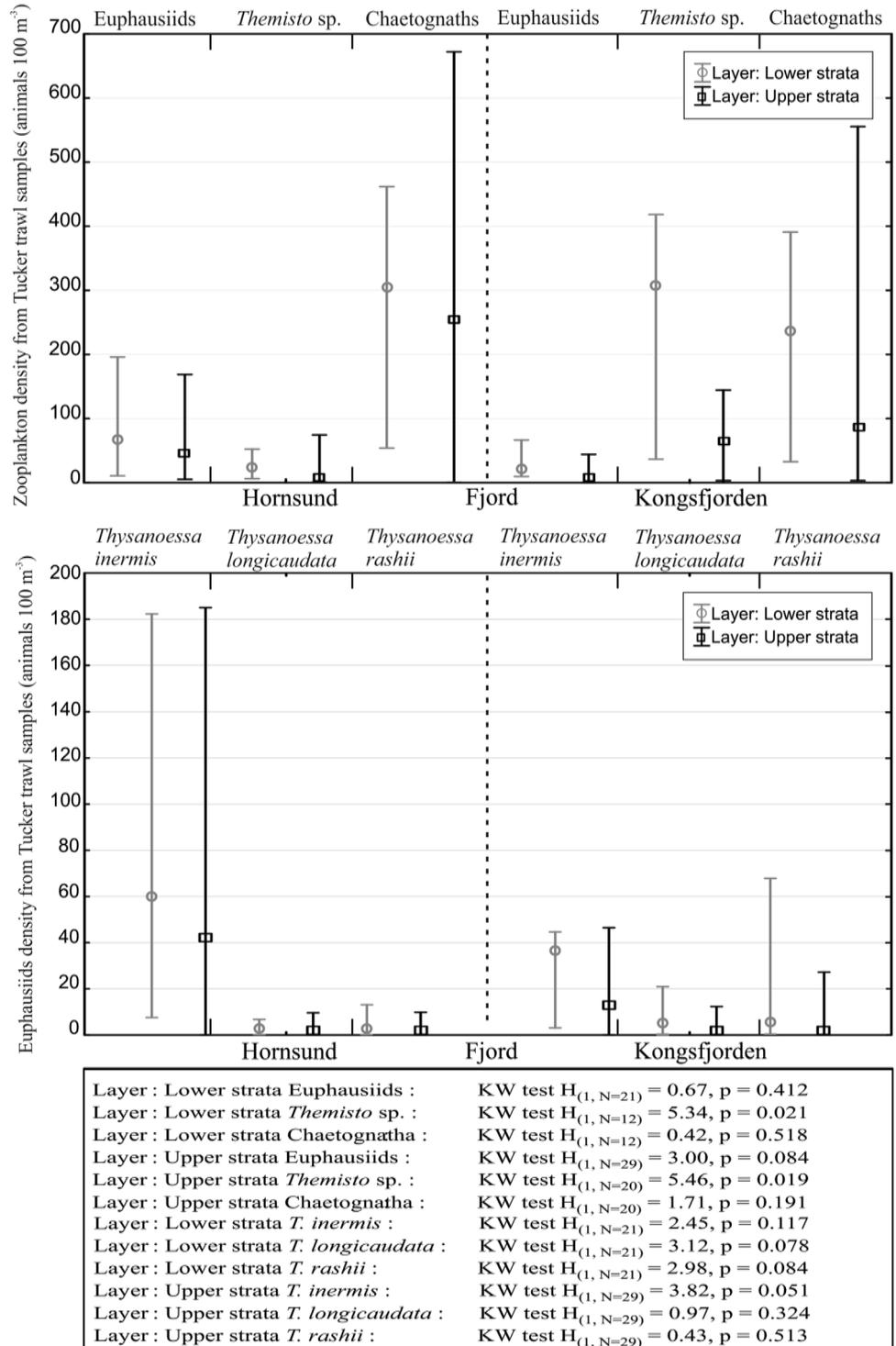
It seems that the local distribution of krill (*T. inermis*) is more associated with close proximity to the glacier front rather than with a depth (Fig. 2). An obvious question arises as to what conditions lead to the formation of bottom aggregations.

Possible scenarios

Predator avoidance strategy

A variety of predator avoidance strategies have been described for krill and fish, the most common of which are

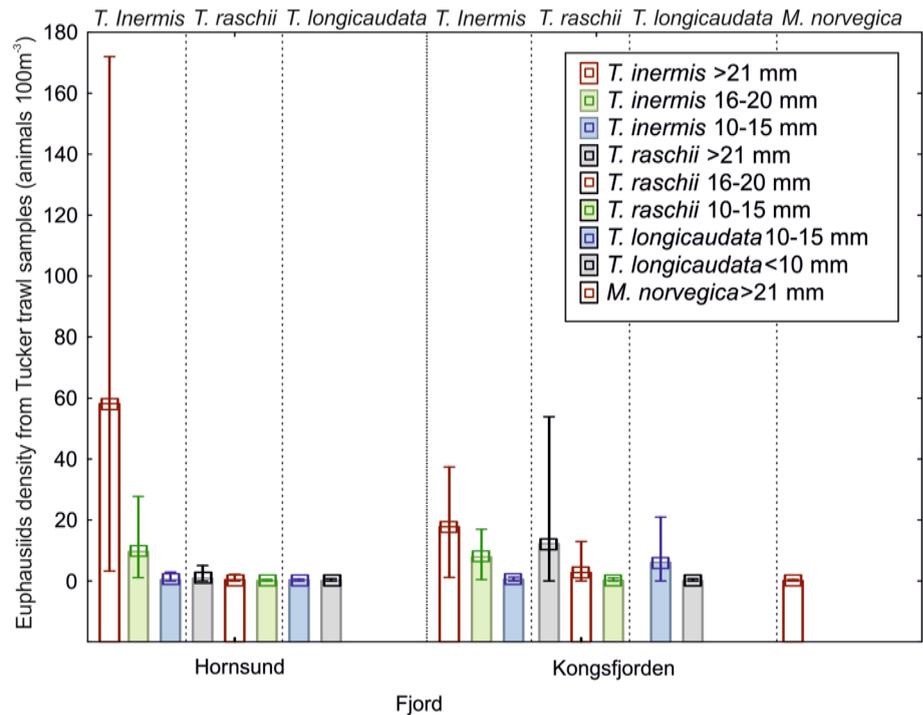
Fig. 5 Whisker plots showing densities of Euphausiids, *Themisto* spp., and Chaetognaths from Tucker trawl samples (upper and lower water column) in both fjords. The concentration of krill was also shown with the division into species (*Thysanoessa inermis*, *Thysanoessa longicaudata*, *Thysanoessa rashii*). Median and range (min max) are shown



swarming and avoiding predators by escaping to the seabed (Verity and Smetacek 1996; Axelsen et al. 2001; Ryer et al. 2004; Simard and Harvey 2010). Krill in the water column may be vulnerable to predation from above, below, and all sides, while krill near the seabed are mainly vulnerable from above. Forming aggregations is another strategy that reduces mortality from predation, so forming aggregations near the

bottom may be especially advantageous as it combines two strategies for avoiding predators. On the other hand, there are cases when swarms of the krill (*Meganyctiphanes norvegica*) were protected by large, piscivorous fish, which uses the krill swarms as a feeding ground in their hunt for planktivores (Kaartvedt et al. 2005). It should be also taken into account that krill interaction with sea floor may actually

Fig. 6 Density and distribution of Euphausiids length in Tucker Trawl samples collected in 2016. Data shown separately for both fjords. Mean and range (min max) are shown



expose to different predators like demersal fishes and sea anemones.

The density of cod feeding on krill is much higher in Kongsfjorden than in Hornsund (Szcucka et al. 2017), which may explain why a larger part of the krill population occurs near the seabed in Kongsfjorden than in Hornsund (which has low numbers of predatory fish). Acoustic data showing the distribution and size of fish in the water column for both of the fjords discussed here (Szcucka et al. 2017) support this idea. The lowest density of fish occurs in the glacial bays is consistent with the maximum occurrences of krill (Brepolen, Samarinvgen in Hornsund and near the glacier front of Blomstrandbreen, Conveybreen in Kongsfjorden) (Fig. 2). Glacial bays are characterized by specific environmental factors, including a large amount of mineral suspension in the water column and a strong gradient between brackish waters at the surface and higher salinity waters at depth. Large predators, such as Atlantic cod, tend to avoid glacial bays (Szcucka et al. 2017).

Sedimentation and glacier trap

Estuarine circulation in the glaciated fjords is driven by cata-batic winds (Węśławski et al. 2000; Lydersen et al. 2014). This process starts in June when ablation intensifies and ends in September when the air temperature drops, leading to a significant decrease in the inflow of suspended sediments and the volume of fresh water (Węśławski et al. 1995). There are also known cases of mass mortality of krill (Węśławski and Legżyńska 1998), phytoplankton (Hernando et al. 2015),

and amphipods (Eiane and Daase 2002) as a result of osmotic shock resulting from the direct proximity of the glacier or the glacial river. On the other hand, previous research demonstrates the high tolerance of the krill *Euphausia superba* to a wide salinity range from 25 to 45 (Aareset and Torres 1989). It is believed that a large amount of suspended material in glacial bays has a negative effect on the functioning of coastal ecosystems (Thrush et al. 2003). High concentrations of suspended material in the water column can adversely affect krill by clogging the filtration apparatus used for feeding. When sediment concentrations are high, krill may ingest predominantly inorganic mineral particles. Additionally, mineral particles of glacial origin ($> 1.1 \times 10^5 \mu\text{m}^3$) with sharp edges can mechanically destroy the krill (Fuentes et al. 2016). Dead zooplankton can be periodically stranded, creating swaths of dead organisms on the shore. This has been recorded in the southern (Fuentes et al. 2016) and northern polar regions (Legeżyńska et al. 2000; Eiane and Daase 2002). Dead krill have also been recorded in large numbers during dredging in an Antarctic fjord, in the form of large aggregations on the seabed (Sicinski personal communication, Balazy unpublished photography). A dense concentration of suspended material in the tidewater glacier area is likely to be a cause of high krill mortality (Lewis and Syvitski 1983; Węśławski and Legeżyńska 1998). Suspended plumes on the surface, which come directly from the outflows of glaciers or glacial rivers, are a common occurrence (Zajaczkowski 2008). Numerous mineral particles from the flocculation process combine in the deeper parts of the water column into large flocs that can build up on the boundary of various water masses thus

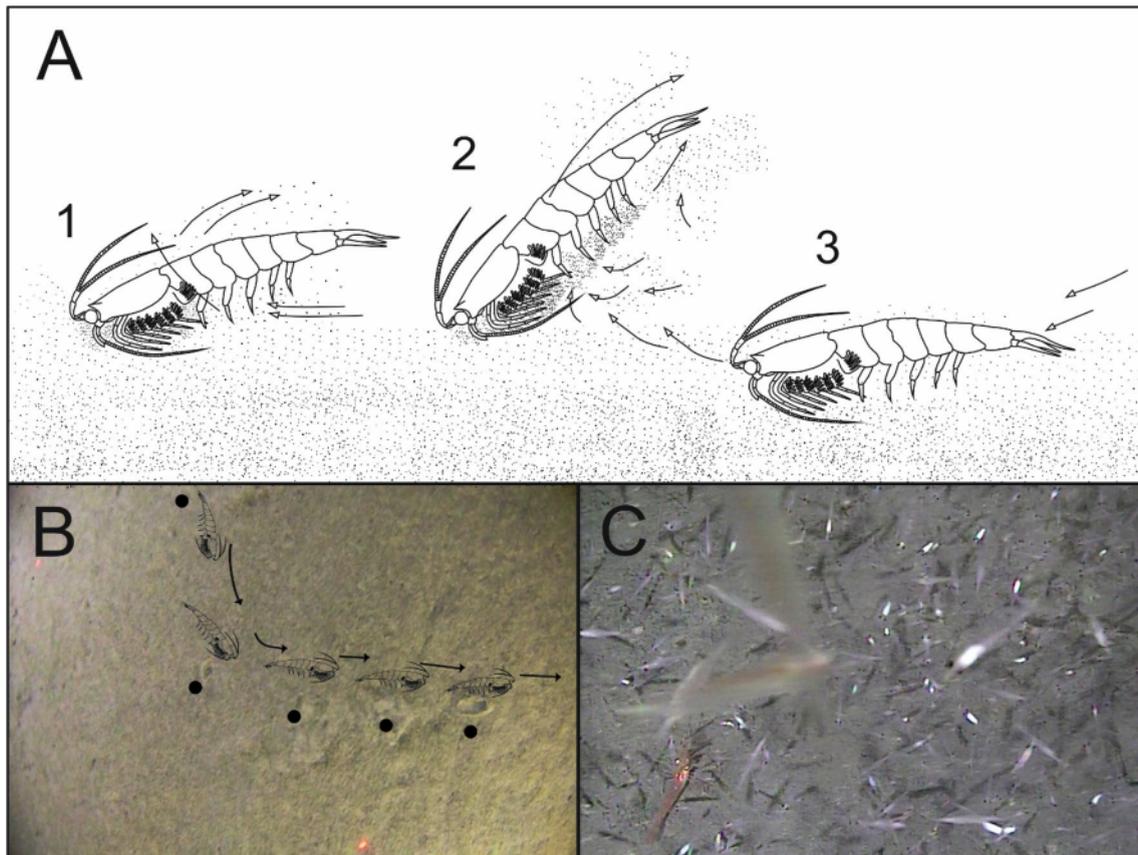


Fig. 7 Three methods of krill feeding at the sea bottom. Methods 1 and 3 may be convergent, and differences in the depth of the individual result from the degree of hydration of the upper layer of the sediment (fluffy, nepheloid layer), edited from Mauchline and Fisher (1969). Behaviour number 3 was first observed by Clarke and Tyler (2008), calling them nose diving. In most observations, feeding activity was calm when there were few krill present and the individuals

delved into the sediment at regular intervals (b); additional data are given in Online Resource 1 "ESM_1.mp4". Black dots symbolize the places where the nose diving activity of one individual occurred. When krill were more abundant, feeding behaviour was more chaotic, nervous (c). A number of krill feeding simultaneously have the potential to resuspend a lot of sediment

creating a reservoir of cleaner water that may trap the planktonic organisms below. The estuarine circulation, driven by a rapid influx of glacial meltwater, may be responsible for zooplankton retention in the inner parts of the fjord (Węśławski et al. 2000). There, the high sediment load and surface salinity gradient result in high zooplankton mortality. Stunned and dead krill are forced to the surface by glacial outflow, where they are an excellent source of food for seabirds (Urbanski et al. 2017). These conditions also create a perfect feeding site for necrophagous crustaceans. Large concentrations of birds in the study area, mainly Black-legged kittiwakes (*Rissa tridactyla*), were recorded in 2015 for both fjords (Urbański et al. 2017) and correlate with the large numbers of krill in the near-bottom aggregations at this time. Analysis of the photos showed large densities of echinoderms and anemones from the genus *Cerianthus* near the glacier, which may also be feeding on dead krill. The population of ophiuroids in the Spitsbergen fjords had very high concentrations near the glacier fronts (Deja et al. 2016), which may be associated

with bottom macrozooplankton aggregations. In Antarctica, dead euphausiids were the main source of food for abyssal ophiuroids (Sokolova 1994).

Parasitoid apostome ciliates

One of the few well-explained causes of mass mortalities is parasitoid apostome ciliates (Gómez-Gutiérrez et al. 2003, 2017). *Thysanoessa inermis* and *Thysanoessa raschii* are infected with parasitoid ciliates of the genus *Pseudocollinia* that kill krill in < 3 days (Capriulo and Small 1986; Capriulo et al. 1991; Lynn et al. 2014). Krill individuals infected with *Pseudocollinia* can be easily visually recognized. Their body loses transparency and changes colour from beige to orange depending on the stage of infection and characteristically swells the cephalothorax (Gómez-Gutiérrez et al. 2003, Gómez-Gutiérrez and Robinson 2006; Lynn et al. 2014). In our studies, distinctive, clearly orange individuals were observed on several dozen video stations and maybe they are

infected (Fig. 3c). Not many such changed individuals were observed; however, there were not registered dead individuals at the bottom, which usually accompanies such infections (Gómez-Gutiérrez et al. 2003).

Possible errors in the methodology

The numbers of krill presented in this work should be interpreted with some caution. Collecting camera images below the euphotic zone necessitates the use of artificial lighting. This method may introduce error that results in overestimating the densities of the individuals. Positive phototaxis of zooplankton in Kongsfjorden in response to ROV lighting has been previously shown (Hirche et al. 2016). Another study also noted the influence of artificial lighting on animal concentrations (Gutt and Siegel 1994). Strategies employed to minimize this error included continuous horizontal drop camera movement over the bottom (0.05–0.1 m/s), absence of propulsors (which can deter zooplankton), and the method of selecting the still photos from the beginning, middle, and end of the recording period. At most of the surveyed stations where large numbers of krill were observed, they appeared immediately after seabed became visible; consequently, the effect of density increasing with the length of the transect was noticeable but small. The coefficient of variation (defined as the ratio of standard deviation to average and expressed in percentage) does not exceed 30%.

Conclusion

This study point out that not using methods allowing to sample also in the bottom layer of water leads to a huge underestimation of the zooplankton biomass in Spitsbergen fjords.

Table 2 Station name, date, depth, location, krill densities, and type of gear from photo stations used in this study (summer season 2013, 2014, 2015, 2016, 2017, and winter 2016); krill densities in indiv. m⁻³

Station	Date	Depth (m)	Latitude	Longitude	Euphausiacea abundance m ⁻³	Gear type
HSD1	27.07.2015	65	77.041	16.027	124	Drop camera
HSD1'	28.07.2015	65	77.041	16.027	156	Drop camera
HSD10	30.07.2015	95	76.926	16.290	731	Drop camera
HSD11	30.07.2015	121	77.023	16.533	6	Drop camera
HSD12	30.07.2015	70	76.989	16.531	0	Drop camera
HSD13	30.07.2015	70	76.973	16.544	12	Drop camera
HSD14	30.07.2015	50	77.019	16.171	12	Drop camera
HSD15	29.07.2016	50	77.058	16.599	2	Drop camera
HSD16	29.07.2016	56	77.056	16.613	0	Drop camera
HSD17	29.07.2016	62	77.056	16.627	0	Drop camera
HSD18	29.07.2016	66	77.054	16.642	1	Drop camera
HSD19	29.07.2016	60	77.044	16.574	1	Drop camera
HSD1S	01.08.2016	106	77.008	15.853	5	Epibenthic sledge
HSD2	28.07.2015	70	77.093	15.963	0	Drop camera
HSD20	01.08.2016	31	76.914	16.283	2	Drop camera

It was estimated that bottom aggregations of krill make up over 39% of the total krill biomass in Hornsund and 41% in Kongsfjorden. Our observations also show that dominated in Spitsbergen euphausiid species—*T. inermis* creates bottom aggregation mainly in close vicinity to glacier front. Recorded behaviour known as "nose diving" suggests that near-bottom habitat is chosen by krill due to the availability of food in this region.

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Compliance with ethical standards

Conflict of interest The authors declare that there is no conflict of interest in presenting this information.

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Appendix

See Tables 2 and 3. 3.

Table 2 (continued)

Station	Date	Depth (m)	Latitude	Longitude	Euphausiacea abundance m ⁻³	Gear type
HSD21	01.08.2016	80	76.925	16.286	16	Drop camera
HSD22	31.07.2016	84	76.973	16.227	0	Drop camera
HSD23	31.07.2016	78	77.094	15.946	1	Drop camera
HSD24	31.07.2016	84	77.066	15.984	0	Drop camera
HSD25	30.07.2014	160	77.082	15.811	20	Drop camera
HSD26	30.07.2014	167	77.075	15.818	10	Drop camera
HSD27	29.07.2014	55	77.046	16.625	0	Drop camera
HSD28	30.07.2013	84	77.001	16.079	0	Lander
HSD29	30.07.2013	107	77.009	16.025	0	Lander
HSD2S	01.08.2016	78	77.059	15.970	0	Epibenthic sledge
HSD3	28.07.2015	55	77.082	15.993	12	Drop camera
HSD30	30.07.2013	105	76.993	16.018	0	Lander
HSD31	31.07.2017	63.5	77.043	15.939	12	Drop camera
HSD32	31.07.2017	46	77.071	16.355	13	Drop camera
HSD33	31.07.2017	59	77.058	16.409	12	Drop camera
HSD34	31.07.2017	88	77.020	16.447	1	Drop camera
HSD35	31.07.2017	145	76.927	16.308	10	Drop camera
HSD36	31.07.2017	118	76.949	16.251	0	Drop camera
HSD37	31.07.2017	30	77.052	16.002	0	Drop camera
HSD38	31.07.2017	64	77.042	16.453	7	Drop camera
HSD39	31.07.2017	80	77.081	15.991	5	Drop camera
HSD4	28.07.2015	32	77.055	15.891	2	Drop camera
HSD40	31.07.2017	75	77.093	15.952	1	Drop camera
HSD41	31.07.2017	110	76.951	16.251	1	Drop camera
HSD5	28.07.2015	34	77.033	15.955	6	Drop camera
HSD6	28.07.2015	53	76.997	16.169	6	Drop camera
HSD7	28.07.2015	90	77.023	16.533	587	Drop camera
HSD8	29.07.2015	22	77.004	15.631	0	Drop camera
HSD9	29.07.2015	54	77.009	15.623	0	Drop camera
ISF1	02.08.2015	40	78.241	15.641	426	Drop camera
ISF2	11.01.2016	56	78.649	16.875	5	Drop camera
ISF3	01.01.2016	64	78.258	13.795	1	Drop camera
KGF1	03.08.2015	25	78.933	11.923	0	Drop camera
KGF11	06.08.2015	100	78.968	11.658	0	Drop camera
KGF12	06.08.2015	100	78.961	11.726	0	Drop camera
KGF13	06.08.2015	100	78.956	11.820	0	Drop camera
KGF14	06.08.2015	100	78.943	11.888	0	Drop camera
KGF15	06.08.2015	100	78.932	11.955	0	Drop camera
KGF16	06.08.2015	100	78.922	12.032	4	Drop camera
KGF17	06.08.2015	100	78.913	12.110	2	Drop camera
KGF18	06.08.2015	100	78.907	12.185	0	Drop camera
KGF19	07.08.2015	74	78.877	12.468	0	Drop camera
KGF1S	04.08.2016	280	78.977	11.945	0	Epibenthic sledge
KGF2	05.08.2015	100	78.980	12.441	105	Drop camera
KGF20	07.08.2015	93	78.885	12.430	0	Drop camera
KGF21	07.08.2015	88	78.954	12.045	12	Drop camera
KGF22	07.08.2015	110	78.964	11.982	44	Drop camera
KGF23	07.08.2015	100	78.991	11.951	0	Drop camera
KGF24	20.01.2016	93	78.933	11.954	0	Drop camera
KGF25	21.01.2016	105	78.917	12.269	0	Drop camera

Table 2 (continued)

Station	Date	Depth (m)	Latitude	Longitude	Euphausiacea abundance m ⁻³	Gear type
KGF26	23.01.2016	44	78.925	12.389	0	Drop camera
KGF27	23.01.2016	44	78.921	12.378	0	Drop camera
KGF28	23.01.2016	72	78.961	12.345	1	Drop camera
KGF29	07.08.2016	67	78.998	11.978	8	Drop camera
KGF2S	05.08.2016	90	78.893	12.439	0	Epibenthic sledge
KGF3	05.08.2015	48	78.978	12.403	4	Drop camera
KGF30	05.08.2016	80	78.967	12.334	16	Drop camera
KGF31	07.08.2016	82	78.894	12.464	2	Drop camera
KGF32	06.08.2016	85	79.070	11.610	1	Drop camera
KGF33	08.08.2016	58	78.958	12.402	6	Drop camera
KGF34	07.08.2016	92	78.977	12.445	157	Drop camera
KGF35	08.08.2016	39	78.951	12.401	4	Drop camera
KGF36	07.08.2016	78	78.898	12.409	1	Drop camera
KGF37	08.08.2016	63	78.973	12.428	2	Drop camera
KGF38	07.08.2016	64	78.893	12.390	0	Drop camera
KGF39	07.08.2016	47.5	78.885	12.511	1	Drop camera
KGF4	05.08.2015	42	78.977	12.381	0	Drop camera
KGF40	07.08.2016	48	78.884	12.498	2	Drop camera
KGF41	07.08.2013	90	78.931	12.145	0	Lander
KGF42	08.08.2013	115	78.921	12.071	0	Lander
KGF43	08.08.2013	98	78.915	12.161	0	Lander
KGF44	10.08.2013	75	78.997	11.943	340	Lander
KGF45	08.08.2017	50	78.971	12.369	1	Drop camera
KGF46	08.08.2017	81	78.961	12.345	100	Drop camera
KGF47	08.08.2017	43	78.924	12.376	0	Drop camera
KGF48	08.08.2017	85	78.885	12.423	5	Drop camera
KGF49	07.08.2017	70	78.956	12.036	0	Drop camera
KGF5	05.08.2015	53	78.983	12.389	12	Drop camera
KGF50	07.08.2017	62	78.962	11.991	0	Drop camera
KGF51	07.08.2017	80	78.991	11.957	2	Drop camera
KGF6	05.08.2015	30	78.987	12.365	58	Drop camera
KGF7	05.08.2015	55	78.978	12.341	8	Drop camera
KGF8	05.08.2015	45	78.975	12.242	12	Drop camera
KGF9.10	06.08.2015	70	79.000	11.977	751	Drop camera
MG1	01.01.2016	98	79.556	11.128	0	Drop camera
RAU1	10.08.2017	52	79.702	12.232	0	Drop camera
RAU2	10.08.2017	67	79.738	12.470	2	Drop camera
RIP1	14.01.2016	84	80.300	22.345	0	Drop camera
SH1	03.08.2015	50	78.206	11.645	0	Drop camera
SH2	03.08.2015	50	78.945	10.274	0	Drop camera
SH3	03.08.2015	50	79.082	10.689	0	Drop camera
SM1	13.01.2016	81	79.790	11.024	0	Drop camera

During the summer season, there was always daylight; during winter there were only darkness

Table 3 Station name, date, depth, location, and krill densities from Tucker trawl samples used in this study (summer 2014, 2015, and 2016); krill densities in indiv. 100 m⁻³

Station	Date	Depth (m)	Latitude (N)	Longitude (E)	Krill 100 m ⁻³ upper strata	Krill 100 m ⁻³ lower strata
14003/GL	7.2014	25	77.046	16.628	62.1	–
14004/GL	7.2014	25	77.040	16.598	5.2	–
14010/GL	7.2014	25	77.073	15.846	11.6	–
14011/GL	7.2014	25	77.056	15.856	21.2	–
14016/GL	8.2014	25	78.979	12.417	40.9	–
14017/GL	8.2014	30–25	78.980	12.417	0.2	–
14,024/GL	8.2014	30	78.896	12.434	1.7	–
14025/GL	8.2014	30	78.884	12.445	43.1	–
H2	30.07.2015	150–200	76.983	15.759	–	10.7
H2	30.07.2015	15–20	76.983	15.759	8.7	–
HGLA1	29.07.2016	68	77.053	16.652	–	63.3
HGLA1	29.07.2016	15	77.054	16.653	185.3	–
HGLA3	29.07.2016	55	77.039	16.599	–	93.4
HGLA3	29.07.2016	15	77.044	16.567	192.8	–
HGLA4	31.07.2016	85	77.094	15.941	–	14.1
HGLA4	31.07.2016	15	77.090	15.949	38.9	–
HGLA5	31.07.2016	86	77.067	15.978	–	13.4
HGLA5	31.07.2016	15	77.089	15.934	20.3	–
HGLA6	01.08.2016	15–40	76.913	16.301	10.8	–
HGLA6	01.08.2016	30	76.925	16.284	0	–
KB3	07.08.2015	250–290	78.941	76.516	–	66.6
KB3	07.08.2015	10–25	78.941	76.516	7.9	–
KB4	07.08.2015	50–60	78.903	12.230	–	22.2
KB4	07.08.2015	10–25	78.903	12.230	0	0
KB5	07.08.2015	15–25	78.885	12.430	44.2	–
KB5	07.08.2015	45–75	78.885	12.430	–	9.7
KB5 SILL	07.08.2015	10–25	78.898	12.318	1.7	–
KGLA1	07.08.2016	50	78.885	12.505	–	64.9
KGLA1	07.08.2016	15	78.884	12.497	15.1	–
KGLA2	07.08.2016	42–74	78.893	12.384	–	51.9
KGLA2	07.08.2016	15	78.892	12.403	53	–
KGLA3	08.08.2016	40–48	78.976	12.441	–	8.9
KGLA3	08.08.2016	15	78.984	12.396	2.2	–
KGLA4	08.08.2016	15	78.973	12.423	59	–
KGLA4	08.08.2016	53	78.956	12.423	–	127.2
MB1	29.07.2015	80–100	77.092	15.962	–	14.7
MB1	29.07.2015	5–15	77.092	15.962	168.7	–
MB2	29.07.2015	50–70	77.092	15.962	–	68
MB2	29.07.2015	5–15	77.092	15.962	103.5	–
MEN1	30.07.2015	50–70	77.022	16.533	–	57.8
MEN1	30.07.2015	5–15	77.022	16.533	9.6	–
MEN2	30.07.2015	30–40	76.989	16.530	–	165.6
MEN2	30.07.2015	5–15	76.989	16.530	50.3	–
P1	29.07.2015	80–100	77.066	15.851	–	77
P1	29.07.2015	5–15	77.066	15.851	89.3	–
P2	29.07.2015	80–100	77.061	15.865	–	196
P2	29.07.2015	5–15	77.061	15.865	93.4	–
S1	30.07.2015	50–40	76.926	16.290	–	120.6

Table 3 (continued)

Station	Date	Depth (m)	Latitude (N)	Longitude (E)	Krill 100 m ⁻³ upper strata	Krill 100 m ⁻³ lower strata
S1	30.07.2015	5–15	76.926	16.290	13.3	–
S2	30.07.2015	80–100	76.939	16.268	–	57.9
S2	30.07.2015	5–15	76.939	16.268	45.1	–

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New strategies for the new environment in Spitsbergen fjords (Arctic). Scattering of the feather star *Heliometra glacialis* (Echinodermata, unstalked crinoid) clinging to a crab

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Abstract

This publication presents an unusual behavior of a comatulid crinoid that was tentatively attributed to *Heliometria glacialis* (Echinodermata, Crinoidea, Heliometrinae). This unstalked crinoid was observed clinging on *Hyas* sp. crabs in the inner part of the Spitsbergen fjords heavily loaded with suspension runoff. In situ observations were made using a 16-h and 45-min time-lapse sequence showing the decompositions of Atlantic cod. During the exposure, apart from typical organisms such as carrion crustaceans, crabs, and starfish, three individuals of crinoids were observed. One of the crinoids was clinging to the edge of the platform for most of the exposure. The remaining two individuals were observed attached to the carapace of *Hyas* sp. crabs for 6 h 55 min. It was also found, based on analysis of the video material from 202 locations examined in the summer season between 2015 and 2020 using a drop camera, two additional locations showing comatulid crinoids. Both locations in the Ekmanfjorden and in the interior of the Vanmijenfjorden are areas under the strong influence of a glacier meltwater plum or a glacial river runoff. So far, comatulid crinoids have been found mainly in locations outside of the influence of turbid waters from fjords. We interpret this new behavior within comatulid crinoids as an adaptation that help colonize new regions gradually exposed by the retreating glaciers.

Keywords Arctic · Spitsbergen · Fjords · Dispersal strategy · Unstalked Crinoidea · Heliometra

Introduction

Due to the global warming, the European Arctic is one of the most changing marine ecosystems in the world (IPCC 2022). The retreat of sea ice, and tidal glaciers (de-icing), associated with increased advection of Atlantic waters is especially visible in coastal waters and fjords of the Svalbard archipelago (Søreide et al. 2021). This rapid change creates unique opportunity to observe how organisms adapt to new environment and emerging niches.

Particularly not only interesting, but also difficult to study are areas located in the direct vicinity of a tidewater glacier or a glacial river. Extreme sedimentation rates create exceptionally soft sediment that does not allow the use of traditional drop cameras with triggering by a weight hitting

the bottom. Visibility in such places often reaches 20 cm and less.

Rapidly melting tidal glaciers on Svalbard discharge huge amount of freshwater, fine, and coarse mineral particles in the vicinity of the glacier front (Lydersen et al. 2014). In areas of high mineral sedimentation rates, colonization by the epibenthic fauna requires an adapted behavior to prevent sinking into the sediment, avoid clogging of filtering apparatus, and being buried under massive rain of particles. Typical adaptations are to be mobile (fast swimming crustaceans) or very small and light (minute bivalves)—(Włodarska-Kowalczyk and Pearson 2004) or being able to turn around and shake the sediment off—like colonial bryozoan *Alcyonidium disciformae* (Kukliński and Porter 2004). Other option is to use large dropstones as a platform above the soft substrate or larger mobile species as a vehicle like organisms colonizing hermit crab shells (Balazy et al. 2015).

Our aim was to study newly exposed areas of coastline and seabed and check how these are becoming colonized by fauna (ACCES project—see Søreide et al 2021). Recording time-lapse videos from the deglaciated fjords, we have

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observed an unusual behavior of the filter feeder crinoid in the turbid coastal environment, which is a new observation of the presumed adaptation helping the colonization of new regions.

There are two species of unstalked crinoids known from Spitsbergen coast (Clark 1970); however, only one, *Heliometra glacialis*, is regarded as relatively common and widely distributed on the outer shelf of Barents and Greenland seas—(Dyer et al. 1984; Graeve et al. 1997; Schander et al. 2010). The most typical bottom for this species is gravel mixed with mud and sand, but it has also been found only on sand, silt, and loose stones (Clark and Clark McGown 1967). Present records of this species typically placed it on mixed to hard bottom out of the fjords turbid waters, so occurrence of *Heliometra glacialis* within inner fjord basin comes as a surprise.

Research area (environmental setting and location)

The research area is the western fjords of Spitsbergen. The Ekmanfjorden is the northern branch of the large centrally located Isfjorden fjord system (Fig. 1). It ends with two bays. One of them is Brevika, ends with a glacier flowing directly into the water, while the other is Mudderbukta ends with a river delta that drains water from glaciers ending on land. The place is heavily loaded with suspension runoff at least periodically since June–August (Fig. 1). This is visible on the water surface in the form of brick-red plumes, which is the result of the erosion of Devonian sandstones lying in the area (Hjelle 1993; Kavan et al. 2022). Median size of suspended particle near glacier area is much bigger than in inner and outer parts of the fjords (Sagan and Darecki 2018). The median size of suspended particles increases in water column due to sedimentation and flocculation processes (Szczuciński and Zajączkowski 2013; Moskalik et al. 2018). In winter, the fjord freezes and the ice recedes at the beginning of June (Kavan et al. 2022). Van Mijenfjord is a medium-sized fjord located south of Isfjord. The station

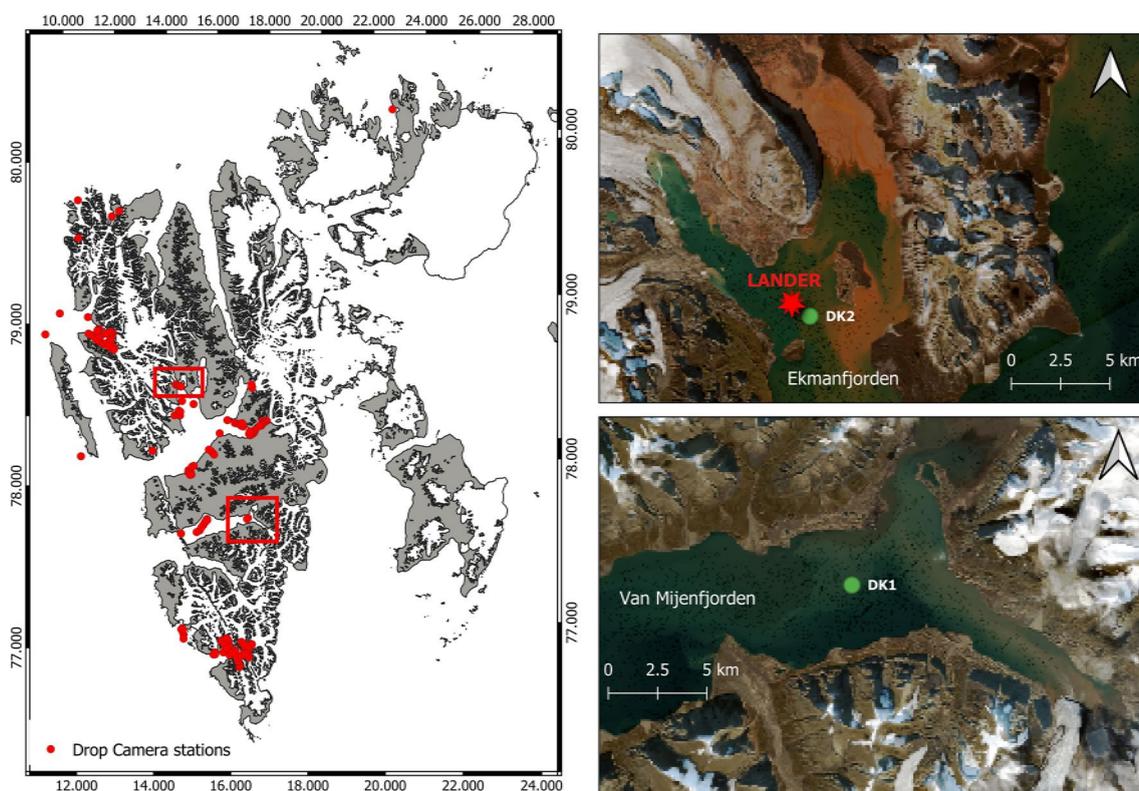


Fig. 1 General map of Spitsbergen (at left) with locations of the drop camera stations and detailed satellite views figured at right. Red dots: drop camera stations, green dots: stations in which the presence of unstalked crinoids was recorded (DK1 and DK2), red aster-

isk: Lander station. The satellite images were taken two days after the Lander experiment and show plumes of sediment reaching the station areas

where the presence of unstalked crinoids was confirmed is situated in the inner part of the fjord between Rindersbukta with a glacier still actively flowing into the bay and Sveabukta, where suspension from the great glacial river Kjellstromdalen is discharged. The innermost part of the fjord usually freezes in winter. The image material was collected in the middle of the ablation season (Holmes et al. 2019) when the sedimentation rate is very high. In Kongsfjorden, the sedimentation rate reaches $20,000 \text{ g m}^{-2} \text{ year}^{-1}$ in the area of the ice front (Svendsen et al. 2002). During the rest of the year the activity of the glacier and therefore the sedimentation rate is much lower. On the basis of research in Adolfbukta, it was found that in the autumn, the particulate matter flux to the bottom decreases by an order of magnitude compared to summer while the concentration of suspended particulate matter (SPM) decreases only twice. The authors explain this phenomenon with less effective flocculation (Szczeniński and Zajączkowski 2013).

Materials and methods

Time-lapse cameras with lighting according to Balazy et al. (2018) were mounted on an adapted Lander structure previously used to take underwater vertical photos. The device was lowered to the seabed from the RV Oceania at the selected location (Fig. 1) at a depth of 35 m. The ship then sailed to another position minimizing its impact. Lander is a construction made of stainless steel, weighted with lead to minimize tipping when lowering to the bottom. Modification of the Lander consisted mainly in building special clamps for two sets of cameras and adding a platform at the height of 30 cm for attaching the bait. Due to the often very hydrated and soft sediment in the inner parts of the Spitsbergen fjords, the heavy lander was sinking into the sediment, and as a result, the bait platform was at the bottom level. Classical benthic gear (box cores) use to sink in the sediment as well. A drop camera with a preview or specially prepared time-lapse video equipment left for a short time up to several days (buried by sediment) will work best. One of the cameras was mounted at an angle, the other directly above the bait. The bait was half Atlantic cod. The exposure time was 16 h 45 min. The camera mounted at an angle worked with an interval of 5 min, which allowed to obtain 205 photos. The vertically mounted camera worked with an interval of 15 min, which allowed to obtain 67 photos. The vertical camera images had a defect due to a trapped air bubble in front of the lens but were still usable. The material was recorded in both JPG and RAW format, which allowed to easily and without loss of quality improve the exposure of photos. From the captured material, a time-lapse movie (15 fps—frame per second) was made showing the course of the entire experiment. Drop camera photos were taken according

to the methodology described by Deja et al. 2019 in the summer season between 2015 and 2020 from the research vessel RV Oceania. In total, material was collected from 202 locations. The bottom was filmed with a camera for 10 min. In the studied locations, CTD (Conductivity–Temperature–Depth) profiles were also made to check the temperature and salinity in the bottom layer.

Results

After 55 min, the first carrion crustaceans appeared on the bait. Mainly *Onisimus* sp. and *Orchomenella minuta*. At the same time, they constituted the main part of the attracted invertebrates. After two hours and 55 min, the first representative of crabs attributed to *Hyas* sp. was recorded. Several large scavenger crustaceans *Anonyx nugax* were also attracted, but in very small numbers (only a few individuals). The bait was also visited once by a starfish, probably *Urasterias lincki*. After 4 h and 35 min from the beginning of the time-lapse sequence, one unstalked crinoid from the Comatulida order attributed to *Heliometra glacialis* was recorded. After the analysis of subsequent frames, it can be seen that the this unstalked crinoid was clinging to the platform edge (Fig. 2) and remained in this position until the Lander was pulled out, i.e., over 12 h. In the eighth hour of exposure, a second specimen of *Heliometra glacialis* was registered. It was clinging to the carapace of a crab *Hyas* sp. For the next hours, this *Hyas* sp. crab with a crinoid attached remained visible in the camera field, and at 14 h a second *Hyas* sp. crab also with a crinoid on its carapace appears (Fig. 2). Until Lander was brought to the surface, the crabs with attached crinoids were feeding on the exposed bait. For a total of 6 h 55 min (131 frames), the assemblage crabs/crinoid or only crinoid arms were recorded in the field of view (which meant that the crab was feeding out of frame on an invisible fragment of the bait).

The analysis of the video material from the drop camera showed that comatulid crinoid was also recorded in two additional locations out of the 202 surveyed places. Both locations (DK1, DK2) are located in the inner part of the fjords and are similar in terms of hydrological conditions (Fig. 1). Temperature and salinity in the bottom layer for station DK1 (72 m depth) are ($-1.45 \text{ }^{\circ}\text{C}$; 34.27) and those for station DK2 (42 m depth) are ($2.7 \text{ }^{\circ}\text{C}$; 33.7), respectively. On the surface layer, temperature varies from $4.59 \text{ }^{\circ}\text{C}$ on DK1 station to 8.03 on DK2, and salinity varies from 28.49 to 16.21 respectively. However, none of the comatulid crinoid observed in these additional locations was seen clinging on a crab.

Observations of crinoids in other glacial bays, the innermost parts of the fjords of western Spitsbergen were confirmed using a drop camera (Fig. 3) and other common

Fig. 2 Photographs showing *Heliometra glacialis* recorded during bait experiment on Lander station. 1a—A crinoid attached with its cirri to the edge of the platform. 2a—Specimen with cirri clinging on *Hyas* sp. carapace. 2b—Arm of a second crinoid also attached to a nearby crab. 3—4—photographs from the horizontal camera, better showing the inter-relationships crinoid/crab

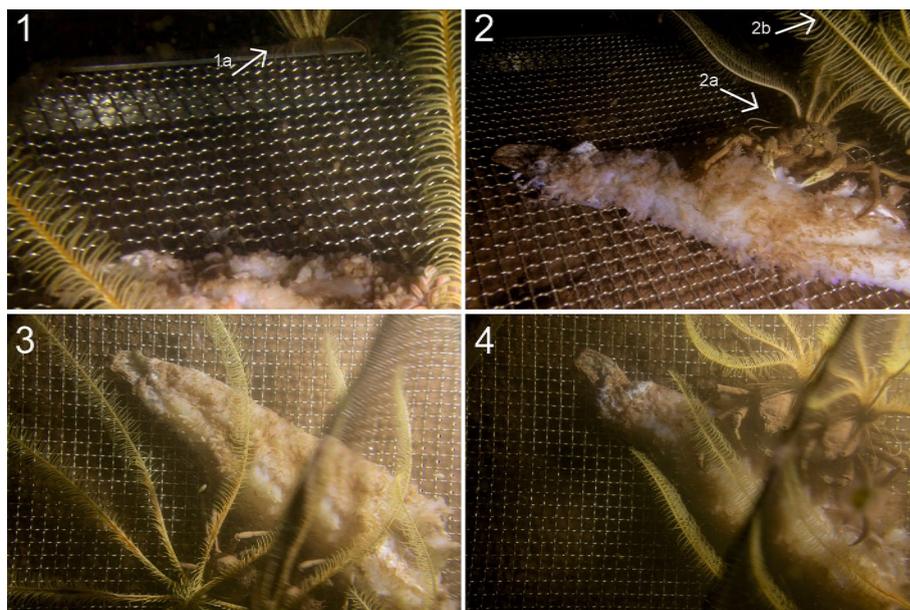
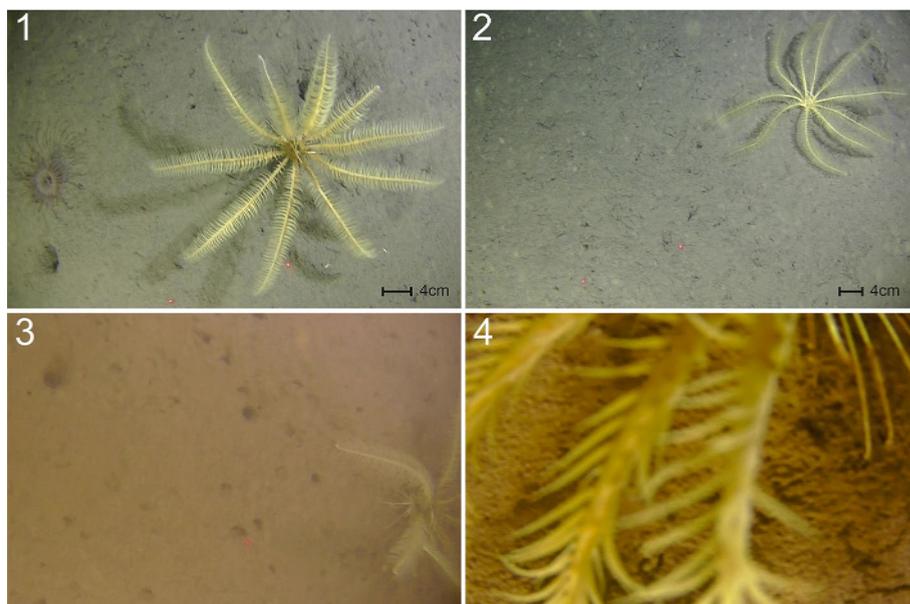


Fig. 3 Specimens of *Heliometra glacialis* registered in the summer of 2020 in Vanmijenfjorden at DK1 station (1;2) at a 72 m depth and in Ekmanfjorden at DK2 station (3;4) at a 42 m depth. Photographs from Ekmanfjorden are not to scale due to very difficult hydrological conditions (strong currents and high suspension)



echinodermata (starfish and brittle stars) were found in large numbers within the glacier basin and glacier front (Deja unpublished data).

Discussion

Comatulids and other invertebrate suspension feeders often colonize elevations on the seabed (Meyer 1980; Messing et al. 1990; Messing 1997, 2004; Meyer et al. 2014, 2021; Meyer and Sweetman 2015). At such heights, the flow of current is faster and more laminar, thanks to which these organisms get a feeding advantage (Genin et al. 1986;

Meyer-Kaiser et al. 2021). We observed one crinoid attached to the edge of the platform and the other two attached to the carapace of a crab (Fig. 2, Online Resource—supplementary time-lapse video material). An experiment conducted in the LTER (long-Term Ecological Research) area of HAUSGARTEN, Meyer-Kaiser et al. (2019) showed that on abandoned steel structure the number of comatulid crinoids attributed to *Poliometra prolixa* was significantly higher than at the bottom surface. In Fram Strait where the hard substrate is limited, *P. prolixa* has been frequently observed on stones and as an epibiont on sponges (Meyer et al. 1984, 2014, 2016; Schulz et al. 2010). Bottom currents are essential for benthic organisms to disperse, reproduce, and feed (Eléaume et al.

2011). Dense aggregations of *Heliometra* have been noted on the elevations of sea bed in oceanic ridge—Mohn area in N Atlantic or on the large colonies of sponges (Schander et al. 2010). In the glacial bay, the hard substrate is also very limited, which may explain to some extent the association with crabs, and the attachment of one specimen to the edge of the platform (Fig. 2). To the best of our knowledge, no similar observation has ever been recorded. Crabs from the Majoidea superfamily, which are also represented by the observed *Hyas* sp., are known for decorating the carapace. An association between *Hyas araneus* and *Hyas coarctatus* with the sea anemones *Cribrinopsis similis*, *Hormathia nodosa*, and *Urticina crassicornis* was previously observed in the study area (Balazy et al. 2014). There are only a few reports of epibiont relationships between echinodermata and sea crabs in general (Ng and Jeng 1999; Lee and Ko 2009). Relationships among Pilumnidae, Portunidae are mainly described. Associations with crinoids (*Harrovia albolineata*, *Harrovia japonica*, *Tiaramedon spinosum*) have also been recorded, but none of these observations concern the Arctic regions.

The dropstone melted from the growler will be quickly buried, but the highly mobile large crab gets rid of the suspended matter, while being a convenient substrate for the crinoids. The notion that Echinodermata prefer non-turbid waters often mentioned in the literature is a misleading generalization (Meyer 1980). Many Echinodermata, including crinoids, live in at least periodically cloudy environments (Meyer 1973, 1980). Such a periodically cloudy environment is precisely the glacier bay, the innermost parts of the fjords.

Comatulids in Svalbard were mainly observed in the deep water region (Anisimova and Cochrane 2003; Meyer-Kaiser et al. 2021), the northern Svalbard shelf (Meyer et al. 2015), Wijdefjorden in the northern part (Gulliksen and Svensen 2004). *Heliometra glacialis* generally prefers open waters and has rarely been observed in bays or fjords. However, its presence was found in Gronfjord (small branch in the entrance of Isfjord) (Clark and Clark McGown 1967) and a study conducted over 100 years ago (Hofsten 1915) also found isolated occurrences of *Heliometria glacialis* in Isfjord. The temperature range in which the species was recorded ranges from -1.90 to 5.80 °C, while the salinity ranges from 32.2 to 34.9. (Clark and Clark 1967) which is consistent with the temperature and salinity values measured during our study.

The area of the fjords, especially the inner parts, still have much to offer and can significantly expand our knowledge about the behavior, interactions, and functioning of benthic organisms in this changing environment.

The melting tidal glacier forms environment that can offer benefits and not only difficulties. First of all, there is massive rain of marine plankton killed at the surface by the osmotic shock (Węśławski and Legeżyńska 1998; Zajaczkowski and Legeżyńska 2001). This large and predictable food source

sustains rich community of mobile carrion feeders and occasionally also krill that is able to collect phytoplankton food from the sediment (Hirche et al. 2016; Deja et al. 2019). This may be not only a convenient niche for crinoids, but also for the broadly defined megafauna throughout the fjord, also because that large benthic predators such as Atlantic cod avoid such environments (Szczycka et al. 2017).

Crinoids seems to use the uncommon method—crab riding, to avoid the problem with unstable bottom and still use the benefits of glacial front. However, it should be taken into account that crinoids can move on their own, and also might be transported with currents to places behind their usual optimal habitats. There the crab riding might be a useful survival strategy.

Conclusion

During recording time laps videos, we observed the presence of crinoids in the inner part of deglaciated fjords, under strong influence of turbid water from glacier meltwater. Known records of this species typically place it on mixed to hard bottom out of the fjords turbid waters, so our finding of *Heliometra* within inner fjord basin comes as a surprise. In addition, we have observed two specimens of the comatulid crinoid *Heliometra glacialis* clinging on crabs. We interpret this yet undescribed behavior as an adaptation to colonization of new habitats and in this case to avoid the problem with unstable bottom and still use the benefits of glacial bay.

An alternative interpretation could be: fjords are not optimal habitats for comatulids but some individuals, transported by currents or by chance end up in there, some are lucky enough to find elevated substrate on which to cling, some of these substrates are crabs and this is possible because this crab accepts symbiotic relationships. This interpretation takes into account all of the data available and points at the idea that this is not an “adaptation” (this needs to be defined) but some sort of colonization by chance that is expected in animal populations, especially in populations composed of many individuals such as *Heliometra*.

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Author contributions KD conducted the experiments, analyzed the data, and designed and wrote the manuscript. KDD wrote and edited the manuscript. JMW reviewed the manuscript. All authors read and approved the final manuscript.

Declarations

Competing interests The authors are required to disclose financial or non-financial interests that are directly or indirectly related to the work submitted for publication. Please refer to “Competing Interests and Funding” below for more information on how to complete this section.

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Observation of discarded appendicularian houses in the benthic and pelagic zones of Spitsbergen fjords using drop-camera imagery

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ABSTRACT: This study documents previously unreported observations of abandoned *Oikopleura vanhoeffeni* (Chordata: Appendicularia: Oikopleuridae) houses accumulating on the seabed of various Spitsbergen fjords. The investigation utilized data from 253 video stations recorded during Arctic summer expeditions from 2015 to 2021. Notably, observations from 2021 revealed that *O. vanhoeffeni* houses were present both on the seafloor and in the pelagic zone, with densities reaching up to 973 structures m^{-2} , occasionally covering the entire surveyed seabed. According to existing literature, such densities could contribute up to 58 mg carbon m^{-2} . In regions of maximum house density, the water column contained significant mineral suspensions, which could potentially influence the rates of house occlusion, production, and sedimentation. This phenomenon underscores a potentially significant link between Arctic plankton and the intensification of melt-water runoff enriched with mineral suspensions, driven by the accelerating effects of climate change. Moreover, this observation may enhance our understanding of the carbon cycle in high-latitude marine ecosystems, such as the Spitsbergen fjords. Although short-lived, this occurrence may play an ecologically significant role for benthic communities and serves as a notable example of benthic–pelagic coupling, emphasizing its ecological significance.

KEY WORDS: Benthic–pelagic coupling · Arctic · Larvaceans · Appendicularia · Gelatinous zooplankton · Carbon biomass · *Oikopleura vanhoeffeni* · Jelly falls

1. INTRODUCTION

Appendicularians are widely distributed throughout the world's oceans and are among the most common components of plankton (Hamner & Robison 1992, Gorsky & Fenaux 1998, Kalarus & Panasiuk 2021). In some regions, such as Baffin Bay, they have been reported to consume up to 10% of the local primary production (Acuña et al. 2002). Appendicularians are known to produce mucous houses, which are filter-feeding structures (Esnal 1999, Sato et al. 2001). These structures trap small food particles, such as nano- and picophytoplankton, bacteria, and even viruses (Flood et al. 1992, Hansen et al. 1996, Aravena & Palma 2002, Tsujimoto et al. 2006, Lawrence et al. 2018, Jaspers et al. 2023). As the house becomes clogged with prey, fecal pellets, and suspended mineral particles, the appendicularian discards it (Flood

& Deibel 1998). This process can occur several to dozens of times per day (Hansen et al. 1996, Sato et al. 2001), and in some species, such as *Fritillaria formica digitata*, up to 40 times per day (Sato et al. 2003). Abandoned houses, containing filtered bacteria, diatoms, cyanobacteria, and dinoflagellates, may periodically constitute a primary component of marine snow under specific conditions (Alldredge & Gotschalk 1988, Gorsky & Fenaux 1998). Moreover, they play a significant role in global vertical carbon export (Vargas et al. 2002, Alldredge 2005, Robison et al. 2005).

Appendicularians possess a fragile body structure that is easily damaged and fragmented when collected using traditional methods, such as plankton nets, with their filter structures being even more fragile. In a study on the carbon biomass of gelatinous zooplankton (GZ), appendicularians were excluded due to significant undersampling in most GZ surveys

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(Luo et al. 2020). The prevailing belief that appendicularians have a low importance for higher trophic levels is likely a result of their rapid digestion and subsequent underestimation in classical gut content studies (Hays et al. 2018, Kodama et al. 2022, Jaspers et al. 2023). Gorsky & Fenaux (1998) demonstrated that appendicularians are an important food source for many planktonic carnivores, including fish larvae. The species *Oikopleura dioica* and *Fritillaria borealis* constitute between 40 and 75% of the prey of Pleuronectiformes larvae (Last 1980). Similarly, the diet of *Paralichthys olivaceus* consists primarily of 87.5% *Oikopleura* spp. and 2.4% *Fritillaria* spp. (Ikewaki & Tanaka 1993). Appendicularians are consumed by more than 80 species of invertebrates and 350 species of vertebrates, mainly fish (Purcell et al. 2005) and serve as an important food source for commercially significant fish species (Suca et al. 2018). Appendicularians have been found in large quantities in the diets of Gadidae (Johnson et al. 2009), Salmonidae (Doubleday & Hopcroft 2015), and Liparidae (Walkusz et al. 2016). For many fish species, including larval stages, appendicularians represent a preferred prey item. Notably, the polar cod *Boreogadus saida*, a key species in the studied region of Spitsbergen, demonstrates this preference (Nakano et al. 2016).

Abandoned appendicularian houses can serve as a food source or an alternative habitat for other organisms (Esnal 1999). During their sedimentation, appendicularian houses provide sustenance for organisms such as copepods and krill (Alldredge 1972, Ohtsuka et al. 1993, Steinberg et al. 1994, Steinberg 1995, Nishibe et al. 2015). An intriguing aspect of appendicularian biology is their ability to form large aggregations. This typically occurs during specific seasons and in areas where other planktonic species are scarce or absent (Björnberg & Forneris 1956a,b, Fenaux 1963, Alldredge 1982, Uye & Ichino 1995).

This study documents the phenomenon by reporting the mass occurrence of appendicularians captured on underwater cameras in Spitsbergen fjords. It also describes the accumulation of abandoned appendicularian houses, which in some areas covered up to 100% of the seafloor. The potential causes and implications of this event are examined.

2. MATERIALS AND METHODS

2.1. Research area

The Svalbard archipelago, situated in the high Arctic, consists of several islands, with Spitsbergen being

the largest (Fig. 1). This region is influenced by 2 contrasting water masses: the warm and saline Western Spitsbergen Current (WSC), which flows northward along the west coast and transports Atlantic water (Walczowski et al. 2012, Lydersen et al. 2014), and the colder, fresher Sørkapp Current, which carries Arctic water from the Barents Sea (Promińska et al. 2017). These currents shape the climate, sea ice conditions, and hydrography of the coastal and fjord systems (Cottier et al. 2007, Walczowski & Piechura 2011, Carmack et al. 2015, Skogseth et al. 2020).

The research stations were primarily located in 5 fjords along the western coast of Spitsbergen: Krossfjorden, Kongsfjorden, Isfjorden (a large fjord system), Van Mijenfjorden, and Hornsund in the south. Despite their proximity, these fjords exhibit substantial differences in water masses, glacial input, geomorphology (including the presence or absence of underwater sills), and biological communities.

Hornsund, the southernmost fjord, is the coldest in the region due to the dominant influence of the Sørkapp Current and the strong Polar Front, which limits the penetration of Atlantic water (Promińska et al. 2017). This sill-free fjord reaches depths of up to 230 m and is characterized as 'maturing,' with Arctic species predominating, high productivity, and notable carbon sequestration (Węśławski et al. 2017, Zaborska et al. 2018). Hornsund is the site of the region's fastest glacier retreat, reaching up to 70 m yr⁻¹. It also displays distinct sedimentation patterns, with high rates in Brepollen (35 cm yr⁻¹) and low rates near the outer fjord (0.1 cm yr⁻¹) (Węśławski et al. 2012, Błaszczuk et al. 2013).

Van Mijenfjorden, partially enclosed by a sill and the islands of Mariaholmen and Akseløya, spans 50 km in length. It is strongly influenced by glacial sedimentation from the Paulabreen glacier and the Kjelleströmelva River. Despite the sill, summer stratification separates warm, fresh surface water from colder, saline waters introduced by tidal mixing (Støylen & Fer 2014). The fjord typically freezes during winter.

Isfjorden, the largest fjord in Spitsbergen, extends 170 km in length, 24 km in width, and reaches depths of up to 455 m. Its sill-free main channel allows warm Atlantic water from the WSC to flow unimpeded into the fjord (Nilsen et al. 2008, Forwick & Vorren 2009). Branches such as Borebukta and Dicksonfjorden contain underwater sills and are influenced by meltwater and glacial river input. This diversity creates varied physical conditions and supports diverse benthic and pelagic communities.

The Kongsfjorden/Krossfjorden system lies in northern Spitsbergen, where the entrance is formed by the

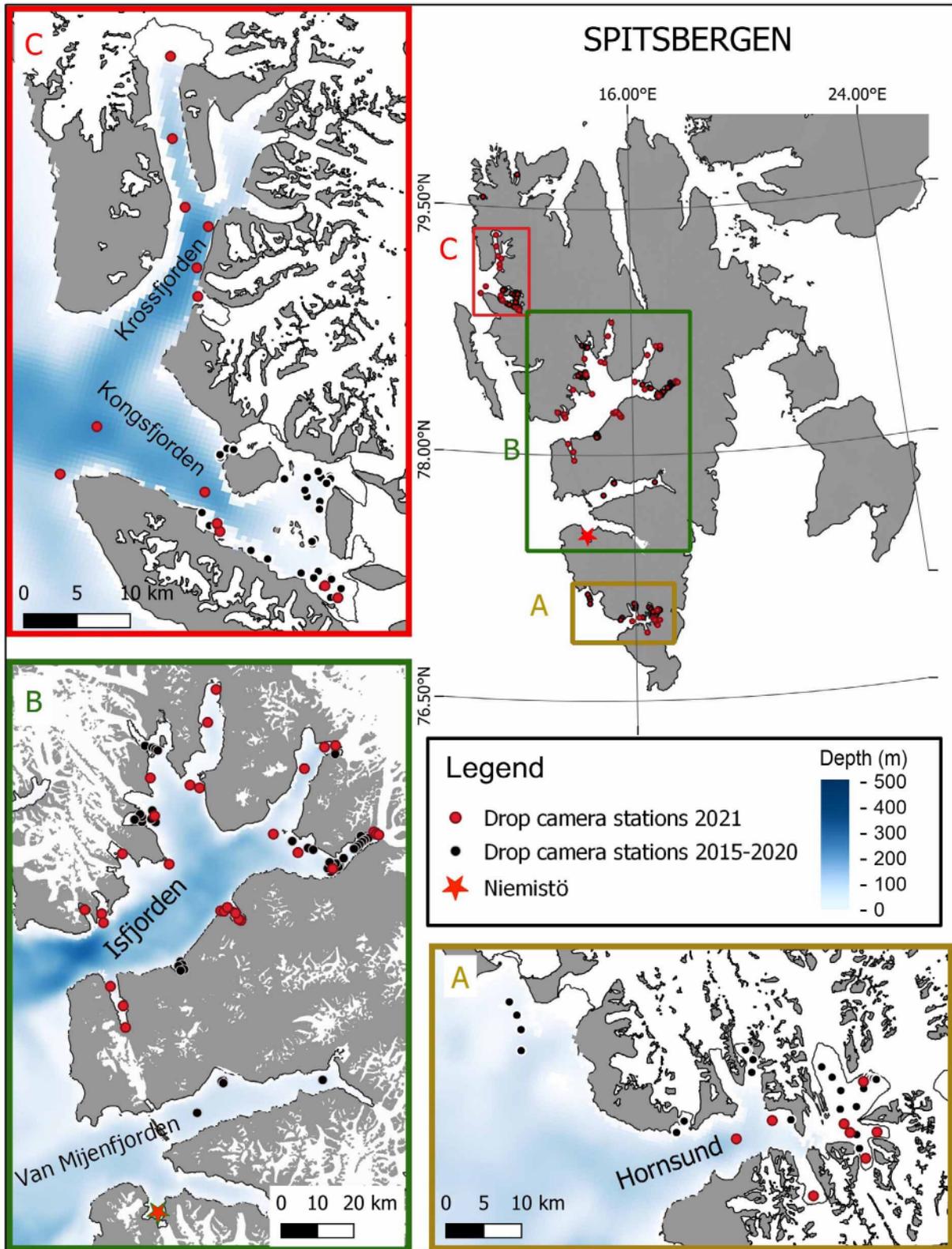


Fig. 1. Spitsbergen, displaying the locations of video stations recorded during Arctic summer expeditions from 2015 to 2021. A red star marks the location of the archival station where the Niemistö core was collected in 2001, revealing a distinct layer of *Oikopleura* sp., most likely *O. vanhoeffeni*

deep glacial channel Kongsfjordrenna. Kongsfjorden stretches approximately 26 km in length and 4–10 km in width, with a maximum depth of 394 m. Krossfjorden is narrower but longer (30 km) and reaches a depth of 374 m. The system is affected by the advection of transformed Atlantic Water, which influences seasonal hydrography and biological communities (Hop et al. 2006, Cottier et al. 2007, Dalpadado et al. 2016). Both fjords receive significant freshwater input from glacial melt (Schellenberger et al. 2015), with Arctic characteristics prevailing in the inner basins, as reflected in mixed Arctic and boreal communities (Maclachlan et al. 2007, Walkusz et al. 2009, Hop et al. 2012).

2.2. Data collection

The present study analyzed video footage collected from 253 stations, predominantly located in the fjords of Spitsbergen, as shown in Fig. 1. The research was conducted aboard the RV 'Oceania' during Arctic summer expeditions (July–August) over 7 yr, from 2015 to 2021, at depths ranging from 18 to 374 m. All video data were acquired using an underwater imaging system, hereafter referred to as a drop camera. The system included a metal frame with 2 cameras: an analog unit with 700 television lines for real-time monitoring and a Panasonic HX-A500 digital camera that recorded high-resolution video (1280×720 pixels) onto a memory card. The setup included 2 independently powered lamps, each operated by separate batteries, and a pair of parallel-mounted lasers for scale calibration. The distance between the lasers was 17 cm. The drop camera was deployed continuously from its release into the water until its retrieval aboard the vessel, descending at an average rate of 0.4 m s^{-1} . Once the camera reached the seafloor, it recorded the benthic surface for approximately 10 min at a frame rate of 100 frames per second (FPS), corresponding to 4-fold slow-motion playback. This recording mode facilitated precise identification and quantification of benthic organisms. The research vessel RV 'Oceania' is not equipped with a dynamic positioning system and therefore drifts passively at an average speed of 0.3 knots (0.15 m s^{-1}). This natural drift enabled the camera to collect video footage along a transect, rather than from a fixed position. The average altitude of the camera above the seafloor was approximately 50 cm. At stations near glacier fronts, the altitude was reduced to 10–30 cm to mitigate visibility issues caused by high concentrations of sus-

pended particulate matter from glacier discharge. The height of the camera above the seafloor was estimated by referencing objects of known size visible in the footage, such as sponges and sea anemones, and by analyzing the spacing of laser points. This method for determining the camera's position relative to the seabed aligns with established approaches reported in previous studies (e.g. Gutt & Siegel 1994, Hirche et al. 2016).

Appendicularian houses were recorded both on the seabed and in the water column, but only during the 2021 season. In previous years, no houses were observed on the seabed, while only a few isolated occurrences were documented in the water column, never exceeding a few individuals per entire water column survey. The houses of the appendicularians and other GZ representatives were counted from the surface to the bottom. However, it remains uncertain whether the observed filtering structures contained living organisms or were empty, thus all houses within the water column were counted. Nine freeze frames were extracted at regular intervals during the portion of the video when the camera was positioned above the seafloor. Appendicularian houses were counted and standardized to an area of 1 m^2 . In the water column, houses were counted continuously. However, quantitative recalculations were not performed due to significant variations in visibility, water transparency, and field of view between stations. The drop camera system was optimized for benthic studies and does not allow for the reliable conversion of recorded pelagic organisms into standardized volumetric units. Additionally, a CTD measurement with a fluorescence sensor was performed at each station. Based on literature data (Deibel 1986, Riehl 1993), abandoned houses were converted into estimated carbon content. Due to substantial variability in water transparency and occasionally unfavorable sea conditions during video recording, including vessel motion and hull swaying, the entire data set was manually analyzed. The analysis of each recording was conducted using VLC Media Player, an open-source software provided under the GPL license. Data were visualized and plotted in Python 3.7 (Van Rossum & Drake 2009) using Matplotlib 3.1.1 (Hunter 2007, Caswell et al. 2019) and Pandas 1.0.5 (McKinney 2010) and in QGIS software where additional spatial analyses were performed. Figures based on drop-camera recording footage were created in CorelDRAW software. Satellite data were obtained from Sentinel-2 natural color composites of the study region and used as a base-map (Fig. 2). The imagery was downloaded from

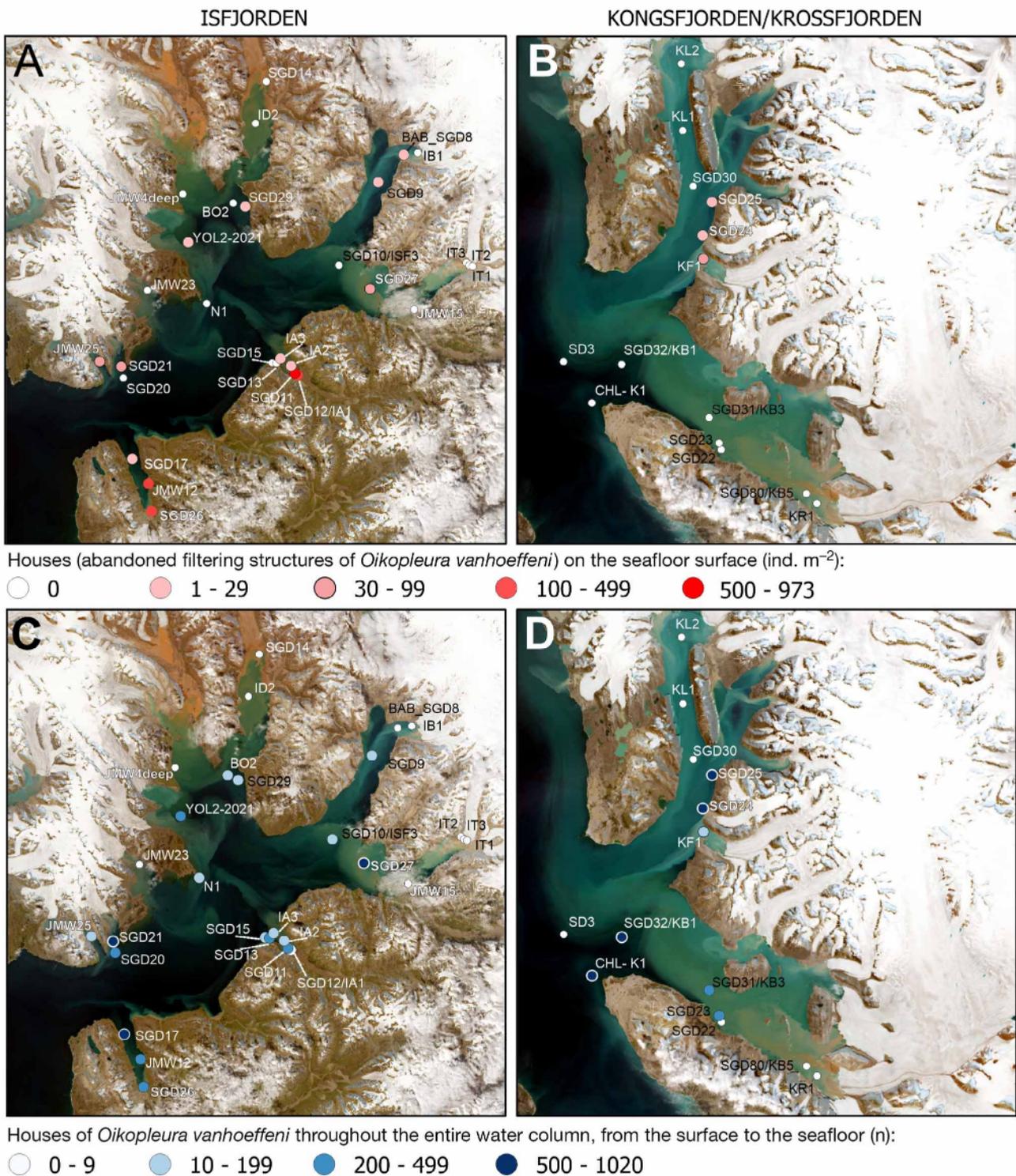


Fig. 2. Location of the stations in (A,C) the Isfjorden and (B,D) the Kongsfjorden/Krossfjorden complex, showing (A,B) the density of abandoned houses on the seabed per m², categorized into 5 intervals, and (C,D) the absolute number of houses recorded in the water column from the surface to the seabed, presented in numerical intervals. The background features a Sentinel 2 natural color composite acquired on 14 August 2021

<https://apps.sentinel-hub.com/eo-browser/> and acquired on 14 August 2021, corresponding to the closest available date to the *in situ* data collection.

These data provided environmental context, particularly regarding suspended sediment runoff in the region.

3. RESULTS

The analysis of material from 253 video stations (see Fig. 1) revealed the presence of appendicularian houses on the seafloor of Spitsbergen fjords and large aggregations of houses in the water column exclusively

in the 2021 season. Additionally, quantitative counts of appendicularians and GZ representatives were conducted in the water column for that year. Detailed counts from the water column and seabed are presented in Table 1. To improve clarity, house densities are expressed as ranges and visualized on the map (Fig. 2).

Table 1. Summary of selected parameters characterizing the surveyed stations in 2021, including the number of *Oikopleura vanhoeffeni* houses and other representative gelatinous zooplankton observed in the water column, as well as the number of abandoned *O. vanhoeffeni* houses recorded on the seafloor (standardized per m²). The values for *O. vanhoeffeni* houses in the water column represent total counts observed throughout the entire surveyed water column at each station and are not standardized to volume units, due to variability in the camera field of view and water clarity. Gelatinous zooplankton taxa include the ctenophores *Beroe cucumis* and *Mertensia ovum*, and the medusae *Halopsis ocellata*, *Halitholus cirratus*, and *Cyanea capillata*. Detailed locations of the stations are shown in Fig. 2

Stn	Location	Date (d.mo)	Depth (m)	Bottom type	Appendicularians in water column	<i>M. ovum</i>	<i>B. cucumis</i>	<i>H. cirratus</i>	<i>H. ocellata</i>	<i>C. capillata</i>	Appendicularian houses at the bottom (ind. m ⁻²)	Bottom carbon (mg C m ⁻²)	
												Min.	Max.
SGD1	Hornsund	25.07	114	Soft	0	0	0	0	0	0	0	0.00	0.0
SGD2	Hornsund	25.07	75	Soft	1	0	0	0	0	0	0	0.00	0.0
SGD4	Hornsund	25.07	167	Soft	8	1	1	0	0	0	0	0.00	0.0
SGD5	Hornsund	25.07	45	Soft	0	0	0	1	0	0	0	0.00	0.0
HB1	Hornsund	25.07	50	Soft	0	0	0	0	0	0	0	0.00	0.0
HM1	Hornsund	27.07	66	Soft	0	0	0	0	0	0	0	0.00	0.0
HM2	Hornsund	27.07	53	Soft	0	0	0	0	0	0	0	0.00	0.0
HS1	Hornsund	27.07	76	Soft	0	0	0	0	0	0	0	0.00	0.0
CHL- K1	Kongsfjord	01.08	68	Hard	700	1	1	0	0	0	1	0.01	0.1
SGD31/KB3	Kongsfjord	01.08	343	Soft	218	0	0	0	1	0	0	0.00	0.0
SGD22	Kongsfjord	01.08	20	Mixed	0	0	0	0	0	0	0	0.00	0.0
SGD23	Kongsfjord	01.08	151	Soft	215	0	0	0	0	0	0	0.00	0.0
SGD32/KB1	Kongsfjord	02.08	374	Soft	740	4	0	0	1	0	0	0.00	0.0
SGD80/KB5	Kongsfjord	03.08	86	Soft	0	0	0	0	0	0	0	0.00	0.0
KR1	Kongsfjord	03.08	59	Soft	0	0	0	0	0	0	0	0.00	0.0
SD3	Kongsfjord	05.08	52	Soft	0	0	0	0	0	0	0	0.00	0.0
KF1	Krossfjord	06.08	60	Soft	47	0	1	0	0	0	58	0.49	3.5
KL1	Krossfjord	07.08	256	Soft	0	0	0	0	0	0	0	0.00	0.0
KL2	Krossfjord	07.08	174	Soft	0	0	0	0	0	0	0	0.00	0.0
SGD24	Krossfjord	07.08	245	Soft	510	5	6	0	0	0	2	0.02	0.1
SGD25	Krossfjord	07.08	141	Soft	910	4	2	0	0	0	2	0.02	0.1
SGD30	Krossfjord	07.08	282	Soft	0	0	0	0	0	0	0	0.00	0.0
SGD12/IA1	Isfjord	10.08	48	Soft	4	13	0	0	0	0	104	0.87	6.2
SGD11	Isfjord	10.08	65	Soft	490	29	2	0	0	0	973	8.15	57.7
N1	Isfjord	11.08	38	Hard	178	8	0	0	0	0	0	0.00	0.0
JMW23	Isfjord	11.08	44	Soft	0	0	0	0	0	0	0	0.00	0.0
SGD21	Isfjord	11.08	103	Soft	520	11	0	0	0	0	43	0.36	2.6
SGD20	Isfjord	11.08	100	Hard	480	18	1	1	0	1	1	0.01	0.1
JMW12	Isfjord	12.08	48	Soft	240	17	2	2	0	0	294	2.46	17.4
SGD26	Isfjord	12.08	55	Soft	320	10	6	2	0	0	207	1.73	12.3
SGD17	Isfjord	12.08	132	Mixed	1020	11	11	0	0	0	5	0.04	0.3
JMW25	Isfjord	13.08	42	Soft	37	2	0	0	0	0	39	0.33	2.3
SGD27	Isfjord	14.08	35	Mixed	730	9	0	0	0	0	75	0.62	4.4
JMW15	Isfjord	14.08	72	Soft	2	12	0	0	0	0	0	0.00	0.0
IT3	Isfjord	14.08	39	Soft	0	0	0	0	0	0	0	0.00	0.0
IT2	Isfjord	14.08	40	Soft	0	0	0	0	0	0	0	0.00	0.0
IT1	Isfjord	14.08	27	Soft	0	0	0	0	0	0	0	0.00	0.0
YOL2-2021	Isfjord	15.08	71	Soft	392	40	0	0	0	1	23	0.19	1.4
SGD29	Isfjord	15.08	37	Mixed	38	1	0	0	0	1	2	0.02	0.1
SGD14	Isfjord	15.08	22	Soft	0	0	0	0	0	0	0	0.00	0.0
JMW4deep	Isfjord	15.08	72	Soft	5	21	1	0	0	0	0	0.00	0.0
ID2	Isfjord	15.08	87	Soft	0	0	0	0	0	0	0	0.00	0.0
BO2	Isfjord	15.08	51	Hard	88	0	0	0	0	3	1	0.01	0.0
SGD10/ISF3	Isfjord	16.08	99	Soft	140	17	0	0	0	0	0	0.00	0.0
SGD9	Isfjord	16.08	146	Soft	100	18	2	0	0	0	3	0.03	0.2
BAB_SGD8	Isfjord	16.08	190	Soft	2	6	14	0	0	0	9	0.07	0.5
IB1	Isfjord	17.08	96	Soft	0	0	0	0	0	0	0	0.00	0.0
SGD15	Isfjord	18.08	18	Hard	110	2	0	0	0	0	0	0.00	0.0
SGD13	Isfjord	18.08	31	Soft	235	7	0	0	0	0	0	0.00	0.0
IA3	Isfjord	18.08	98	Soft	150	14	0	0	0	0	2	0.01	0.1
IA2	Isfjord	19.08	74	Soft	150	20	1	0	0	0	4	0.04	0.3

Out of the 51 stations surveyed in 2021, appendicularians were recorded at 31 stations in the water column, with 21 stations having more than 100 filtering structures recorded during the descent of the drop camera. These values represent absolute counts, not standardized volumetric densities, due to variability in field of view and optical conditions between deployments. The highest number of appendicularian filtering structures in the water column was recorded at Stns SGD17 (Isfjorden) and SGD25 (Krossfjorden), with 1020 and 910 filtering structures, respectively. Fig. 3 presents freeze frames from 4 selected stations showing houses in the water column. The distribution pattern of filtering structures within the water column was influenced by local stratification. At shallow stations with weak thermohaline structure, houses were observed throughout the entire water column, from the surface to the seafloor, at similar densities and without distinct aggregations (e.g. Stn SGD27). In contrast, at deeper stations with pronounced stratification, most houses accumulated at the pycnocline and began sinking after

acquiring additional weight from mineral particles (e.g. Stn SGD25).

In addition to appendicularian filtering structures, the ctenophore *Mertensia ovum* was recorded at 26 stations, with a maximum of 40 individuals observed at Stn YOL2-2021 (Isfjorden). The presence of *Beroe cucumis* was documented at 14 stations, with a maximum count of 14 individuals at Stn BAB-SGD8 (Isfjorden). Additionally, 3 other GZ species were identified: *Halitholus cirratus*, *Halopsis ocellata*, and *Cyanea capillata* (see Table 1).

At 24 stations, the remnants of appendicularian houses, either whole or decaying, were found at the bottom. The maximum density was observed at Stn SGD11 (Isfjorden), with a concentration of 973 houses m^{-2} , nearly covering the entire seafloor (Fig. 4; Video S1 in the Supplement at www.int-res.com/articles/suppl/m771p071_VS1.mp4). Notable differences were observed between stations located in relatively close proximity, such as Stn SGD12/IA1 and SGD11. At both locations, the houses were well-preserved in terms of shape and remained intact.

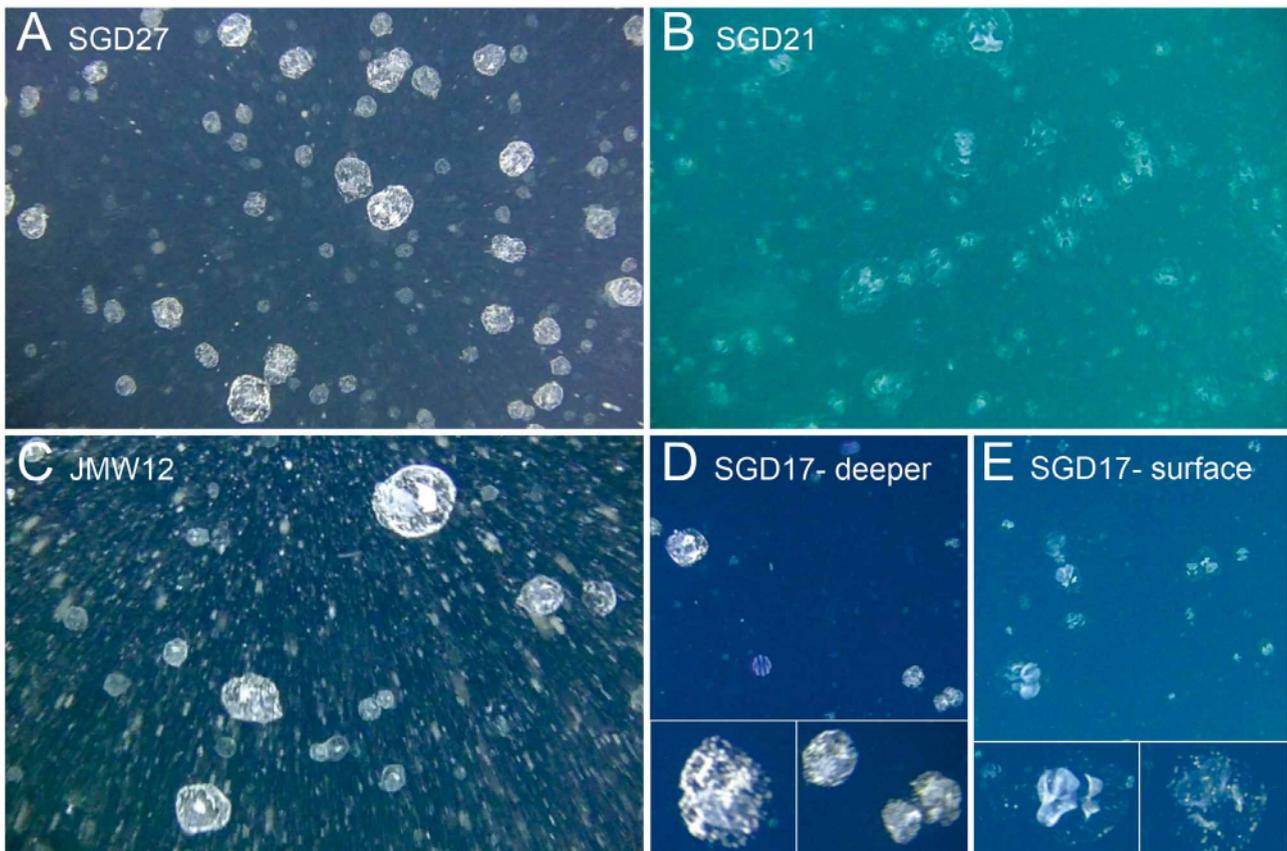


Fig. 3. Freeze frames capturing *Oikopleura vanhoeffeni* houses in the water column. Stn SGD17 (D,E) includes snapshots from both the surface layer and 100 m depth to illustrate differences in the appearance of the houses, particularly in terms of suspension coverage

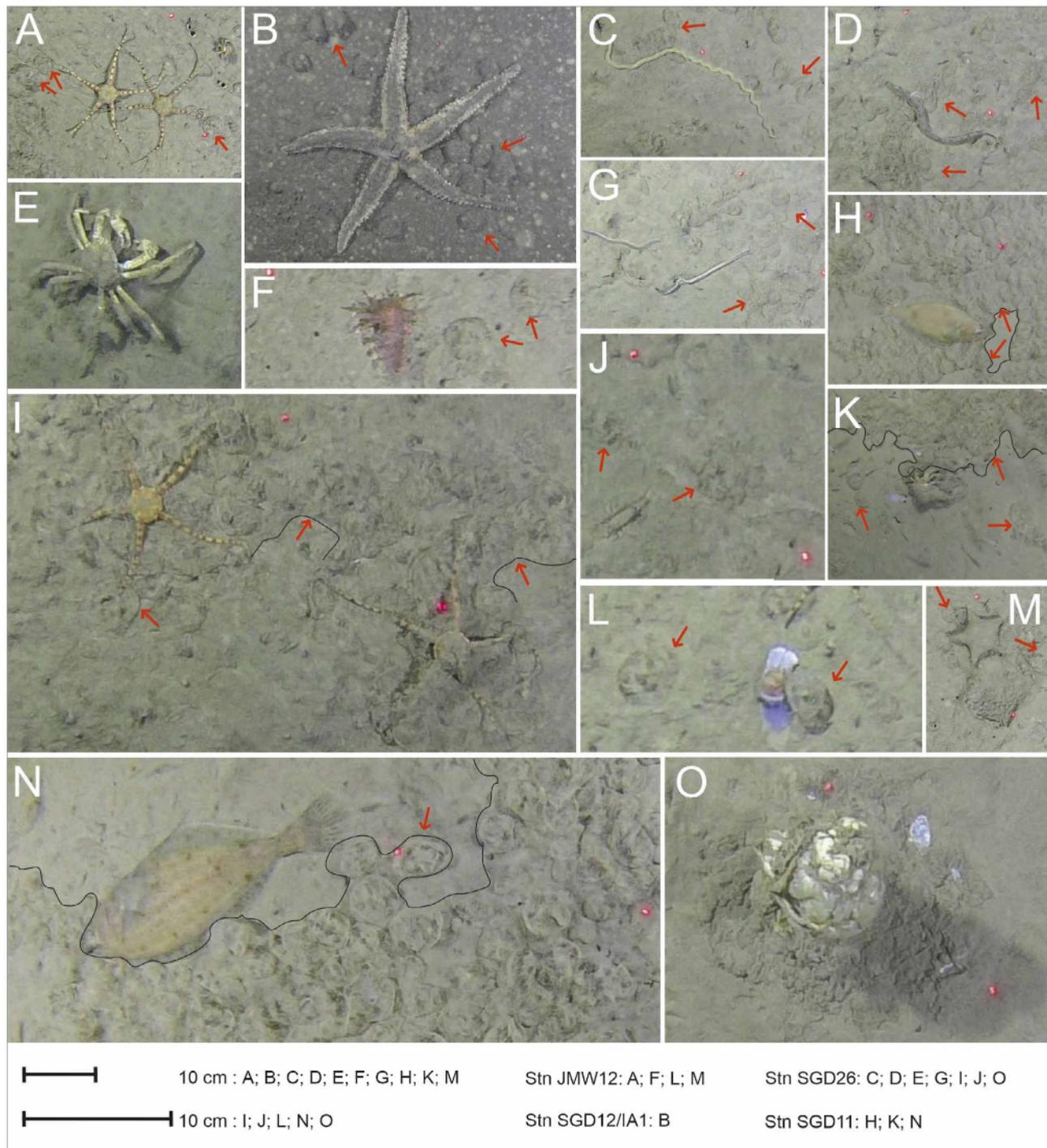


Fig. 4. Freeze frames from 4 stations where the highest densities of abandoned *Oikopleura vanhoeffeni* houses were recorded. The distance between the red laser dots is 17 cm, serving as a scale reference. Viewing Video S1 (as well as the full-sized panels in the Supplement at www.int-res.com/articles/suppl/m771p071_supp.pdf), is strongly recommended to facilitate the identification of appendicularian houses depicted in these frames. To aid readers in locating the houses on the seafloor, selected examples are marked with red arrows, and curved black lines delineate areas of house aggregations from relatively clear seafloor. Each panel also features representatives of benthic megafauna observed at the respective locations: (A,I) *Ophiocten sericeum*, (B) *Urasterias lincki*, (C) *Phyllodoce* sp., (D) Pisces, (E) *Hyas* sp., (F) *Dendronotus frondosus*, (G) Nemertea, (H,N) Pleuronectidae, (J) Decapoda, (K) *Pagurus* sp., (L) Naticidae, (M) *Ctenodiscus crispatus*, and (O) *Buccinum* sp. egg capsule cluster. In panels E and O, only fragments of appendicularian houses are visible, entangled around the walking legs of a crab and attached to the *Buccinum* sp. egg capsule cluster, respectively

However, at Stn SGD12/IA1, the houses were partially covered with suspended material, suggesting a higher accumulation of trapped particles also within their structure. This observation is illustrated in Fig. 4B and Video S1. Differences between the 2 stations were also evident in the water column. Only 4 houses were identified at Stn SGD12/IA1, compared to 490 at the nearby Stn SGD11. At 9 stations where *Oikopleura vanhoffeni* houses were found on the seafloor, their density exceeded 20 ind. m⁻². At 3 stations, only remnants were observed, appearing as degraded houses attached to protruding structures and benthic organisms, such as polychaete tubes, sea urchins, and scallops. The estimated amount of carbon on the seafloor at this station, depending on the conversion factor applied (Deibel 1986, Riehl 1993), ranged from 8.15 to 57.7 mg C m⁻². Comparable densities were documented at Stns JMW12, SGD26, and SGD12/IA1 (all in Isfjorden), exhibiting 294, 207, and 104 filtering structures m⁻², respectively (Fig. 4; Video S1). Consequently, the estimated quantities of bottom carbon at these stations were up to 17.4, 12.3, and 6.5 mg C m⁻², respectively. The estimated bottom carbon is directly proportional to the number of houses remaining and is presented as a range from the minimum to maximum values in Table 1.

The condition of the houses recorded on the seafloor varied significantly, ranging from well-preserved (e.g. Fig. 4, Stns SGD11, SGD12/IA1) to severely degraded (e.g. Fig. 4, Stn SGD26) (see Video S1). At Stn SGD12, some houses were found to be intact, while at Stn SGD26, only detached fragments were observed (Fig. 4). Among the examined fjords, Hornsund stands out, as no Appendicularia were recorded either in the water column or on the bottom. At locations where appendicularian jelly falls (JFs) were observed, a diverse array of epifauna and demersal fish from the family Pleuronectidae was also recorded, as shown in Fig. 4. In addition to these benthic organisms, interactions with near-bottom pelagic species were also documented. At Stn SGD11, krill were observed actively pecking at the appendicularian houses covering the seafloor. Fig. 4 includes freeze frames from 4 stations, illustrating representatives of benthic megafauna among the abandoned appendicularian filtering structures.

Hydrological data and fluorescence measurements are presented in Fig. 5, visualized for the Isfjorden and Kongsfjorden/Krossfjorden areas, corresponding to regions where occurrences of organisms or their houses were recorded in the water column or on the seafloor. Water temperature was relatively consis-

tent across study locations. The mean salinity measured in the surface water layer (upper 10 m) was significantly reduced due to glacial meltwater and river discharge. Chlorophyll *a* fluorescence was highest in the upper 40 m layer of Isfjorden, with peak values reaching 0.8, while in Kongsfjorden/Krossfjorden, the highest values were found in the upper 20 m layer, with a relatively higher value of up to 2.0.

4. DISCUSSION

GZ, including cnidarians, ctenophores, and pelagic tunicates, are characterized by highly dynamic population fluctuations (Purcell 2012, Lucas et al. 2014, Luo et al. 2020). These organisms are composed primarily of water with a minimal carbon content, enabling them to thrive in nutrient-poor environments. However, when food availability increases, they can efficiently exploit these resources (Acuña et al. 2011, Pitt & Lucas 2014). GZ bloom events often end in mass mortality events known as JFs, when food supplies are exhausted (Lebrato et al. 2011). This phenomenon has been documented using various methodologies, including video-based techniques such as remotely operated vehicles, yo-yo cameras, towed cameras, and *in situ* photography during diving expeditions (Cacchione et al. 1978, Duggins 1981, Miyake et al. 2002, Sweetman & Chapman 2011). Additionally, other methods such as bottom trawls, direct visual observations, sediment traps, and stomach content analyses have provided insights into the occurrence of JFs (Cowper 1960, Sartor et al. 2003, Sexton et al. 2010, Takahashi et al. 2013). Lebrato et al. (2012) provided a comprehensive overview of JF events. Field observations indicate that the bodies of GZ are often well preserved and show minimal decomposition (Billett et al. 2006, Sweetman & Chapman 2011). However, to date, no studies have explicitly documented the involvement of appendicularian houses in JFs. One possible explanation for this absence is the fragile nature of appendicularians and, in particular, their mucous filter structures, which are highly susceptible to damage during conventional sampling, such as with plankton nets (Hamner et al. 1975).

4.1. Appendicularian houses in the water column and on the seafloor — past observations

References to abandoned filter structures on the seafloor mainly concern large appendicularians of the genus *Bathochordaeus* observed in Monterey

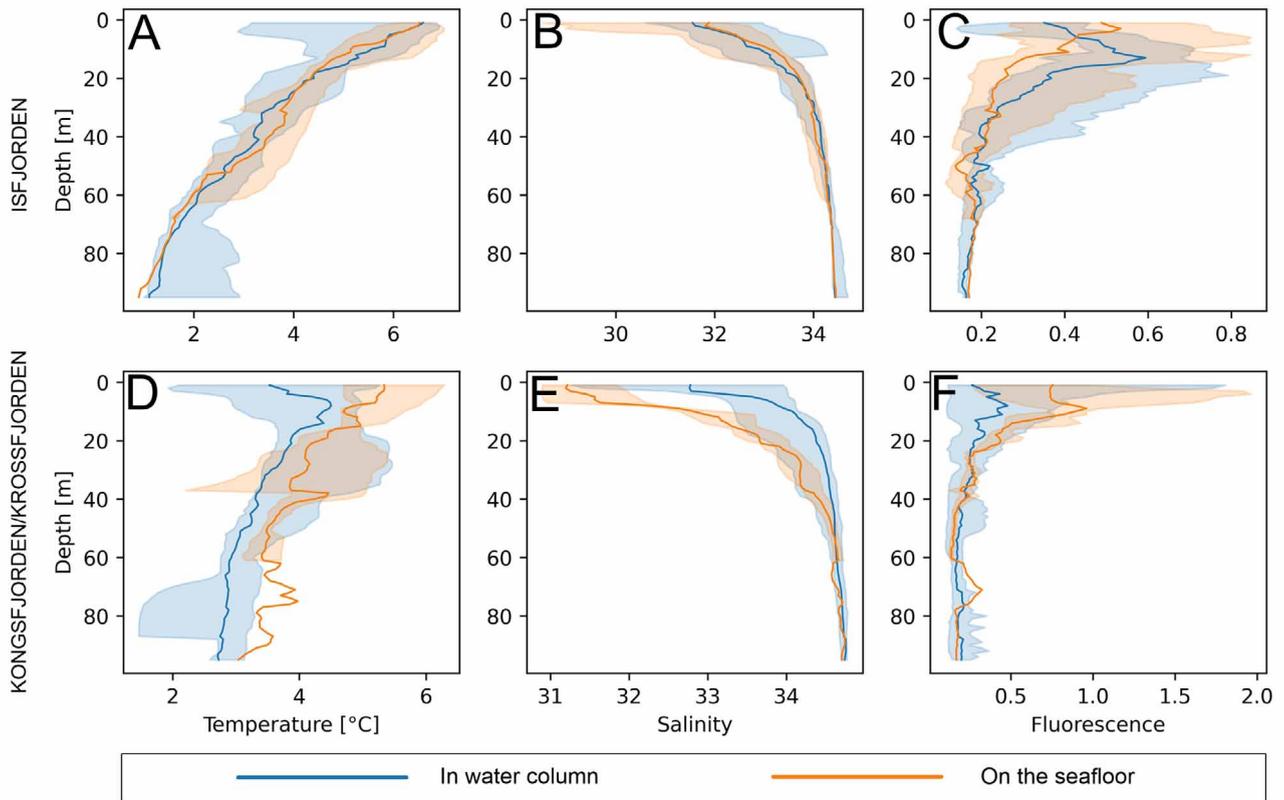


Fig. 5. Vertical profiles of average values (solid lines) of (A,D) temperature, (B,E) salinity, and (C,F) fluorescence with minimum–maximum ranges (shading) are presented for (A–C) Isfjorden and (D–F) Kongsfjorden. These profiles are averaged for the stations where *Oikopleura vanhoffeni* houses were observed in the water column (blue) and on the bottom surface (orange). Data below 80 m were excluded, as they do not provide significant information beyond this depth

Canyon (Hamner & Robison 1992), which were recorded at maximum densities of up to 1 structure m^{-2} during MIR I submersible dives in 1990. In Newfoundland and Nova Scotia, during blooms of *Oikopleura vanhoffeni* and *O. labradoriensis*, abandoned houses accumulated as 'slub' (slime) on fishing nets, reducing their effectiveness and making them more visible to fish (Mahoney & Buggeln 1983, Taggart & Frank 1987). Both fishermen's observations and subsequent scientific research linked the mass occurrence of this species to the appearance of a cold water mass in the region (Mahoney & Buggeln 1983, Choe & Deibel 2008). A similar phenomenon was observed and documented using an underwater video camera in the summer of 2019, when appendicularian blooms clogged Inuit fishing nets in the western Canadian Arctic, preventing fishing for a period of 40 d (Pettitt-Wade et al. 2020). Although the phenomenon of houses sinking to the seafloor in Svalbard has been previously mentioned (Gulliksen & Svensen 2004), no photographic or video documentation exists, nor any data on house density. Similar appendicularian blooms were reported earlier in the Spitsbergen region, in-

cluding observations from the 1990s in Smerenborgfjorden and in January 2016 in the marginal ice zone of Fram Strait (S. Kwaśniewski pers. comm.). The occurrence of appendicularian blooms near the marginal sea ice zone is further supported by studies (Arashkevich et al. 2002, Deibel et al. 2017, Pantiukhin et al. 2024). Abandoned houses of *O. vanhoffeni* were also observed during core sampling conducted aboard RV 'Oceania' in 2001 in Recherchefjord. This observation was documented in a photograph showing appendicularian houses resting on sediment collected using the Niemistö core sampler from a depth of 70 m (Figs. 1 & 6).

4.2. Identification of the species responsible for jelly falls

The size of the recorded houses (Figs. 4 & 6), together with existing knowledge of appendicularian species in the study area, suggests that *O. vanhoffeni* is primarily responsible for the observed JF. This species produces mucous houses measuring approx-

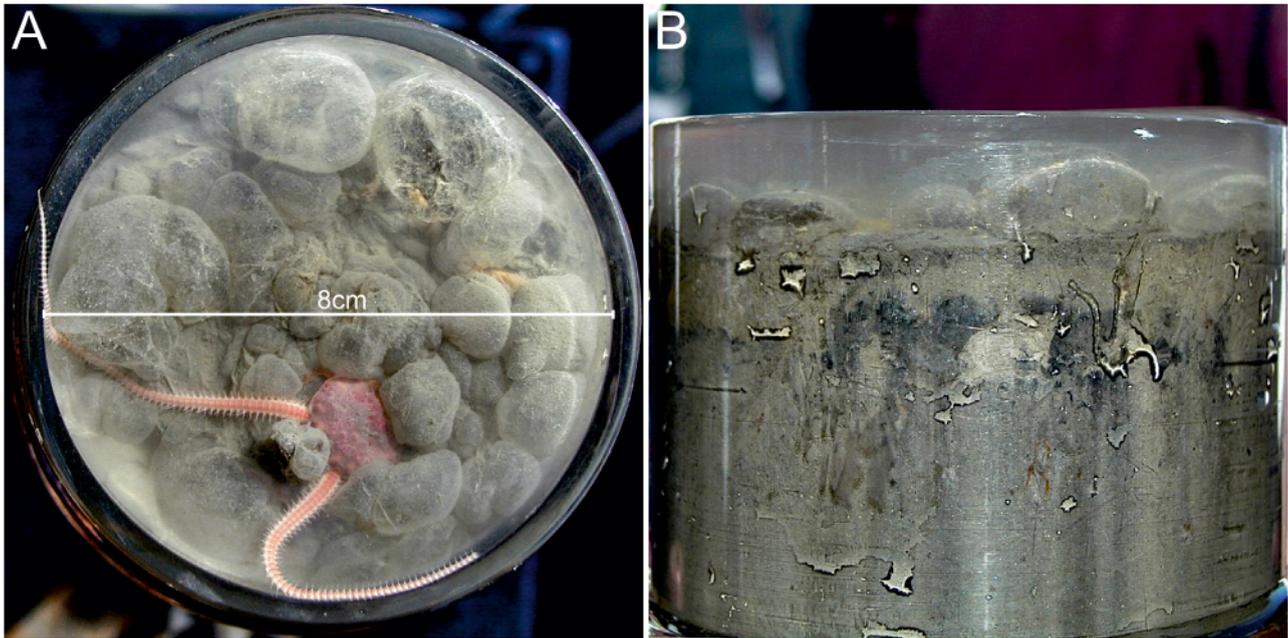


Fig. 6. (A) Top and (B) side views of a core sample collected using the Niemistö probe in Recherchefjorden reveal a distinct layer of abandoned *Oikopleura* spp. houses. The sizes of the structures suggest that they predominantly belong to *O. vanhoeffeni*. Photographs by Sławomir Kwaśniewski

imately 40–60 mm in diameter (Knoechel & Steel-Flynn 1989). It is notable for its relatively large body size, with a tail length of around 13 mm (Deibel 1986, Knoechel & Steel-Flynn 1989) and for its stenothermy, meaning that it develops within a relatively narrow temperature range compared to other members of the Oikopleuridae family (Broms & Tiselius 2003). Additionally, it is a cryophilic species and the dominant appendicularian in Arctic seas (Udvardy 1954, Shiga 1993, Deibel & Daly 2007). *O. vanhoeffeni* can produce up to 6 new houses per day (Deibel 1987). The concentration of this species observed in coastal waters of Newfoundland reached up to 2000 ind. m⁻³ (Deibel 1987), a value comparable in order of magnitude to the numbers observed in our study, despite differences in methodology and volume standardization.

4.3. Potential impact of turbid meltwater

As they sink, appendicularian houses act as mucous traps, capturing larger particles that adhere to their surfaces (Kjørboe et al. 1996). This phenomenon is illustrated in Fig. 3, which shows a distinct difference in the appearance of houses in the surface layer compared to the deeper layer at Stn SGD17. Estimates of particle capture by abandoned houses suggest that most particles in the house and on its surface were collected while the appendicularian was still inside

(Hansen et al. 1996). It is likely that most of the houses found in the deeper part of the water column with a large number of filtered particles are devoid of their hosts. The rate at which marine snow particles fall is heavily dependent on their properties such as particle size and shape, apparent density and porosity, as well as the content of lithogenic or calcite material that acts as ballast (Francois et al. 2002, Klaas & Archer 2002, De La Rocha & Passow 2007). All recorded occurrences of abandoned *O. vanhoeffeni* houses on the seafloor were within the direct influence zone of a glacier or a large glacial river (Stns SGD26, JMW12, SGD27, JMW25, SGD21, SGD11, SGD12/IA1, KF1; Fig. 2). The presence of a substantial amount of mineral suspension in this area may lead to faster clogging of structures, increase the rate of house replacement, and significantly accelerate the sinking rate of abandoned houses due to ballasting with lithogenic material from melting glaciers. The median particle size of the suspension studied in the fjords of Spitsbergen ranges from 81.06 to 123.38 µm (Dragańska-Deja 2024). The pore size of the incurrent filter in *O. vanhoeffeni* houses averages 163 ± 65 µm in length and 81 ± 34 µm in width (Deibel 1986). These values are relatively comparable, suggesting that glacial-origin suspensions may easily clog the incurrent filter. Oikopleuridae are capable of partially preventing the clogging of a house by directing water currents using specialized ciliated spiracles in the

opposite direction (Alldredge 1976). However, this mechanism is effective only up to a certain density of filtered cells, beyond which the rate of house replacement increases significantly and the development of individuals or populations may decline (Sato et al. 2001). In this study, significant differences in the distribution of appendicularian houses were observed between Stns SGD12/IA1 and SGD11. This disparity can be attributed to the positioning of Stn SGD12/IA1, which is 17 m shallower and situated closer to the mouth of the Adventelva River. This river delivers substantial amounts of suspended material, with the highest concentrations recorded at 826 mg l⁻¹ and vertical fluxes exceeding 1000 g m⁻² d⁻¹ (Zajaczkowski & Włodarska-Kowalczyk 2007). These conditions likely contribute to greater accumulation of suspended particles within the houses at Stn SGD11, which may explain the observed differences in house abundance between the 2 stations.

4.4. Depth factor

Depth may be a significant factor influencing accumulations of appendicularian houses on the seafloor, which have been recorded at depths ranging from 40 to 70 m (Table 1, Fig. 6). At these depths, the impact of wave action is minimized, facilitating the direct deposition of sinking houses near the origin of the water mass where the bloom occurred. This enables the formation of the observed aggregations. In contrast, deeper locations may be less conducive to such accumulations, as the probability of house drift within the water column over a broader seabed area increases. Additionally, abandoned houses undergo physical changes during their descent: they experience rapid deflation shortly after being discarded, followed by gradual compression and loss of buoyancy over time (Lombard & Kiørboe 2010). While these processes increase the sinking velocity of houses, allowing them to settle faster, the initial period of slower sinking and reduced density permits significant horizontal displacement before compression is complete. This reduces the likelihood of concentrated accumulation on the seafloor at greater depths. At Stns SGD17, SGD20, CHLK1, and SGD32, located farther from the source of suspension and at greater depth, either no houses or only a few (<5 m⁻²) were recorded on the seafloor, despite the presence of a large number of appendicularians in the water column (Fig. 2, Table 1).

Glacial runoff can positively influence nutrient availability and labile carbon transport to upwelling zones near tidewater glaciers (Urbanski et al. 2017),

which can lead to increased biological productivity (Hood et al. 2009, Hawkings et al. 2015, Wadham et al. 2016). Consequently, these areas may be favorable for the mass development of zooplankton, including Appendicularia. The association between high densities of *O. vanhoeffeni* and upwelling events has also been reported by Taggart & Frank (1987). Additionally, strong tidal currents and the presence of underwater sills can further intensify mixing and nutrient delivery to surface waters (Etherington et al. 2007). It is likely that the occurrence of a JF composed of Appendicularia requires the simultaneous presence of several of the aforementioned factors.

4.5. Interactions with other organisms

The preservation state of the houses is influenced by various physical and biological factors, such as hydrodynamic forces, the concentration of suspended mineral particles, depth, and the actions of marine organisms like crabs, echinoderms, and fish. In waters with a temperature of 2°C, the bacterial decomposition of *O. vanhoeffeni* houses would take approximately 2 to 3 wk (Deibel 1987). In the Spitsbergen region, however, due to the rapid sinking of the houses, a more significant factor may be their burial by sedimentation from suspended particulate matter or mechanical degradation by megabenthic organisms. Abandoned sinking houses serve as habitats and food sources for numerous marine organisms, including harpacticoids, poecilostomatoid copepods, and invertebrate larvae (Alldredge 1972, Ohtsuka et al. 1993, Steinberg et al. 1994, Steinberg 1995, Nishibe et al. 2015). At all stations where numerous *O. vanhoeffeni* houses were recorded, high densities of *Mertensia ovum* were also observed. Several GZ taxa co-occurred with *O. vanhoeffeni*, including the ctenophores *Beroe cucumis* and *Mertensia ovum*, and the medusae *Heliopsis ocellata*, *Halitholus cirratus*, and *Cyanea capillata*. While *B. cucumis* is a specialist predator that feeds exclusively on other ctenophores (Falk-Petersen et al. 2002, Haddock 2007), the remaining species are likely predators of appendicularians (Pettitt-Wade et al. 2020). At Stn SGD11, active interactions between krill and the appendicularian houses accumulated on the seafloor were observed. The behavior of krill closely resembled benthic foraging strategies previously described in both the Arctic and Antarctic. These include 'nose diving' (Deja et al. 2019), 'skimming', and 'balling' — a group behavior in which krill stir up sediment collectively to feed on suspended material (Kane et al. 2021) In our ob-

servations, krill individuals displayed a clear preference for seafloor patches covered with *O. vanhoefeni* houses over barren areas (see Video S1). During descent, the filtering structure left behind a trail of released particles and dissolved substances, which may attract and influence the movement of zooplankton. Assuming a sinking rate of 30 to 40 m d⁻¹ (Alldredge & Gotschalk 1988, Koski et al. 2007), zooplankton feeding on the descending material can reduce the carbon content in the house by 20 to 30%. However, in glacially influenced environments such as the fjords of western Spitsbergen, where suspended mineral loads are high (Zajaczkowski & Włodarska-Kowalczyk 2007), the actual sinking rate may be substantially higher — potentially exceeding 100 to 150 m d⁻¹ — due to lithogenic ballasting (Lombard et al. 2013).

GZ are thought to play a significant role in the biological pump; however, their overall contribution to global carbon flux remains poorly understood (Luo et al. 2020). JFs represent an understudied source of particulate organic matter (Lebrato et al. 2012). The large biomass and rapid sinking capacity of GZ aggregations suggest that JFs and feces play a critical and underestimated role in the biological pump and sea–air carbon balance (Lebrato & Jones 2009, Sweetman & Chapman 2015, Steinberg & Landry 2017, Lebrato et al. 2019, Luo et al. 2020). GZ are highly efficient at assimilating nano- and picoplankton (King et al. 1980, Deibel 1988, Acuña et al. 1996), which allows them to quickly remove small cells from the euphotic zone and exert a greater influence on vertical carbon flux than copepod-dominated communities (Urban et al. 1992, Hansen et al. 1996, Vargas et al. 2002). GZ can filter submicron particles, which enables efficient energy extraction from the microbial system and transfer to larger metazoans (Gorsky & Fenaux 1998). This process significantly shortens the food chain and may even enhance the transfer of colloidal organic matter to higher trophic levels, including fish (Flood et al. 1992, Bedo et al. 1993). The abandoned houses on the seafloor, primarily composed of mucopolysaccharides, still contain digestible and nutritionally valuable producers such as diatoms and dinoflagellates. A study by Beroujon et al. (2022) revealed a strong correlation between the high density of appendicularian 'banks' on the Greenland shelf and the abundance of benthic fauna in the region. Appendicularians occur in large numbers in areas of high productivity and through their specific way of feeding, enhance benthic–pelagic coupling (Beroujon et al. 2022). Under favorable conditions, appendicularians can consume up to 50–66% of the standing crop of

phytoplankton (Alldredge 1981, Deibel 1988, Maar et al. 2004). The remineralization of JF biomass releases dissolved organic matter, creating a 'jelly carbon shunt' (Condon et al. 2011). The carbon derived from GZ reaching the seafloor can rapidly release dissolved organic carbon, which stimulates benthic microbial communities and may indirectly support benthic scavengers via microbial production (Titelman et al. 2006, Sweetman et al. 2014, Luo et al. 2020). Research by Luo et al. (2020) indicates that the transfer efficiency of GZ particulate organic carbon (POC) is 5 times greater than that of non-GZ POC.

4.6. Episodic nature and ecological implications of appendicularian jelly falls

The documented appendicularian JF episode and the associated carbon deposition on the seabed (see Table 1) represent only a transient snapshot of the ecosystem's condition. The frequency, duration of house persistence on the seafloor, and the timing of blooms and subsequent deposition remain largely unknown. Only 2 studies in the literature have quantified the carbon content in *O. vanhoefeni* houses (Deibel 1986, Riehl 1993), both of which examined clean structures that exhibited signs of prolonged filtration activity. *O. vanhoefeni* defecates approximately every 16 min (Bochdansky & Deibel 1999), suggesting that, in addition to abandoned houses, the studied area should also contain significant amounts of fecal matter. Patchiness is a well-documented feature of marine ecosystems, affecting both benthic and planktonic organisms, and is particularly evident in the case of GZ (Graham et al. 2001, Robinson et al. 2021). Traditional plankton nets may fail to detect or effectively sample such aggregations, leading to potentially misleading conclusions (Majaneva et al. 2013). The integration of modern video-based methodologies with conventional sampling techniques can provide a more comprehensive understanding of the scale and mechanisms driving these aggregations.

The phenomenon of abandoned houses covering the seabed, co-occurring with the massive development of Appendicularia in the water column, as described in this study (Table 1, Figs. 3 & 4), appears to be highly irregular and episodic. Across the 7 observed seasons, a mass occurrence of Appendicularia was recorded in only one. It is possible that similar events occurred outside the study period. The study by D'Angelo et al. (2024) also emphasizes the generally high episodic occurrence of *O. vanhoefeni* in the studied region. Data from a long-term time series

(2010–2018) using a sediment trap deployed on a mooring in the inner part of Kongsfjorden revealed a single pronounced peak between October 2010 and January 2011, with maximum values reaching $138 \text{ ind. m}^{-2} \text{ d}^{-1}$ in December 2010 (D'Angelo et al. 2024). Literature data support the observations made in this study (Table 1), indicating that Hornsund exhibits significantly lower abundances of *Oikopleura* spp. compared to other studied fjords, with differences reaching up to an order of magnitude in both abundance and biomass (Gluchowska et al. 2016, Ormańczyk et al. 2017).

Although the year 2021 clearly stands out in the data set used, no major anomalies in hydrography or environmental conditions were recorded. The observed event likely reflects the episodic and under-documented nature of appendicularian blooms and JF deposition, which may occur more frequently than previously recognized.

Data/code availability. All data included in this study are available from the corresponding author on reasonable request.

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Surface lebensspuren and their tracemakers in Arctic fjords of Spitsbergen: Patterns, diversity, and environmental controls

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Abstract: This study presents a comprehensive analysis of epibenthic lebensspuren, *i.e.*, biogenic surface traces, and their tracemakers in the fjords of Svalbard. Data were collected over six Arctic summer seasons (2015–2017, 2019, 2020, and 2023) and one winter season (2016), across 206 stations, 57% of which exhibited lebensspuren. Nineteen distinct lebensspuren morphotypes were identified, including eight newly described forms. Tracemakers were identified for 18 of these types, and specific species or genera determined for 10. Echinoderms were the dominant group, responsible for 55% of all traces, followed by decapods (20%) and gastropods (17%). The study documents lebensspuren morphology and ethology along with their associated tracemakers, offering insights into their abundance and spatial distribution within fjord ecosystems. Notable findings include the high frequency of lebensspuren produced by the sea star *Urasterias lincki*, along with significant contributions from brittle stars, shrimps, and gastropods. Distribution patterns were influenced by environmental factors such as proximity to glaciers and river mouths; however, non-metric multidimensional scaling analysis revealed no clear community separations. This dataset can serve as a valuable resource for the interpretation and classification of trace fossils (*i.e.*, fossil analogues of lebensspuren), while highlighting the ecological and paleoenvironmental importance of lebensspuren in Arctic marine systems.

Keywords: Arctic, glacial bays underwater imagery, biogenic surface traces, epibenthic megafauna, bioturbation.

Introduction

Benthic organisms, through activities such as locomotion and burrowing, bioturbate sediments and consequently produce a variety of traces. These traces, known as lebensspuren, are defined as any biogenic structures resulting from the interaction of living organisms with the substrate, primarily sediment (Ewing and Davis 1967). One of the pioneering classifications of lebensspuren was based on the organism behavior during their formation (Seilacher 1953). Resting traces are imprints left by temporarily stationary organisms, with the most common examples being those of asteroids (sea stars) and ophiuroids (brittle stars). Crawling traces result from movement across the sediment surface and are often marked by impressions of limbs or podia, such as the tube feet of sea stars or the appendages of mobile crustaceans. Grazing traces are surface trails that reflect both locomotion and feeding activity, typically pro-

duced by snails or sea urchins. Dwelling traces are burrows that serve as domiciles for their tracemakers and are represented the burrow openings of polychaetes, anemones, or fish. These structures arise from the interactions of both epifauna and infauna with the sediment; however, the most readily observable and morphologically distinctive are those produced by epibenthic megafauna (Young *et al.* 1985). A separate category of lebensspuren includes digestion traces, also referred to as defecation traces (Miguez-Salas *et al.* 2024c), which encompasses fecal casts and pellets, such as the coiled castings of lugworms (*Arenicola marina*) or the fecal deposits of holothurians.

According to new classification proposed by Miguez-Salas *et al.* (2024c), marine lebensspuren are categorized based on three components: morphology, ethology, and tracemaker identity. For the latter two components, the use of open nomenclature is possible when precise identifica-



tion is uncertain. This classification framework is adopted in the present study.

Current knowledge of lebensspuren primarily stems from the analysis of photographs or various types of casts (Bell *et al.* 2013; Ishida *et al.* 2022; Miguez-Salas *et al.* 2023b). Neiochnological studies remain limited due to high operational costs and observational challenges (Kaufmann *et al.* 1989; Przeslawski *et al.* 2012; Miguez-Salas *et al.* 2024b). Much of the existing research has focused on more accessible shallow marine environments or has been carried out under experimental conditions (Uchman and Pervesler 2006; Brom *et al.* 2018). In contrast, relatively few studies have addressed lebensspuren in deep-sea environments (Wheatcroft *et al.* 1989; Przeslawski *et al.* 2012; Miguez-Salas *et al.* 2022, 2024a, 2024c; Brandt *et al.* 2023).

Identifying the organisms responsible for producing lebensspuren remains a significant challenge (Ewing and Davis 1967). In the deep-sea environment, only a limited number of tracemakers have been definitively associated with the structures they produce (Miguez-Salas *et al.* 2024b). A well-known example is *Paleodictyon*, a trace fossil whose maker has long eluded discoveries despite considerable effort (Rona *et al.* 2009; Przeslawski *et al.* 2012; Miguez-Salas *et al.* 2023b). In some cases, similar traces may be produced by multiple taxa, complicating identification. For instance, the crawling lebensspuren of holothurians and echinoids are often difficult to distinguish (Dundas and Przeslawski 2009; Bell *et al.* 2013). In this context, photographs that capture both the trace and the trace-making organism are particularly valuable for improving identification accuracy and advancing neiochnological studies.

The ability to directly identify the trace-making organism and observe its behavior is one of the key distinctions between lebensspuren and trace fossils (Miguez-Salas *et al.* 2022, 2023a). These traces can provide valuable insights into the relationship between organisms and environmental conditions, such as the availability and distribution of organic matter (Miguez-Salas *et al.* 2022). Such observations allow for the inference of environmental factors in both modern settings (neiochnology) and past environments through comparison with trace fossils (Buatois and Mángano 2011). Documenting and cataloging new examples of lebensspuren plays a crucial role in bridging the fields of neiochnology and paleoichnology (Bromley 1996).

The fjords of Svalbard (the high Arctic archipelago), unique in many aspects, offer an excellent natural laboratory for collecting and study of lebensspuren. This is particularly relevant in the current era of climate change, as increased sedimentation due to glacial melt is altering fjords ecosystems. Notable trends include the influx of new species and the northward shift of species ranges (Deja *et al.* 2016). A key question remains whether there is a correlation between the abundance and diversity of lebensspuren, and the abundance and biodiversity of megafauna. Current studies have not reached a definitive conclusion, suggesting instead that a complex interplay of biotic and abiotic factors influences this relationship

(Kitchell *et al.* 1978; Young *et al.* 1985; Wheatcroft *et al.* 1989; Turnewitsch *et al.* 2000; Hughes and Gage 2004; Miguez-Salas *et al.* 2024b). The link between lebensspuren and benthic fauna suggests that these traces can serve as useful proxies for assessing species richness and community structure, particularly in patchy environments where megafauna may not be visible and traces may be the only indicators of biological activity (Heezen and Hollister 1971; Mauviel *et al.* 1987; Kaufmann *et al.* 1989).

This study is based on the hypothesis that the prevailing abiotic and biotic conditions in the fjords of Svalbard favor the preservation of lebensspuren. Building on this premise, it presents the most frequently observed lebensspuren in these fjords and, where possible, identifies their tracemakers. In addition, it describes several new types of lebensspuren, not previously reported in the literature. The resulting dataset is particularly valuable, as high-resolution video observations enabled the assignment of traces to their producers and even documented the process of trace formation *in situ*. Furthermore, the study investigates potential correlations between the number and diversity of lebensspuren and the composition of epibenthic megafauna. The findings highlight the importance of incorporating neiochnological analysis into studies on benthic biodiversity and behavior.

Study area

Spitsbergen, the largest island of the Svalbard archipelago, is located in the high Arctic and is characterized by a dynamic interplay of various water masses, including the warm Western Spitsbergen Current and the colder Sørkapp Current (Walczowski *et al.* 2012; Promińska *et al.* 2017). These currents play a crucial role in shaping the island's climate, sea ice conditions, and marine ecosystems (Cottier *et al.* 2007; Walczowski and Piechura 2011; Carmack *et al.* 2015). The island hosts a complex network of fjords, each exhibiting distinct hydrological and geological features influenced by their proximities to glacial inputs and exposure to ocean currents. Variability in water mass influence and the presence or absence of underwater sills create diverse ecological niches that support rich and varied marine communities (Svendsen *et al.* 2002; Nilsen *et al.* 2008). Spitsbergen a key research area for studying interactions between Arctic marine and glacial systems, offering critical insights into the impacts of climate change on polar environments. This unique geographic and oceanographic settings make Spitsbergen an essential location for understanding Arctic ecological dynamics and their broader climatic implications. The data presented in this study were collected from several fjords and adjacent marine areas around Spitsbergen, each offering distinct environmental settings shaped by oceanographic and glacial influences.

Hornsund

Recognized as the coldest fjord, Hornsund is primarily influenced by the Sørkapp Current. It is distinguished by a high rate of glacial retreat and plays a notable role in

regional carbon sequestration (Promińska *et al.* 2017; Węśławski *et al.* 2017).

Van Mijenfjord

This fjord is characterized by a stratified water column due to the presence of a sill and is subjected to significant glacial inflows. It also experiences pronounced seasonal freezing, making it an unique Arctic system (Støylen and Fer 2014).

Isfjorden

The largest fjord in the region, Isfjorden lacks a sill at the mouth, allowing for extensive advection of Atlantic waters. Its multiple glacier-fed branches contribute to diverse physical conditions and a rich mosaic of benthic and pelagic communities (Nilsen *et al.* 2008).

Kongsfjord

Known for substantial Atlantic water influence, Kongsfjord's hydrography and biological communities are shaped by the interplay between warm Atlantic inflows and glacial meltwater, which enhances Arctic conditions in the inner fjord (Hop *et al.* 2006; Cottier *et al.* 2007).

Additional data were collected near the Torellbreen glacier and on the adjacent shelf (nine stations), as well as from isolated stations located in Magdalenfjorden, Raudfjorden, Smerenburgfjorden, and Rijpfjorden. These varied locations collectively provide a comprehensive representation of Svalbard's fjord ecosystems and contribute to understanding spatial patterns of lebensspuren and their environmental drivers.

Methods

Field sampling

The photographic material presented in this study comprises of 206 video transects recorded in the fjord regions of Svalbard (Fig. 1). Most of the data were collected from the deck of the RV *Oceania* during six Arctic summer expeditions (2015–2017, 2019, 2020, 2023). One additional video transect (station GR7_2023) was conducted from a small boat *Gavia Immer*. These summer stations are complemented by 10 stations recorded in 2016 aboard the R/V *Helmer Hansen* (Supplementary Material, available from <https://opendap.iopan.pl/opendap/data/csv/Lebensspuren/contents.html>).

All footage was captured using an underwater imaging system referred to here as a drop camera. The device con-

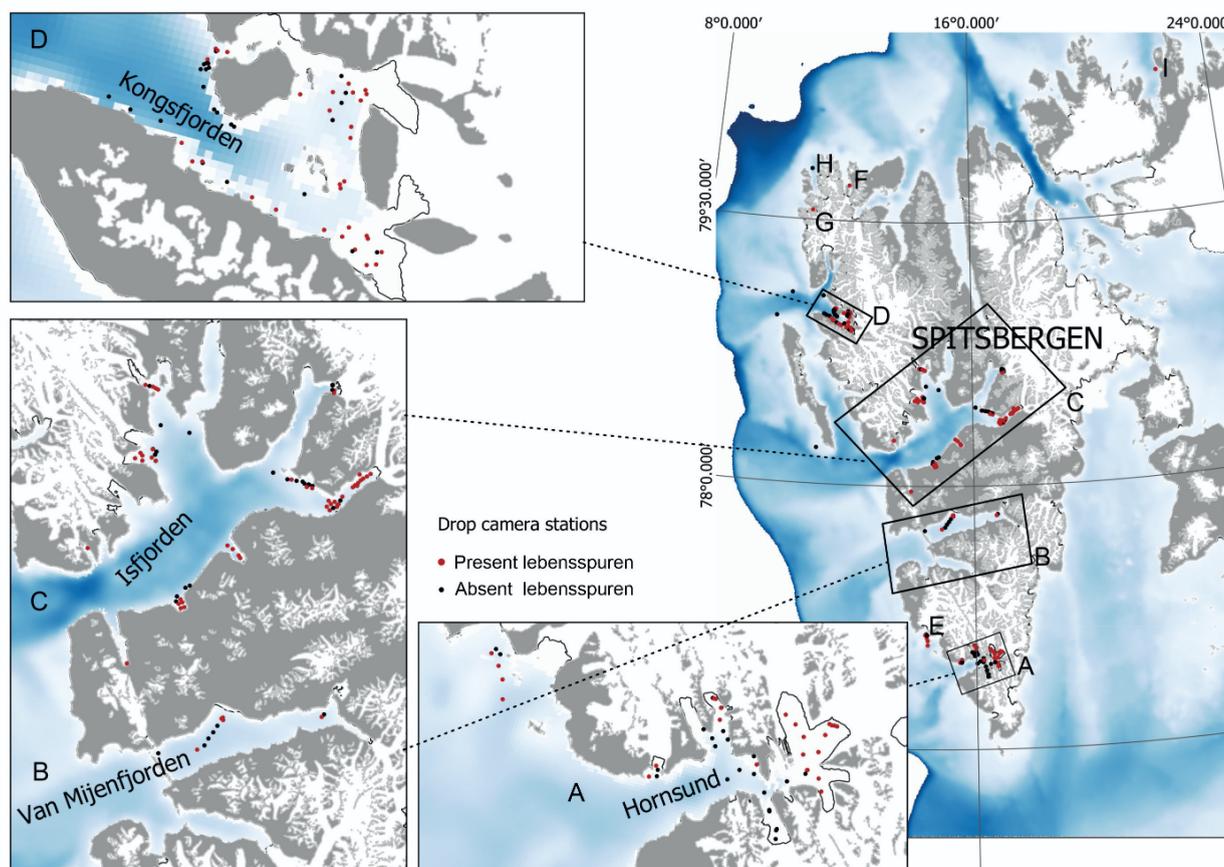


Fig. 1. Map of the Svalbard archipelago showing the locations of stations surveyed using a drop camera. Red dots indicate stations where lebensspuren were recorded, while black dots represent stations where no traces were observed. Letter symbols correspond to the following regions: A – Hornsund Fjord; B – Van Mijenfjorden Fjord; C – Isfjorden Fjord; D – Kongsfjorden and a fragment of Krossfjorden; E – Torellbreen and shelf; F – Raudfjorden; G – Magdalenfjorden; H – Smerenburgfjorden; I – Rijpfjorden.

sists of a metal frame housing two cameras: an analog camera with a resolution of 700 TVL for live monitoring, and a digital Panasonic HX-A500 camera that recorded high-resolution video (1280×720 px) to a memory card. The system is also equipped with two batteries, each powering an independently operated lamp, and a pair of parallel-mounted lasers used for scale calibration.

Each transect recorded approximately 10 min of seabed footage while the camera was towed at a speed of approximately 0.3 knots (0.15 m s⁻¹) and maintained at an average height of 50 cm above the seafloor. In stations near glacier fronts, the camera height was reduced to 10–30 cm due to poor visibility caused by high concentration of suspended glacial particulates. The height of the camera above the seabed was estimated using visible referencing objects of known size, such as sponges and sea anemones, as well as with the spacing of laser points – a method consistent with approaches used by other researchers (Gutt and Siegel 1994; Hirche *et al.* 2016).

The surveyed depth range extended from 22 m at the shallowest location to 280 m at the deepest, with a median depth of 70 m (Supplementary Material, see above). Video footage from the digital camera was recorded in fourfold slow motion, which facilitated detailed post-processing and minimized blurring and out-of-focus frames. This is especially important in turbid areas affected by glacial discharge, where water clarity and camera drift often posed challenges to capturing high-quality imagery.

Video analysis

Each station was then analyzed for the abundance and biodiversity of megafauna, as well as for the presence of lebensspuren preserved on the seabed – primarily resting lebensspuren, locomotion lebensspuren, and grazing traces. Due to the considerable variability in water transparency and occasionally unfavorable sea conditions during video acquisition, *e.g.*, swaying of research vessel’s hull, all footage was analyzed manually. Each video was reviewed multiple times using VLC media player, an open-source software licensed under the GPL.

At certain stations, the usable portion of the footage, and consequently the analysis duration, was slightly reduced due to poor visibility or recording artifacts. The exact duration of the analyzed footage for each transect along with the estimated area of the seafloor surveyed (expressed in m²) was calculated based on the vessel’s average drift speed and the camera’s field of view. The values are provided in Supplementary Material (see above).

Additionally, bottom turbidity at each station was visually assessed using a four-level scale (0–3): (i) 0 (No Suspension): no visible particles suspended in the water column; the water appeared clear; (ii) 1 (Low Suspension): minimal particle suspension observed; water remained predominantly clear with slight turbidity and good visibility; (iii) 2 (Moderate Suspension): noticeable particle suspension resulted in moderate turbidity, with a marked re-

duction in visibility; (iv) 3 (High Suspension): a high concentration of suspended matter was visible, often significantly disrupting the image quality; at some stations, lowering the camera closer to the seafloor was required to improve visibility.

Due to the extensive volume of material collected, the analysis excluded certain types of traces, such as openings of burrows and various surface traces. These included depressions or openings produced by anemones of the family Cerianthidae, tube openings of polychaetes from the families Terebellidae and Sabellidae, probable fish burrow openings, likely produced by species from the family Lumpenidae, and fecal mounds produced by polychaetes of the family Arenicolidae.

Representative examples of the most common recorded lebensspuren, along with their tracemakers, are shown in Figs. 2–5. In these still frames, image contrast was enhanced to compensate for poor water clarity and to reduce the visual effect of backscatter caused by suspended particles. All illustrations were produced using QGIS and Corel Draw software. For statistical analyses, PRIMER 7 software with the PERMANOVA+ add-on was employed. Spearman’s rank correlation coefficient was used to assess the significance of the relationships among the measured variables. The data collected were divided into three subsets: (i) “Lebensspuren”: this subset consists of data from 117 stations where traces were recorded. Each trace was counted and identified to the lowest possible ethological and taxonomic category (Table 1); (ii) “All Megafauna”: this subset comprises all benthic fauna identified at the same 117 stations where lebensspuren were observed; (iii) “Tracemakers”: this subset also draws from the same 117 stations but includes only mobile species capable of producing the analyzed traces. A list of these potential tracemakers is provided in Supplementary Material, see above.

Distances from each station to the nearest glacier front or glacial river mouth were measured using QGIS software. Based on this information, stations were categorized under the factor “Station Type” into one or three groups: “Glacier Influence” “River Influence” or “No Direct Influence”.

Results

Spatial distribution and multivariate patterns of lebensspuren

Out of the 206 analyzed stations, clear examples of lebensspuren were identified at 117 stations, representing 55% of total (Table 1). The recorded traces were assigned to 19 distinct types. For 18 of them, still-frame examples and corresponding tracemakers were documented. Each trace was assigned a morphotype, a taxonomic identification of the trackmaker, where possible, and behavioral category.

In ten types of lebensspuren, the tracemakers could be confidently identified to the genus or species level. For the remaining types, precise taxonomic identification was not

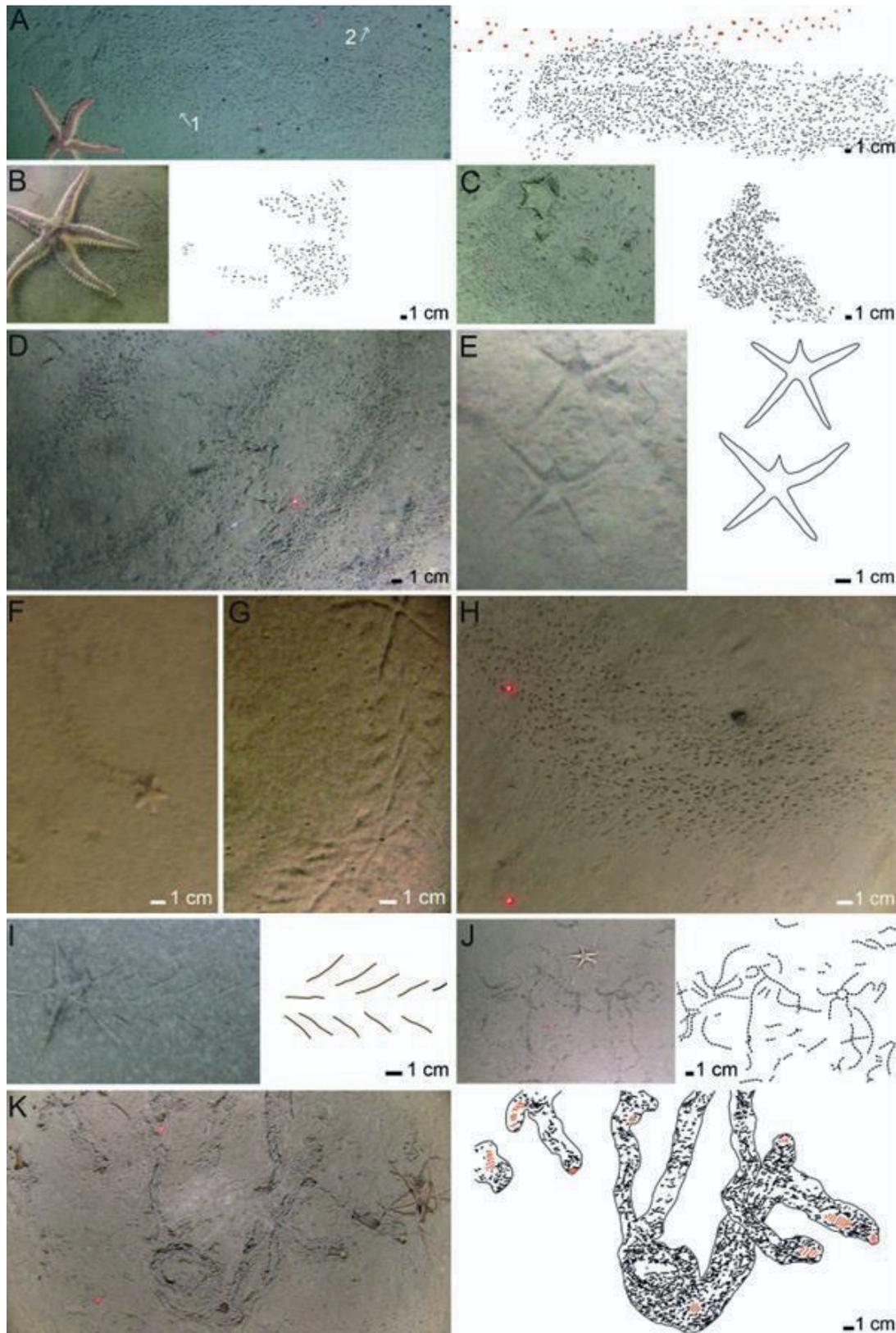


Fig. 2. Recorded lebensspuren – part one. High-density punctuated trail produced by the sea star *Urasterias lincki*, shown both with its tracemaker (A₁, B) and without (D, H). (C) High-density punctuated trail produced by *Ctenodiscus crispatus*, shown with its tracemaker. (E) Sea star impression of an unidentified sea star with an arm undergoing regeneration. (F) High-density punctuated trail produced by of juvenile, indeterminate asteroid, shown with its tracemaker. (G, I) Herringbone trails produced by *Ophiuridae* spp., both with visible tracemakers. (J) Discontinuous, winding trail produced by *Ophiuridae* spp., shown with its tracemaker. (K) Irregular M-ridged trail attributed to the sea cucumber *Myriotrochus rinkii* (indicated with red shading), along with well-developed associated lebensspuren. (A₂) Step trail produced by *Pagurus* spp.

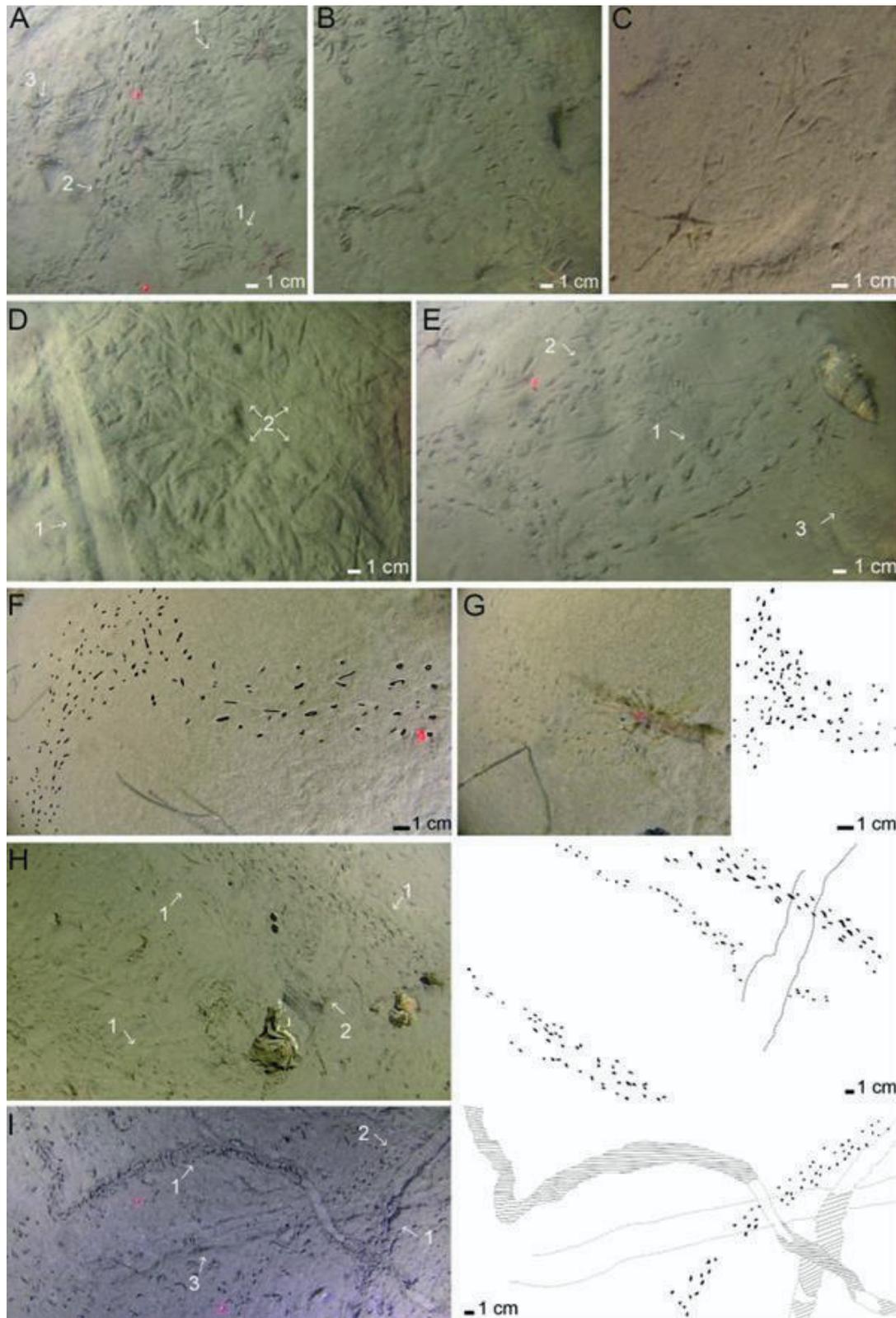


Fig. 3. Recorded lebensspuren – part two. (**A₁**, **B**, **E₃**) Railroad trail produced by the brittle star *Stegophiura nodosa*, shown with the tracemaker. (**A₃**) Ophiuroid impression left by *Stegophiura nodosa*. (**C**) Herringbone trail attributed to Ophiuridae spp., with a visible tracemaker, likely *Ophiura robusta*. (**D₂**) Irregular intersecting trail formed by Ophiuridae spp. (**D₁**) Flat, shallow trail produced by Gastropoda. (**A₂**, **E₂**, **I₂**) Step trails produced by *Pagurus* spp., shown without visible tracemakers. (**H₁**) Step trail of *Pagurus* spp. with visible tracemakers. (**F**, **G**) Step trail created by Caridea, with and without visible tracemakers. (**I₃**) Furrow trail produced by indeterminate *Pagurus* spp., shown with the tracemaker; this type of trail results from the hermit crab dragging its shell across the sediment (**H₂**). (**E₁**) Bilateral step trail produced by *Pagurus* spp., also resulting from shell dragging, shown with the tracemaker. (**I₁**) Composite sinuous fractured-flat trail formed by Naticidae spp.

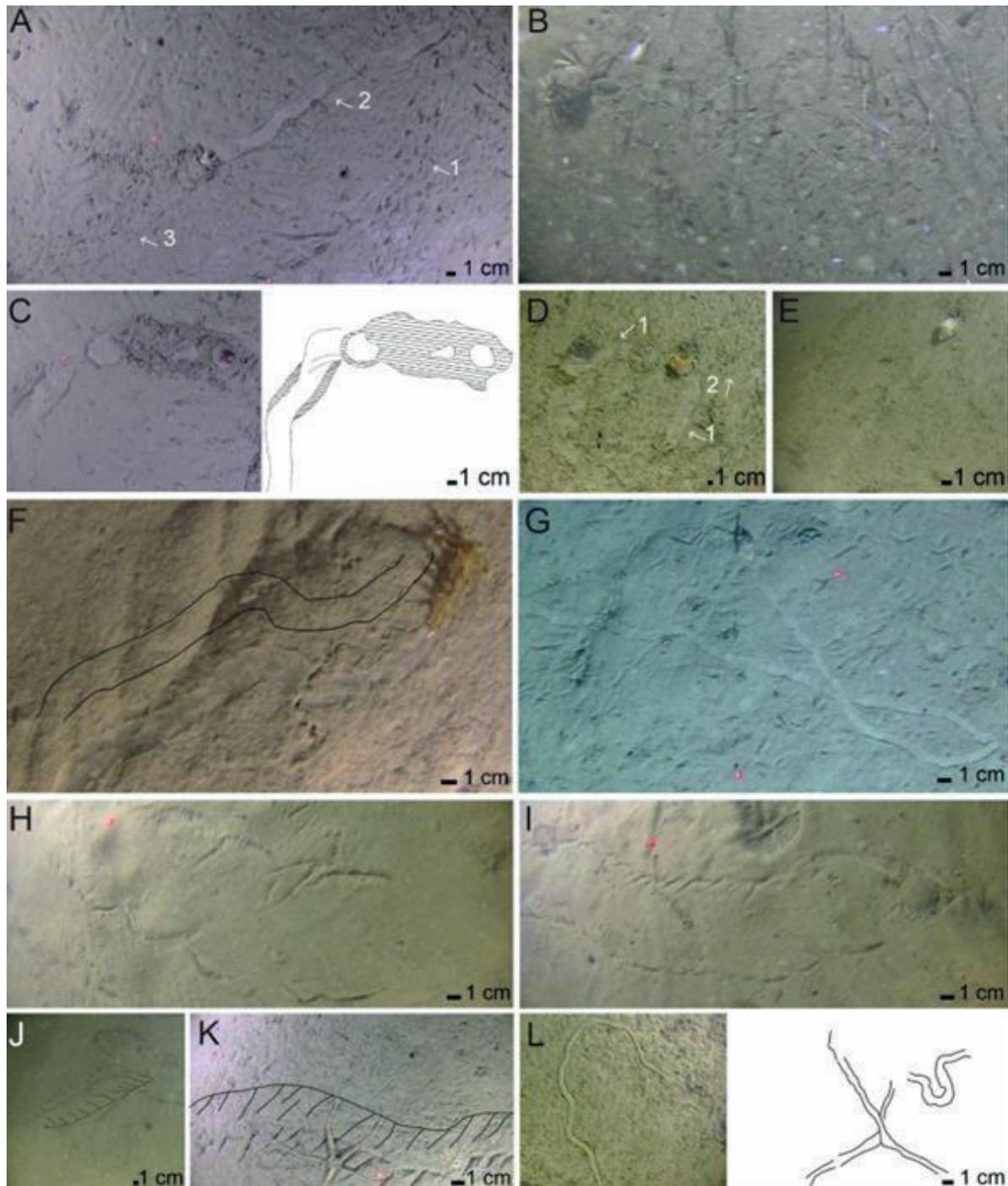


Fig. 4. Recorded lebensspuren – part three. (A₁, D₂) Step trail produced by *Pagurus* spp.; the tracemaker is visible only in panel D₂. (A₃) Bilateral step trail left by *Pagurus* spp., formed by shell dragging. (A₂) Flat, shallow trail produced by an indeterminate Gastropoda. (B) Step trail produced by the crab *Hyas* sp. (C) Composite, winding, fractured-flat trail produced by a gastropod of the family Naticidae spp., shown with its tracemaker. (D₁, E, G) Flat, shallow trails produced by *Buccinum* sp., each accompanied by the tracemakers. (F) Flat, shallow trails of the nudibranch *Dendronotus frondosus*, with the tracemaker present. (J, K) Ribbed, curved trails attributed to Pleuronectinae spp., with the tracemaker visible in panel J. (H, I) Segmented, winding twin trails produced by Pleuronectinae spp. (L) Irregular shallow trail formed by *Phyllodoce* sp., accompanied by its tracemaker.

possible due to limitations in visual resolution. For instance, within Naticidae, two snail species, *Euspira pallida* and *Cryptonatica affinis*, are morphologically similar and indistinguishable in the video material. Similarly, Caridea indet. includes members of the families Pandalidae and Thoridae. While most observed individuals are likely *Pan-*

dalus borealis, conclusive identification would require specimen collection and laboratory analysis. This is also true for individuals of Nemertea indet. Other ambiguous categories include juvenile representatives of Asterozoa and Ophiurozoa, which comprise three species – *Ophiura sarsi*, *Ophiura robusta*, and *Ophiocten sericeum*. Although

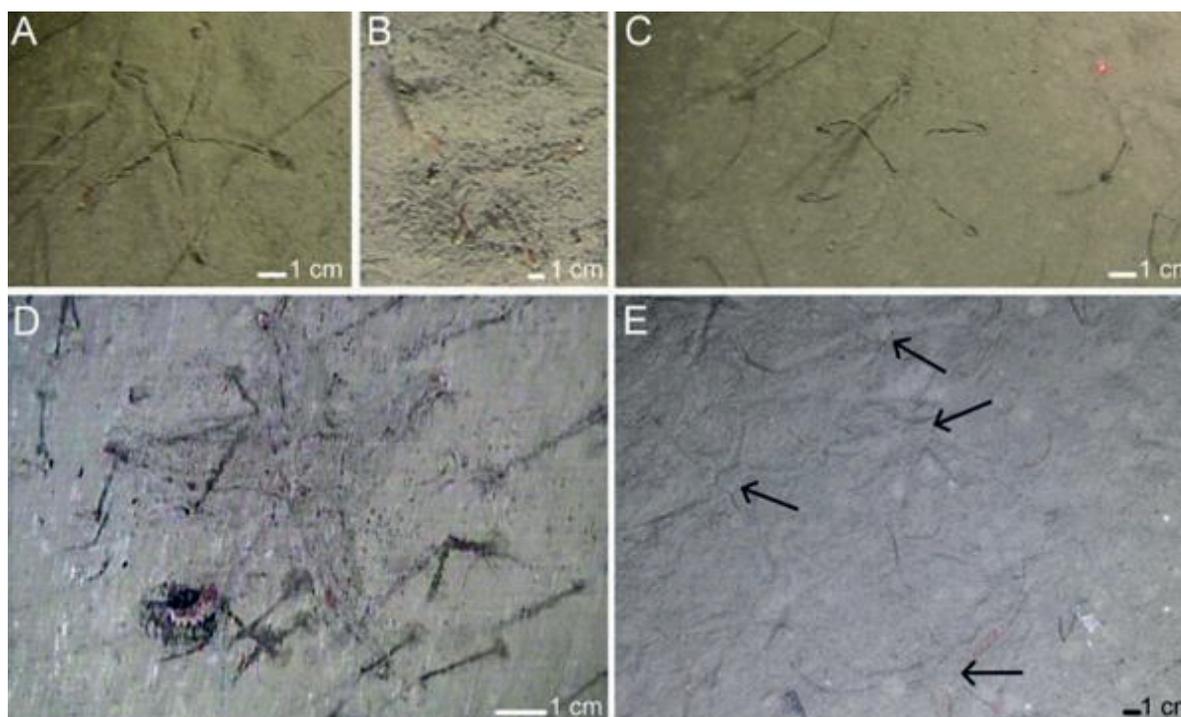


Fig. 5. Resting traces produced by nearly completely buried echinoderms. (A–D) Sea star impressions left by individuals of *Urasterias linckii* almost entirely buried beneath the sediment surface. (E) Impression created by a nearly completely buried, undetermined brittle star.

these species are morphologically distinct under laboratory conditions, they are difficult to differentiate in video footage and were therefore grouped under a single general category.

Identified lebensspuren were further grouped into four major biological categories based on the likely trace-makers. The most numerous group was Echinodermata, responsible for 691 traces, accounting for 55% of all recorded lebensspuren. Decapoda formed the second largest group with 249 occurrences (20%), followed by Gastropoda with 207 occurrences (17%). The remaining 8% (105 traces) included those produced by *Phyllococe* sp., Nemerita indet., Pleuronectinae (*Hippoglossoides platessoides* and *Reinhardtius hippoglossoides*), and unidentified traces (Table 1). Notably, no fecal casts attributable to holothurians were observed in the analyzed video material, despite the confirmed presence of species such as *Myriotrochus rinkii* and occasional occurrences of *Cucumaria frondosa*. This absence may reflect species-specific defecation behavior, rapid degradation of fecal structures, or limitations of the video resolution.

Non-metric multidimensional scaling (NMDS) analysis conducted for lebensspuren, epibenthic megafauna and tracemaker subset did not reveal distinct community groupings. Instead, the stations in all three datasets appear to form a single, continuous community. However, a clear spatial organization is evident when considering environmental factors, particularly proximity to glaciers and glacial rivers. Stations are distinguishably structured according to the predefined station-type categories: River Influence, Glacier Influence, and No Direct Influence (Fig. 6).

Figure 7 illustrates the percentage distribution of individual lebensspuren types across the studied locations. In the inner parts of the fjords, traces attributed to the sea star *Urasterias linckii* predominate. In the immediate vicinity of the most active glacier fronts, such as Kongsfjorden (Kronebreen) and in Hornsund (Hornbreen), *Urasterias* traces remain dominant, but traces attributed to the *Cariidea* group also represent a significant portion of the total. *Ophiuridae* are commonly observed near glacier-affected sites, including Austreburgerbukta and Hornbreen (Hornsund), Yoldiabukta (Isfjorden), and Blomstrandhamna (Kongsfjorden).

Statistical analysis revealed a statistically significant positive correlation between the abundance of lebensspuren and their morphological diversity ($\rho = 0.62$, $p < 0.05$), as well as between lebensspuren richness and the number of distinct tracemaker taxa ($\rho = 0.27$, $p < 0.05$) (Fig. 8). A moderate and statistically significant positive correlation was also observed between lebensspuren abundance and the abundance of identified tracemaker organisms ($\rho = 0.37$, $p < 0.05$), suggesting that areas with a higher density of potential tracemakers tend to exhibit more biogenic surface traces. Conversely, a moderate negative and statistically significant correlation was found between station type and bottom turbidity ($\rho = -0.58$, $p < 0.05$), with glacier-influenced stations exhibiting elevated levels of suspended sediment. Additionally, a moderate negative and statistically significant correlation between the species richness of benthic fauna and bottom turbidity ($\rho = -0.53$, $p < 0.05$) suggests that high turbidity—particularly near glacier fronts—may suppress overall faunal diversity (Fig. 8).

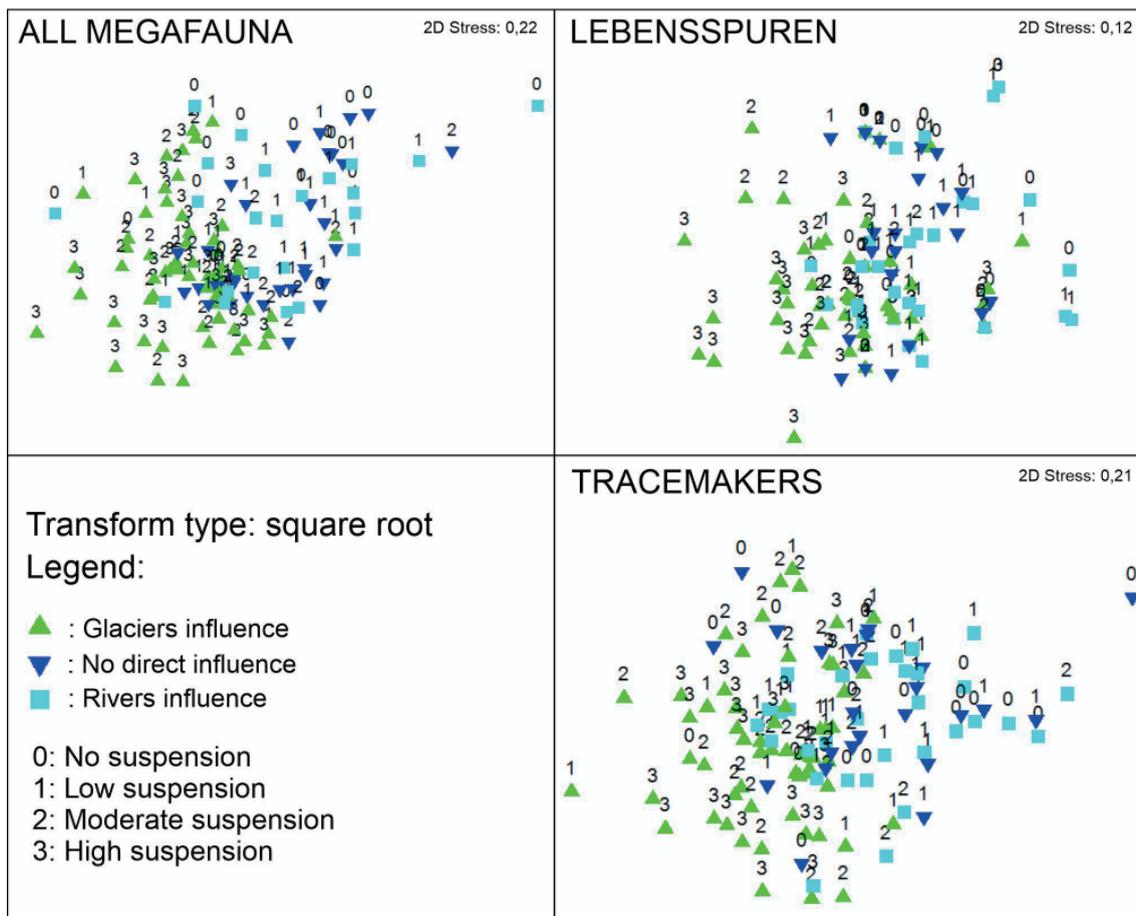


Fig. 6. Results of the n-MDS analysis showing patterns in lebensspuren, epibenthic megafauna, and identified tracemakers.

Lebensspuren and their tracemakers

Following the classification system proposed by Miguez-Salas *et al.* (2024c), the names of the lebensspuren presented in this study are based on three components/labels: (i) morphological characterization, (ii) inferred behavior, and (iii) tracemaker taxonomy. For clarity and consistency, these components are separated by semicolons.

This study introduces eight new morphological components: Herringbone trail, Discontinuous irregular winding trail, Irregular intersecting trail, Ribbed curved trail, Bilateral step trail, Composite sinuous fractured-flat trail, Irregular shallow trail, and Segmented sinuous twin trail. In several cases, direct video documentation of the tracemaker responsible for these traces is provided, offering rare and valuable evidence for linking morphology to behavior and producer identity.

Star-shaped depression; resting; *Asteroidea indet.* (Figs. 2E and 5A–D)

This is a typical resting trace of sea stars (Miguez-Salas *et al.* 2024a), with in 91 examples recorded in the entire dataset. One of the identified tracemaker is *Urasterias lincki*, which was observed to be partially buried in the sediment. Two twin traces captured in the same image (Fig. 2A) likely may reflect both arm regeneration processes of the arms (as one arm appears shorter) and a change in position by the sea star.

High-density punctuated trail; locomotion; *Urasterias lincki* (*Asteroidea*) (Fig. 2A₁, B, D, H)

Lebensspuren left by the sea star *Urasterias lincki* (*Asteroidea*) are the most commonly encountered traces in the collected material. Like other sea stars, this species uses its water vascular system for locomotion, resulting in distinct trace pattern in areas where it is present. These traces are broad, corresponding to the maximum arm span of the individual, and consist of numerous small holes, which represent impressions of tube feet in the sediment. These impressions are elliptical rather than circular, with the longer axis aligned in the direction of movement. The holes occur at nearly uniform density, except in the central part of the lebensspuren, where a characteristic smooth strip is typically observed. This strip forms behind the oral opening during locomotion, as tube feet are absent around the mouth, resulting in a gap in the trace. These traces were primarily recorded in the inner parts of fjords, particularly in the areas of glacial bays (Fig. 6). A total of 354 occurrences of this high-density punctuated trail were identified across 70 stations (Table 1).

High-density punctuated trail; locomotion; *Asteroidea indet., juv.* (Fig. 2F)

This group includes the lebensspuren of juvenile sea star. These traces are of the same type as those produced by adult individuals but are noticeably more delicate and

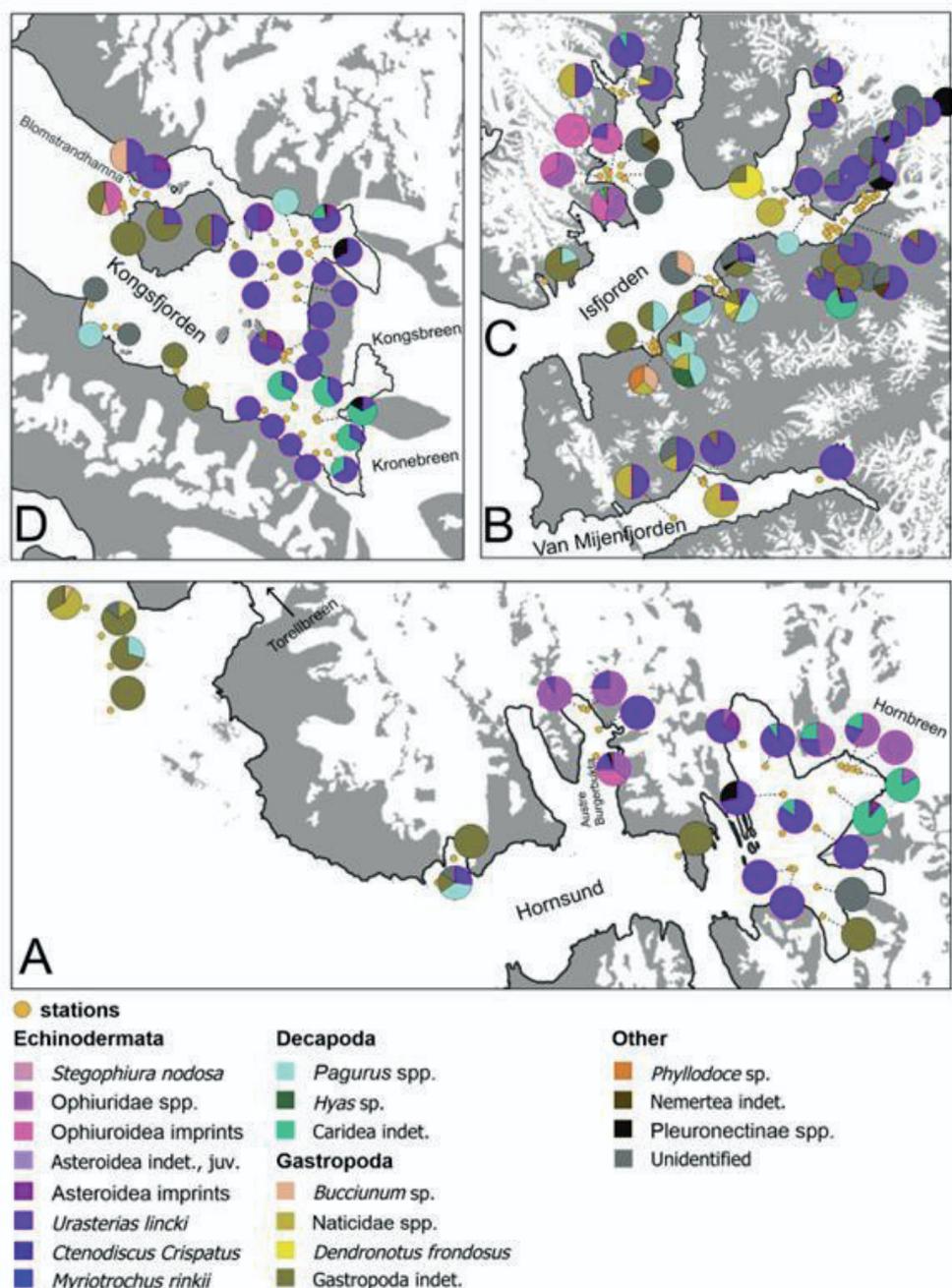


Fig. 7. Percentage distribution of identified lebensspuren across the four most extensively sampled fjords.

smaller in scale. The illustrated juvenile specimen of *Astroidea*, measuring just over 1 cm in diameter, was nonetheless capable of leaving visible imprints of its tube feet on the sediment surface. Across the entire analyzed material, only two such cases were recorded, both at a single station in Isfjorden (Table 1).

High-density punctuated trail; locomotion; *Ctenodiscus crispatus* (*Astroidea*) (Fig. 2C)

Ctenodiscus crispatus, a relatively common sea star, was rarely observed in the recordings. This non-selective deposit feeder (Shick *et al.* 1981) typically remains buried in the sediment for extended periods. Its trace is somewhat similar to that produced by *Urasterias lincki*, but the spa-

cing between tube foot impressions is smaller, and their density per unit area appears higher. This difference may reflect the generally smaller body size of *C. crispatus*. However, only two such traces were identified in the entire dataset, both from a single station (ISF26-2019), which limits the possibility for detailed comparisons.

Irregular M-ridged trail; locomotion and feeding; *Myriotrochus rinkii* (*Holothuroidea*) (Fig. 2K)

Traces of *Myriotrochus rinkii* were discovered at only two stations. These characteristic lebensspuren are deeply incised into the sediment, forming looping and overlapping patterns. The disturbed sediment often displays longitudinal cracking. In some cases, up to eight living specimens

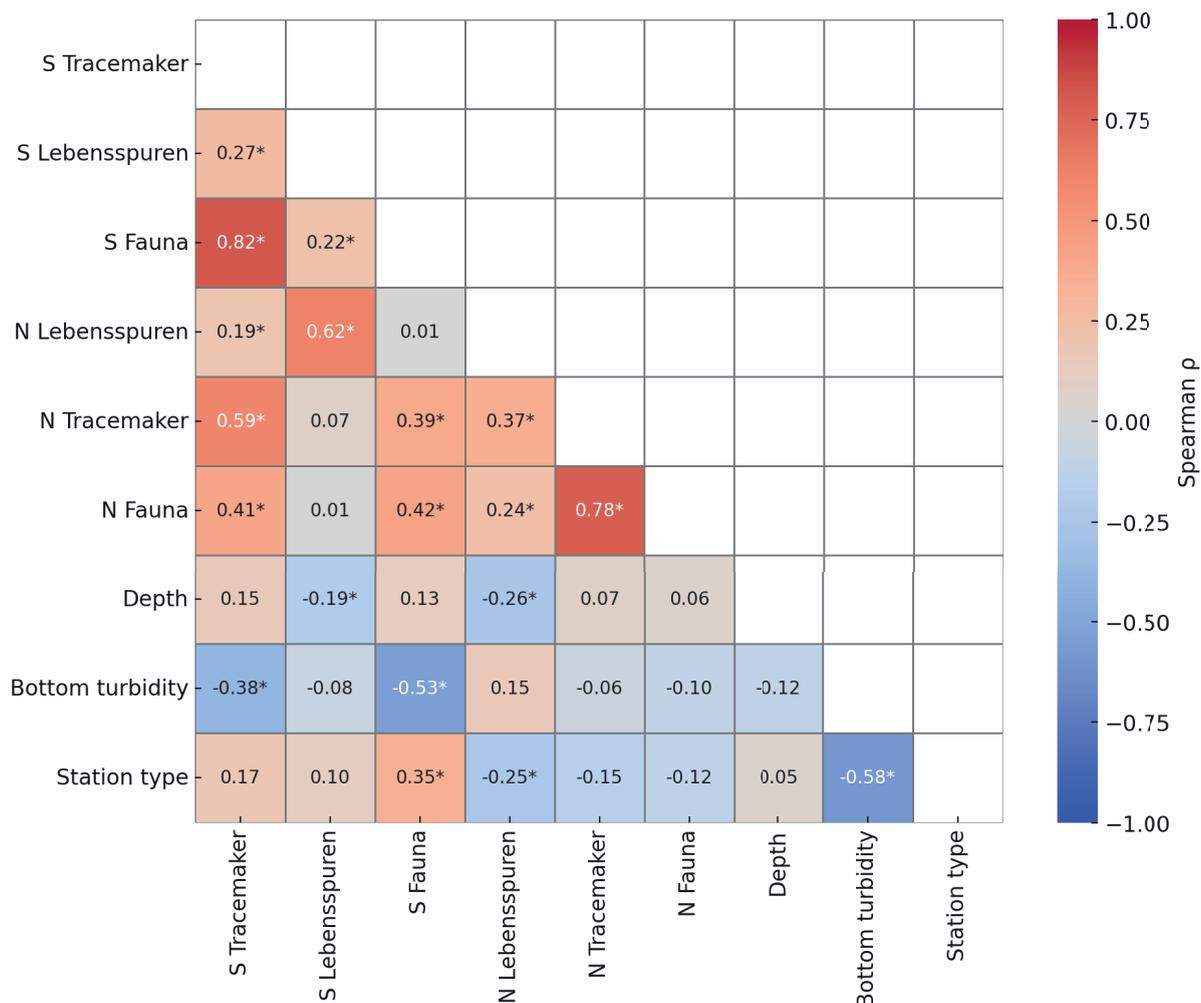


Fig. 8. Spearman correlation matrix showing relationships among the number of species (types) of lebensspuren, megafauna, tracemakers (prefixed with S), their abundance (prefixed with N), depth, bottom turbidity, and station type (Glacier Influence, River Influence, No Direct Influence). Statistically significant correlations ($p < 0.05$) are marked with an asterisk.

of this species were observed along the traces within a single field of view of the camera (Fig. 2K, red hatching indicates individuals of *M. rinkii*).

Ophiuroid-shaped depression; resting; Ophiuroidea indet. (Figs. 3A₃ and 5E)

This is a typical resting trace of brittle stars (Miguez-Salas et al. 2024a). It consists of a central disc-shaped depression with radiating arm impressions, reflecting the characteristic body plan of ophiuroids. A total of 76 such traces were recorded across ten stations. One of the most clearly defined examples (Fig. 3A₃) was created by a living individual of *Stegophiura nodosa*. Another case (Fig. 5E) shows a nearly buried, unidentified ophiuroid within the depression.

Railroad trackway; locomotion; Stegophiura nodosa (Ophiuroidea) (Fig. 3A₁, B, E₃)

Stegophiura nodosa, along with its distinctive lebensspuren, was recorded exclusively at a single station (GR7). During locomotion, this species produces relatively deep

grooves in the seabed using only tips of its arms. Along the longer axis of symmetry, a distinct depression extends beyond the central disc of the organism. As a surface deposit feeder, *S. nodosa* is likely to produce this depression through sediment intake during feeding activity. Notably, such a depression is not produced by other recorded representatives of Ophiuroidea. This brittle star is highly distinctive due to short arms and small body size. However, because of the small scale of both the organism and its trace, the movement pattern could not be accurately reconstructed due to the limited resolution of the video material.

Herringbone trail; locomotion; Ophiuridae spp. (Figs. 2G, I and 3C)

This is a locomotion trace is produced by three species of Ophiuridae (*Ophiocten sericeum*, *Ophiura sarsii*, and *Ophiura robusta*) when the organism is elevated above the substrate and “walks” using its arms. Although these species exhibit notable morphological differences under laboratory conditions, their small size in the video footage makes it impossible to assign traces to individual species

with complete certainty. In total, 92 such traces were identified across 13 stations.

Discontinuous irregular winding trail; locomotion; Ophiuridae spp. (Fig. 2J)

The tracemakers are the same as for the previous trace. This type of trace likely was produced in environments with high sedimentation rates, where the individual remains elevated on its arms for extended periods and shifts its position at irregular intervals.

Irregular intersecting trail; locomotion; Ophiuridae spp. (Fig. 3D₂)

The tracemakers are the same as for the previous two traces. Unlike the previously described patterns, this trace typically covers a much larger area, with the seabed appearing uniformly disturbed across a localized zone.

Step trail; locomotion; Pagurus spp. (Malacostraca) (Figs. 3A₂, E₂, H₁, I₂ and 4A₁, D₂)

This trace was recorded 157 times at 16 stations. It is produced by a complex of hermit crab species from the genus *Pagurus*, specifically *Pagurus pubescens* and *P. bernhardus*. The trace consists of fairly regularly spaced limb impressions left as the organism moves across the substrate. The width of the trace varies depending on the size of the individual.

Step trail; locomotion; Hyas sp. (Malacostraca) (Fig. 4B)

This trace is attributed to crabs of the genus *Hyas*. It consists of irregularly spaced and disorganized limb impressions formed during locomotion across the substrate. It clearly differs from trails produced by *Pagurus* spp., which are typically more linear and regularly patterned. The width of the trace varies depending on the size of the individual. This lebensspuren was recorded only four times at two stations within the entire dataset.

Bilateral step trail; locomotion; Pagurus spp. (Malacostraca) (Figs. 3E₁ and 4A₃)

Visible modifications of the step trail trace, resulting from the dragging of adapted snail shells, primarily from the family Buccinidae, by the hermit crab were observed. The attached shell can alter the trace by smearing the sediment or creating additional longitudinal grooves and forms. This type of lebensspuren often co-occurs with traces left by gastropods.

Step trail; locomotion; Caridea indet. (Malacostraca) (Fig. 3F, G)

This group includes traces from two families of shrimps: Pandalidae and Thoridae. These organisms are difficult to distinguish in camera images. The lebensspuren are long, typically winding trackways composed of a series of depressions left by the walking limbs. Observations by the author indicate that these shrimps frequently change direction, moving backward, sideways, or forward, which can result in larger areas densely limb impressions. Such

traces were only recorded at stations with very soft, malleable sediments (Fig. 7).

Flat shallow trail; locomotion; Buccinum sp. (Gastropoda) (Fig. 4D₁, E, G)

Unlike the lebensspuren produced by gastropods of the family Naticidae, this trace lacks distinctive features that would allow confident attribution to the genus *Buccinum* without direct observation of the organism creating it. The trace remains clearly visible on the sediment surface, with its width corresponding to the size of the individual's foot.

Composite winding, fractured-flat trail; locomotion; Naticidae spp. (Gastropoda) (Figs. 3I and 4C)

The tracemakers include two co-occurring species found in the Svalbard region: *Euspira pallida* and *Cryptonatica affinis*. These gastropods produce a distinctive trace by ploughing deeply into the seabed, resulting in characteristic sediment disturbances. The surface of the trace is often coated with mucus. These features help distinguish it from lebensspuren left by other snails, such as those of the family Buccinidae. A total of 39 occurrences of this trace were recorded across fifteen stations (Table 1).

Flat shallow trail; locomotion; Dendronotus frondosus (Gastropoda) (Fig. 4F)

These are very delicate traces, similar in appearance to those left by gastropods of the family Buccinidae. However, these are much more subtle, disturbing only a very thin layer of sediment. The affected area is typically coated with mucus.

Winding shallow trail; locomotion; Phyllodoce sp. (Polychaeta) (Fig. 4L)

This trace is similar to those produced by Gastropoda and Nemertea but exhibits notable variation in width, which may help distinguish it from the lebensspuren of those groups. Nevertheless, it remains relatively subtle, and accurate identification is not possible without direct observation of the tracemaker. Across the entire analyzed material, this trace was recorded only three times, all at a single station (Table 1).

Ribbed curved trail; locomotion Pleuronectinae spp. (Teleostei) (Fig. 4J, K)

This trace is produced by fins of flatfish species belonging to the *Hippoglossoides platessoides* and *Reinhardtius hippoglossoides* complex. These species create long linear traces, which are likely characteristic of other members within the family Pleuronectidae.

Segmented winding twin trail; locomotion: Pleuronectinae spp. (Teleostei) (Fig. 4H, I)

The tracemakers are the same as in the previous trace. The trace is produced when the individual attempts to bury itself in the upper sediment layer of the sediment or moves in a "jumping" motion across the seabed surface. A total of 14 such traces were identified across 11 stations (Table 1).

Discussion

The region of the Svalbard fjords described in this study exhibits a high abundance and diversity of lebensspuren (Table 1; Figs. 2–5), supporting the hypothesis that prevailing abiotic and biotic factors in this area promote their production, even by relatively small tracemakers such as shrimp (Fig. 3F, G), sea stars (Fig. 2A₁, B–D, H), and nudibranchs (Fig. 4F). These traces are primarily concentrated in the inner parts of the fjords (Figs. 1 and 7). On the shelf areas, traces were recorded only near the Torellbreen glacier and were predominantly associated with gastropod activity.

Trace resident time

The Svalbard fjords exhibit a notably low rate of sedimentation – two orders of magnitude lower than fjords of a comparable size in Greenland or Alaska (Zaborska *et al.* 2006). This extended “trace resident time”, the period during which a trace remains visible on the seabed before being destroyed (Wheatcroft *et al.* 1989) or buried, likely contributes to the preservation of lebensspuren in this region. As a result, traces are less rapidly degraded.

Trace resident time is influenced by both abiotic and biotic factors. Abiotic influences include sedimentation rate, hydrodynamics, substrate consistency, and grain size, while biotic factors involve microbiological degradation and the erasure of traces by other mobile organisms (Wheatcroft *et al.* 1989). For instance, meiofauna can smooth and ultimately obliterate lebensspuren by shifting individual sediment grains (Cullen 1973), while infauna may impact surface traces through horizontal movement within the sediment (Wheatcroft *et al.* 1989).

Some authors (Bell *et al.* 2013) have suggested that abiotic processes degrade lebensspuren at a uniform rate. However, more recent studies (Miguez-Salas *et al.* 2020) demonstrate that sudden events, such as benthic storms, can entirely erase traces from the seabed. In the studied Svalbard region, iceberg scouring may also disrupt the seabed, though such events are typically evident in the sedimentary record.

No single factor can be identified as dominant in determining the preservation potential or duration of trace visibility. For example, in the Adolfbukta (a small glacial bay in Isfjorden) high densities of brittle stars, primarily *Ophiocten sericeum* (unpublished data from dredge and video surveys), were observed, yet no distinct ophiuroid lebensspuren were documented. In contrast, in Hornbukta – a glacial bay in the Hornsund with lower brittle star densities, ophiuroid traces were abundant. Kitchell *et al.* (1978) explained such paradoxes by suggesting that trace resident time may be longer in areas with lower biomass, implying a negative correlation between the lebensspuren and faunal density.

In the current study, analyses revealed a positive correlation between the abundance and diversity of lebensspuren ($\rho = 0.62$), indicating that higher trace density tends to co-occur with greater morphological variability. A moder-

ate negative correlation was also found between station type and bottom turbidity ($\rho = -0.58$), with glacially influenced stations showing higher suspended sediment levels (Fig. 8). Additionally, bottom turbidity was negatively correlated with benthic species richness ($\rho = -0.53$). A moderate positive correlation was observed between the abundance of lebensspuren and the abundance of identified tracemakers ($\rho = 0.37$), suggesting that greater numbers of known trace-producing taxa are associated with more traces.

Previous studies have reported mixed results regarding the relationship between lebensspuren and benthic megafauna. Kitchell *et al.* (1978) suggested an inverse relationship, while Young *et al.* (1985) and Wheatcroft *et al.* (1989) attributed weak correlations to the rapid erasure of traces by deposit feeders. Similarly, Jumars and Wheatcroft (1989) proposed that no consistent (monotonic) relationship existed between trace abundance and faunal density. More recently, Miguez-Salas *et al.* (2024b) recommended limiting such analyses to confirmed tracemakers rather than the entire benthic community. This distinction is crucial, as comparisons involving all megafauna may be confounded by the presence of non-tracemaking species. The difficulty in defining clear correlations also stems from the fact multiple organisms can produce morphologically similar trace types, while a single species may produce a variety of lebensspuren (Miguez-Salas *et al.* 2024b).

The relationship between benthic fauna and lebensspuren appears more complex than originally postulated by Kitchell *et al.* (1978) and Young *et al.* (1985). Later studies reported no significant correlation (Turnewitsch *et al.* 2000; Miguez-Salas *et al.* 2024b), while emphasizing the multitude of factors that influence trace preservation and interpretation (Przeslawski *et al.* 2012; Miguez-Salas *et al.* 2024b). The connections between traces and epibenthic megafauna are clearly multifaceted, making it difficult to identify a single controlling parameter. Continued identification of new trace types and their associated tracemakers is essential for improving our understanding of benthic ecosystems and drawing more accurate conclusions about their dynamics.

Tracemakers and their lebensspuren

The dominant group of tracemakers in the study area is Echinodermata (55%, 691 trace occurrences) (Fig. 7; Table 1 for occurrences; Table 2 for frequency and dominance). This dominance of echinoderms in tracemaker assemblages is consistent with additional findings from other regions worldwide (Hollister *et al.* 1975; Gage and Tyler 1991; Smith *et al.* 1993; Lauerma and Kaufmann 1998; Turnewitsch *et al.* 2000; Vardaro *et al.* 2009). In contrast to deep-sea environments, where the most common sea star trace is the resting impression, often referred to as star-shaped traces (Fig. 2E) (Kitchell *et al.* 1978; Wheatcroft *et al.* 1989; Durden *et al.* 2020; Miguez-Salas *et al.* 2020, 2024a), the most frequently observed lebens-

spuren in the studied Svalbard region is the trace left by a moving sea star, specifically *Urasterias lincki* (Fig. 2A₁, B, D, H). This trace showed a frequency of 60% and dominance of 28% across all stations where lebensspuren were recorded (Table 2).

Sea stars produce not only resting traces related to stationary behavior or feeding but also distinctive traces associated with locomotion on the seabed. Examples of such traces have been described as trace fossils by Mángano *et al.* (1999), with neoichnological and experimental studies documenting these patterns (Gingras *et al.* 2008; Ishida *et al.* 2017). Przeslawski *et al.* (2012) also discussed perforated traces created by sea stars. The closest analogues to the traces presented here are those recorded in the Aleutian Trench (Miguez-Salas *et al.* 2024a), where tube feet impressions are clearly visible.

Star resting impressions of this type have been observed relatively infrequently. However, several near-complete burials of *Urasterias lincki* (Fig. 5A–D) and brittle stars (Figs. 3A₃ and 5E) have been documented, all exclusively in the inner fjord areas near glaciers (Fig. 7). This

distribution may reflect fundamentally different environmental conditions in these zones, notably high sedimentation rates during the Arctic summer. Species inhabiting special adaptations (Kvitek 1989; Kukliński and Porter 2004) or increased mobility, as seen in brittle stars and sea stars.

The observed individuals of the sea star *Urasterias lincki* may have been dead, or the traces could be linked predation or scavenging activity shallowly buried mollusks and crustaceans. Similar traces evidence was presented by Howell *et al.* (2003) and Miguez-Salas *et al.* (2024a). After prey consumption, organisms likely digest *in situ*, explaining burial by suspended sediment (Blake 1989).

In addition to echinoderms, numerous individuals of *Caridea* indet., likely *Pandalus borealis* (Fig. 7), were observed near glaciers. Given their sensitivity to inorganic particles (Dale *et al.* 2008), their presence in these high-sedimentation environments is somewhat unexpected but aligns with observations by Meyer and Sweetman (2015).

Table 2. Frequencies (F%) and dominance (D%) of identified lebensspuren in individual fjords and across the entire dataset. Frequencies (F%) represent the percentage of samples containing specimens of a given species, while dominance (D%) indicates the proportion of a species' abundance relative to the total megafauna abundance. The label "Others" refers to the fjords Smeerenburgfjorden, Rijpfjorden, and Krossfjorden (each with a single seafloor recording), as well as Magdalenfjorden and Raudfjorden, each with two recorded stations.

Lebensspuren:	All stations		Hornsund		Kongsfjorden		Isfjorden		Van Mijenfjorden		Schelf & Torellbreen		Other	
	F%	D%	F%	D%	F%	D%	F%	D%	F%	D%	F%	D%	F%	D%
<i>Stegophiura nodosa</i>	1	8	-	-	-	-	2	13	-	-	-	-	-	-
Ophiuridae spp.	11	7	40	33	-	-	10	3	-	-	-	-	-	-
Ophiuroidea imprints	9	6	5	6	3	3	14	7	-	-	-	-	17	5
Asteroidea indet., juv.	1	0.2	-	-	-	-	2	0.3	-	-	-	-	-	-
Asteroidea imprints	5	1	10	2	12	7	-	-	-	-	-	-	-	-
<i>Urasterias lincki</i>	60	28	70	35	76	63	49	18	100	71	-	-	33	29
<i>Ctenodiscus crispatus</i>	1	0.2	-	-	-	-	2	0.3	-	-	-	-	-	-
<i>Myriotrochus rinkii</i>	2	4	-	-	-	-	4	7	-	-	-	-	-	-
<i>Pagurus</i> spp.	14	13	5	5	6	1	20	18	-	-	25	10	33	10
<i>Hyas</i> sp.	2	0.3	-	-	-	-	4	1	-	-	-	-	-	-
Caridea indet.	14	7	30	11	18	12	6	4	-	-	-	-	17	31
<i>Buccinum</i> sp.	6	1	-	-	6	1	6	1	-	-	25	3	17	2
Naticidae spp.	13	3	-	-	-	-	18	3	60	19	50	27	17	2
<i>Dendronotus frondosus</i>	4	2	-	-	-	-	10	3	-	-	-	-	-	-
Gastropoda indet.	33	10	15	4	24	10	39	10	20	3	100	57	67	19
<i>Phyllococe</i> sp.	1	0.2	-	-	-	-	2	0.4	-	-	-	-	-	-
Nemertea indet.	3	0.2	-	-	-	-	6	0.4	-	-	-	-	-	-
Pleuronectinae spp.	9	1	10	1	9	2	12	1	-	-	-	-	-	-
Unidentified	28	7	10	2	6	2	53	10	20	6	25	3	17	2

Ichnological aspect

The most well-known ichnogenus of sea stars and brittle stars in paleoichnology is *Asteriacites* von Schlotheim, 1820 (Knaust and Neumann 2017). This cosmopolitan resting trace is commonly found in the fossil record from the Cambrian to the Neogene (Crimes and Zhiwen 1986; Mikuláš 1992; Knaust and Neumann 2017). The ichnofamily Biformitidae (Knaust and Neumann 2016) includes impressions interpreted as locomotion traces produced by ophiuroids and asteroids. The locomotion traces documented in this study, from species such as *Urasterias lincki*, *Ctenodiscus crispatus* (Fig. 2C) and juvenile, unidentified individuals (Fig. 2F), further support the question raised by Miguez-Salas *et al.* (2024a): „we open the question, based on the current observations, if the inclusion of unnamed trace fossils produced by sea star podia locomotion as the ones exposed by Mángano *et al.* (1999), should be included within Biformitidae ichnofamily by erecting new ichnogenera that embrace these asterozoan locomotion traces, *i.e.*, not arcuate or hook-shaped imprints, or if they should be assigned to other established ichnofamily with similar morphological features and add asterozoan as possible tracemakers”. As demonstrated in this publication, the inner parts of the Svalbard fjords (Fig. 7) are rich in such traces. With continued advances of video recording technologies, we can expect increasingly frequent documentation of these types of lebensspuren, not only in the Arctic region or the deep-sea floors of the Aleutian Trench.

Behavioral insights from lebensspuren

Studying lebensspuren provides new insights into the behavior of benthic fauna that produce these traces (Prześlowski *et al.* 2012; Miguez-Salas *et al.* 2022, 2024a; Brandt *et al.* 2023). For instance, in the case of lebensspuren produced by *Pagurus* sp., it has been observed that in two instances, individuals follow the trail of a snail (Fig. 4A₂, D₁). In one case, it is likely a snail of the genus *Buccinum*. The genus *Pagurus* is known for its highly developed chemoreceptor senses and ability to locate snails and their empty shells (Rittschof 1980; Gherardi and Tiedemann 2004). Based on the assessment of the traces alone, one can attempt to draw conclusions about species co-occurrence and behavioral interactions (Fig. 3I).

Community-level patterns and tracemaker differentiation

The n-MDS analysis did not reveal distinct clusters among stations, indicating a general lack of sharp community boundaries between different fjord zones. While this absence of clear differentiation may seem unexpected, it carries ecological significance. It suggests a relatively homogeneous distributions of tracemaker types across sites, or alternatively – a continuous gradient in community composition that is not easily captured through categorical separation. Instead of discrete groupings, the n-MDS ordination reveals a continuum of similarity among stations (Fig. 6).

Nonetheless, when n-MDS results are interpreted alongside trace composition and site metadata, certain patterns become apparent. In the glacial bays, lebensspuren are predominantly associated with Echinodermata, particularly *Urasterias lincki*. Additional notable traces in these areas include those attributed to indeterminate Ophiuroidea and Caridea. In contrast, areas near river mouths (*e.g.*, Colesbukta, Adventfjorden) and regions located outside of the fjords (such as the Torellbreen area) are primarily characterized by traces from snails (Naticidae and other indeterminate Gastropoda) and hermit crabs, including *Pagurus pubescens* and *P. bernhardus* (Fig. 7).

Glacial bays are characterized by high concentrations of suspended sediment throughout the water column (Drańska-Deja 2024), which can serve as a limiting factor for many benthic organisms (Görllich *et al.* 1987). However, this turbidity may also function as a refuge from large predators such as Atlantic cod, a species frequently recorded in the fjord region (Bengtsson *et al.* 2024). In contrast, river mouth environments tend to exhibit higher sediment suspension near the surface than at the seabed (Zajączkowski *et al.* 2010), making them more accessible to a broader range of organisms, including large predators.

Bioturbation impact

Benthic and benthic-pelagic fauna play a crucial role in shaping sediments structure, with the extent of their impact depending on the size, abundance, and activity levels of the organisms involved (Murray *et al.* 2002). The analysis of lebensspuren offers valuable insights into bioturbation processes. While most studies on bioturbation focus on its vertical dimension (Oleszczuk *et al.* 2019; Solan *et al.* 2019), trace fossil analysis can also illuminate patterns of horizontal and near-surface bioturbation (Belley *et al.* 2010; Miguez-Salas *et al.* 2024d). Jumars and Wheatcroft (1989) even suggested that horizontal bioturbation may occur at a much higher intensity than vertical mixing.

The depth and visibility of surface disturbances in sediments vary widely depending on the tracemaker. The most subtle traces are produced by nudibranchs such as *Dendronotus frondosus* (Fig. 4F), nemerteans, and polychaetes of the genus *Phyllodoce* (Fig. 4L). In contrast, lebensspuren left by sea stars (Fig. 2A₁, B–F, H), caridean shrimps (Fig. 3F, G), ophiuroids (Figs. 2G, I, J, 3A₁, A₃, B, C, D₂, E₃ and 5E), and hermit crabs (Figs. 2A₂, 3A₂, E₂, H₁, I₂ and 4A₁) result in highly distinctive and often extensive surface disturbances. Snails from the family Naticidae (Figs. 3I₁ and 4C) and the sea cucumber *Myriotrochus rinki* (Fig. 2K) are capable to disturbing sediments to depths exceeding 1 cm. By analyzing the spatial extent of these traces, the biomass of tracemaking organisms, the thickness of sediment they ingest or displace, and their levels of mobility, we can gain a more comprehensive understanding of bioturbation processes in the fjord ecosystems of Svalbard.

Conclusions

This study presents one of the first detailed, video-based documentations of lebensspuren from shallow fjord environments in the Svalbard region, based on observations from 206 stations. Traces were identified at 57% of the sites, revealing notable diversity and abundance across fjord systems. In total, 19 distinct types of lebensspuren were described, with 18 linked to directly observed tracemakers. The majority of these traces were attributed to representatives of Echinodermata, particularly *Urasterias lincki*, whose locomotion traces dominated the dataset. The study introduces eight new lebensspuren morphotypes and provides rare *in situ* documentation of trace-producing behavior. These observations offer valuable insights into both behavioral patterns and taxonomic identities of the tracemakers. By integrating morphological, behavioral, and taxonomic data, this work advances our understanding of benthic community dynamics in Arctic fjords and contributes novel material relevant for ichnological classification and future neoichnological research.

Although statistical analyses did not reveal strong correlations between lebensspuren and megafaunal abundance, the data exhibit spatial patterns that align with environmental gradients, particularly those associated with glaciers influence. The variability observed in trace-type distribution underscores the significance of environmental factors, such as sediment properties and turbidity, in determining the preservation and visibility of traces, *i.e.*, trace resident time.

Crucially, the integration of direct video observations enabled reliable interpretation of tracemaker identity and behavior, effectively bridging a key gap between ichnological classification and ecological function. These findings demonstrate that neoichnological analysis, especially when supported by real-time imagery, offers substantial potential for reconstructing benthic activity and bioturbation processes in both modern and ancient glaciomarine settings.

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OŚWIADCZENIE WSPÓLAUTORSKIE

Niniejszym oświadczam, że mój wkład w pracę:

Deja, Kajetan, Jan Marcin Węslawski, Tomasz Borszcz, Maria Włodarska-Kowalczyk, Piotr Kukliński, Piotr Bałazy, and Patrycja Kwiatkowska. 2016. "Recent Distribution of Echinodermata Species in Spitsbergen Coastal Waters." *Polish Polar Research* 37(4): 511–526. doi: 10.1515/popore-2016-002

obejmował: opracowanie koncepcji publikacji, częściowy zbiór danych, analizę danych, napisanie manuskryptu oraz przygotowanie rysunków i tabel.

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obejmował: zbiór próbek organizmów bentosowych oraz wsparcie przy recenzji i redakcji manuskryptu.



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obejmował: zbiór próbek organizmów bentosowych oraz wsparcie przy recenzji i redakcji manuskryptu.

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obejmował: zbiór próbek organizmów bentosowych oraz wsparcie przy recenzji i redakcji manuskryptu.

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obejmował: zbiór próbek organizmów bentosowych oraz wsparcie przy recenzji i redakcji manuskryptu.



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OŚWIADCZENIE WSPÓLAUTORSKIE

Niniejszym oświadczam, że mój wkład w pracę:

Deja, Kajetan, Mateusz Ormańczyk, and Katarzyna Dragańska-Deja. 2019. "Plankton or Benthos: Where Krill Belongs in Spitsbergen Fjords? (Svalbard Archipelago, Arctic)." *Polar Biology* 42(8):1415–1430. doi: 10.1007/s00300-019-02524-1

obejmował: opracowanie koncepcji publikacji, zebranie danych z wykorzystaniem kamery opuszczanej (drop camera), przygotowanie części rysunków i tabel oraz napisanie manuskryptu.

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obejmował: zbiór i analizę próbek zooplanktonowych oraz wsparcie przy edycji i redakcji manuskryptu.



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obejmował: wsparcie przy edycji i redakcji manuskryptu oraz przeprowadzenie analiz przestrzennych.

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Niniejszym oświadczam, że mój wkład w pracę:

Deja, Kajetan, Katarzyna Dragańska-Deja, and Jan Marcin Węslawski. 2023. "*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* 46(10): 1137–1143. doi: 10.1007/s00300-023-03171-3

obejmował: opracowanie koncepcji publikacji, zbior i analizę danych, napisanie manuskryptu oraz przygotowanie rysunków i tabel.



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obejmował: wsparcie przy edycji i redakcji manuskryptu.



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obejmował: wsparcie przy redakcji manuskryptu.



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OŚWIADCZENIE WSPÓLAUTORSKIE

Niniejszym oświadczam, że mój wkład w pracę:

Deja, Kajetan. 2025. "*Observation of Discarded Appendicularian Houses in the Benthic and Pelagic Zones of Spitsbergen Fjords Using Drop-Camera Imagery.*" *Marine Ecology Progress Series* 771: 71–88. <https://doi.org/10.3354/meps14946>

obejmował: opracowanie koncepcji publikacji, zbior i analizę danych, napisanie manuskryptu oraz przygotowanie rysunków i tabel.

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OŚWIADCZENIE WSPÓLAUTORSKIE

Niniejszym oświadczam, że mój wkład w pracę:

Deja, Kajetan, and Alfred Uchman. 2025. "*Surface lebensspuren and Their Tracemakers in Arctic Fjords of Spitsbergen: Patterns, Diversity, and Environmental Controls.*" *Polish Polar Research* 46(3): 147–165. doi: 10.24425/ppr.2025.154567

obejmował: opracowanie koncepcji publikacji, zbior i analizę danych, napisanie manuskryptu oraz przygotowanie rysunków i tabel.

Kajetan Deja

Kraków, 2.03.2026 r.



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Niniejszym oświadczam, że mój wkład w pracę:

Deja, Kajetan & Uchman, Alfred. 2025. *Surface lebensspuren and Their Tracemakers in Arctic Fjords of Spitsbergen: Patterns, Diversity, and Environmental Controls*. Polish Polar Research 46(3): 147–165. doi: 10.24425/ppr.2025.154567

obejmował: współredakcję manuskryptu i wsparcie przy recenzji.

Prof. dr hab. Alfred Uchman

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