



Bayesian analysis of biodiversity patterns via beam trawl versus video transect—a comparative case study of Svalbard rhodolith beds

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Received: 2 May 2023 / Revised: 18 December 2023 / Accepted: 14 January 2024 / Published online: 4 March 2024
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Abstract

Knowledge of spatial biodiversity patterns is important for ecosystem assessment. Rhodoliths, free-living calcareous algae, are biotic components that structure the sea floor through their complex calcareous skeletons and their tendency to accumulate in an area to form rhodolith beds. Thereby, rhodoliths are considered to act as ecosystem engineers promoting local biodiversity. In this study, the biodiversity of rhodolith beds in Mosselbukta, Svalbard, was investigated to analyse the proposed link between local biodiversity and the presence of rhodoliths by evaluating beam trawl and underwater video transect data. The comparative analysis of two sampling methods addressing the same research question allowed us to assess the suitability of these two methods. To test our hypothesis and the utility of the two methods, evaluations of the two data sets were carried out separately by using Bayesian statistics. The results confirm a positive relationship between the presence of rhodoliths and local biodiversity with a posterior probability of 70% for the video transects and 85% for the beam trawl data. The similarity of the results of the two methods suggests that both methods are well-suited for the analysis of local biodiversity patterns. The combination of the two methods, with their individual strengths and weaknesses, has provided stronger support for the results and a broader view on different components of the biodiversity in the Svalbard rhodolith beds.

Keywords Arctic · Method comparison · Rhodoliths · Quantitative analysis · Crustose coralline algae

Communicated by Vinicius Giglio.

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Introduction

Biodiversity is an important indicator for the type, functionality and health of ecosystems. Enhancing our comprehension and promoting awareness of the link between biodiversity and rhodoliths carries immense significance. Rhodolith beds play a vital role in both ecological and geochemical processes within the ocean, due to their properties as ecosystem engineers, their massive calcium carbonate skeletons and their wide distribution (Nelson 2009; Amado-Filho et al. 2012; Teichert et al. 2014; Fragkopoulou et al. 2021). It is crucial to understand their important role as they are being threatened by global change and direct human impact (McCoy and Kamenos 2015; Teichert et al. 2020; Fragkopoulou et al. 2021). Rhodoliths are defined as free-living structures that are built by crustose coralline algae and may or may not have a nucleus in their interior (Bosence 1983). The nucleus can be versatile, ranging from rock material (cobbles, pebbles) over bioclasts (bivalve shells) to dead algal material. Moreover, there are hollow rhodoliths which lost their former nucleus at some state of their development (Teichert et al. 2014). Crustose coralline algae have a good fossil record since the Silurian (Teichert et al. 2019) but rhodoliths appear much later and differ from litho- or bioclasts covered with algal crusts, so-called ‘coated grains’, by consisting of at least 50% algal material (Bosence 1983; Foster 2001). The massive skeletons of rhodoliths generate large amounts of calcium carbonate per year, making them the main photoautotrophic carbonate producers of the Svalbard archipelago (Teichert and Freiwald 2014). The annual carbonate production from one square metre of seafloor covered with rhodoliths, mostly belonging to the species *Boreolithothamnion glaciale* (Kjellman) Gabrielson et al. (2023) (Basionym *Lithothamnion glaciale* Kjellman 1883), ranges between 100 and 200 g CaCO₃ m⁻²yr⁻¹ (Teichert and Freiwald 2014). The ability of rhodoliths to build these complex skeletons with their irregular surfaces and their partly hollow form contributes significantly to the structuring of the surrounding environment. With these properties, they create an attractive habitat and an important ecological niche for plenty of organisms, being characterised as important autogenic ecosystem engineers (sensu Nelson 2009; Teichert 2014; Teichert et al. 2020).

Earlier studies have addressed the link between the biodiversity of some taxonomic groups and the occurrence of rhodoliths (Nelson et al. 2012; Teichert 2014; Wisshak et al. 2019; Wisshak et al. 2021; Neves and Costa 2022). Teichert (2014) and Wisshak et al. (2019) focused on the mobile macrobenthos based on dredge samples and/or video transects and found a positive link between rhodoliths and biodiversity in Svalbard waters. Wisshak et al. (2021) looked at the sessile micro- and macrobenthos by evaluating long-term settlement experiments placed within and adjacent to the Mosselbukta rhodolith beds and found elevations in the biodiversity of epiliths and bioeroders to be insignificant. Here we follow the approach to evaluate this link through the application of Bayesian statistics by using larger data sets based on two different sampling methods. The advantage of using Bayesian statistics in this regard is that it does not rely on large data sets. Despite having larger data sets than the aforementioned studies, these are still not sufficient for a reliable frequentist statistical approach.

Enhancing the understanding of the role rhodoliths play in ecosystems is a crucial step to help improving advice for the conservation and management of these important habitats, so that actions for their protection could be taken (Vale et al. 2022; Tuya et al. 2023). Rhodoliths are threatened by climate change alongside manifold threats from direct human impact,

including destructive fishing activities, fish and mussel farming and extractive industries (mining, gas and oil exploitation) (Halpern et al. 2015; Nilssen et al. 2015; Legrand et al. 2021; Tuya et al. 2023). One particular threatening human impact for rhodolith beds is bottom trawling (Fragkopoulou et al. 2021). The damage caused by this type of fishing is dramatic and effects ecosystems for a long time (Bernard et al. 2019). Trawling, in addition to the obvious loss of the habitat built by these organisms, results in an overall increase in rhodolith mortality and consequently a reduction in the photosynthetic activity and the associated primary production within rhodolith beds (Martin et al. 2005, 2007; Bernard et al. 2019). Furthermore, Bernard et al. (2019) observed a decrease of habitat complexity and associated flow-reducing capacity, which can affect the erosion and sedimentation rates in these habitats. Consequently, this results in the destruction of ecological niches and size reduction of suitable habitats which impacts biodiversity in these ecosystems (Bernard et al. 2019; Fariols et al. 2022). Moreover, this destruction could have severe consequences for the overall population sizes of economically important species, such as scallops and gadoids, as well as for invertebrates in general, since rhodolith beds can serve as nursery grounds for them (Kamenos et al. 2004a, b; Moura et al. 2021).

Traditionally, also in scientific context trawling or dredging is used as a classical sampling technique to assess diversity of fish and invertebrate assemblages (Eleftheriou and Moore 2013). However, the destructive nature of these sampling methods makes them less suitable for monitoring complex and sensitive habitats such as rhodolith beds. The identification of less invasive sampling strategies is thus requested in international management policies such as the European Union's Marine Strategy Framework Directive (EC, 2008). Accordingly, underwater video techniques are increasingly used for investigating habitat diversity and to monitor benthic ecosystems. In general, these methods provide a cost-effective, non-destructive alternative monitoring method, which allow rapid acquisition of a large amount of high-resolution information on biodiversity even at sites that are difficult to sample with classic methods (Mallet and Pelletier 2014; Taormina et al. 2020). However, one major shortcoming of underwater video techniques is often the reduced taxonomic identification level that resulted from insufficient video/image resolution or water turbidity (Mallet and Pelletier 2014; Flannery and Przeslawski 2015). Many authors therefore conclude to use several methods complementary to balance the advantages and disadvantages and to achieve the most comprehensive assessment of habitat biodiversity (Bosch et al. 2017; Esmaeili et al. 2021; Jac et al. 2021). While using a combination of sampling techniques helps to achieve a more comprehensive data set, it does not solve the problem of using invasive sampling techniques. Therefore, to allow for a reasonable decision on which method to use, quantitative studies with a direct method comparison within the same environmental setting are needed. Such quantitative comparative studies are crucial for assessing the effectiveness, accuracy and practicability of methods for specific research questions. However, investigations of this regard are rather rare, especially of video transects.

Accordingly, we use two different sampling methods (beam trawl and video transect) to analyse the biodiversity in Mosselbukta at the North of Spitsbergen Island, Svalbard, which is characterised by its extensive rhodolith beds (Wisshak et al. 2019; Schlüter et al. 2021). We aim (1) to compare these two epibenthic sampling methods to assess the differences between them. Furthermore, this comparison is based on a case study, with the aim (2) to determine the biodiversity at different sampling points and water depths in the study area and (3) to examine a potential link between higher biodiversity and the occurrence of rho-

doliths, accounting for other environmental conditions. This case study therefore provides further information on how the biodiversity in a high Arctic ecosystem may be underpinned by rhodoliths, raising awareness for protection of these ecosystems and their engineers, particularly in terms of reducing destructive trawl sampling in future studies on rhodolith beds.

Methods

Sampling area and seafloor mapping

All data used in this study were obtained during the “Arctic Carbonate Factories” (ARCA) expedition with the research vessel *Maria S. Merian* in 2016 (Wisshak et al. 2017). The expedition targeted the Arctic Svalbard archipelago a thousand kilometres north of Norway. Mosselbukta (79°53'N, 15°50'E), the sampling site, is an up to 8 km wide and 5 km long bay. It is located in the north of Ny-Friesland at the western part of the Mosselhalvøya peninsula, a part of Spitsbergen Island (Fig. 1). The water in Mosselbukta is dominated by modified Atlantic water from the Arctic Ocean at depth. In shallower waters, the main source is Atlantic water and warm polar surface water dominates the surface (Rudels et al. 2000; Wisshak et al. 2019). The influence of the Atlantic water becomes predominantly noticeable during times of intense expression of the seasonal West Svalbard Current (Sapota et al. 2009). The water parameters for the Mosselbukta rhodolith beds, at a water depth of 46 m, show a seasonal fluctuation in temperatures between a maximum of 6 °C in summer and a minimum of 2 °C in winter. The salinity (PSS) in this area at the same depth (46 m) ranges between 34 and 35 with slightly elevated values in summer (Wisshak et al. 2019). The formation of sea ice usually starts in December – January and ends in May – July (Spren et al. 2008). The seafloor in Mosselbukta is characterised by abundant glaciogenic pebbles to boulders providing suitable hardground for different kinds of organisms, especially for crustose coralline algae, which form extensive rhodolith beds (Teichert et al. 2014; Wisshak et al. 2019) that were first discovered by Kjellman (1875).

During the expedition, seafloor mapping was performed with a Kongsberg EM 1002 multibeam echosounder operating at 95 kHz. It is characterised by an electronic roll stabilisation, a maximum of 111 beams and 2° beam-width. The post-processed topographical map of the seafloor in Mosselbukta served as the basis to plan the beam trawl sampling and video transects (Fig. 1).

Megafauna beam trawl and video data

Mosselbukta was sampled with the beam trawl at 11 different stations MSM55/418-1, 431-1, 443-1, 443-2, 456-1, 456-2, 468-1, 468-2, 475-1, 480-1, 480-2 that are spread across the bay (Fig. 1), ranging from 24 to 153 m water depth, including areas with and without the presence of rhodoliths. Benthic megafauna was sampled with a 2 m beam trawl (Fig. 2a), equipped with a 1 cm mesh size net and attached tickler chains. The beam trawl had a weight of 139 kg and was dragged at a speed of about 1 knot for 5 min starting from the moment of contact with the ground, which corresponds to a track length of approximately 150 m. Megafauna identification was done on board to the lowest possible taxonomic level and after identification, most organisms were returned to the ocean, only few specimens were

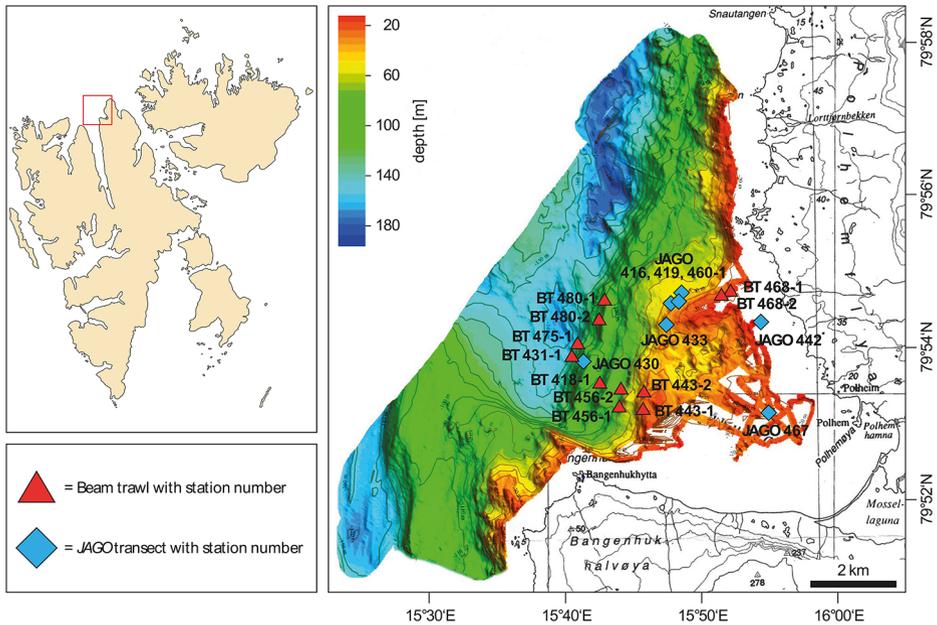


Fig. 1 Location and multibeam map of the study site: Mosselbukta at the Svalbard archipelago. Highlighted with a red triangle are the beam trawl locations and with a blue rhombus the dives of the *JAGO* submersible that were analysed in this study (modified after Wisshak et al. (2017))

collected and preserved in alcohol for further research purposes. The abundance data were standardised to a tow length of 120 m (area sampled = 240 m²). Non-countable taxa, such groups as Bryozoa or Porifera, were excluded from the analysis. Station 475-1 had to be deleted from the data set because the net was torn during deployment of the beam trawl.

Video footages were taken during the dives of the manned submersible *JAGO* with a 1920 × 1080 pixel resolution camera (CANON XA25 HD-Camcorder). The submersible was also equipped with a triangular laser point projection system for scaling purposes (Fig. 2b). The video material evaluated for this study was recorded during 7 dives at stations MSM55/416, 419, 430, 433, 442, 460 and 467 (Fig. 1). These dives were chosen to cover a broad depth range from 10 to 127 m and to cover areas where rhodoliths were present and absent. The material was evaluated by manually analysing numerous sequences per video transect. The sequences were selected according to the dive protocols to assure an accurate depth specification. Each sequence consisted of three freeze frames spanning a 10 s interval and were individually evaluated by counting the number and type of organism groups present as well as by measuring the maximum and minimum grain size in each frame. The organism groups are composed of actinians, asteroids, balanids, bivalves, bryozoans, crustaceans, echinoids, gastropods, non-calcifying algae, ophiuroids, serpulids and sponges (Fig. 3). Fish were not included in the analysis as the noises and lights of the submersible would trigger their reflexes to escape before the submersible was able to catch them on camera. The number of organism groups visible per freeze frame was determined by counting organism group assemblages, to enable also the quantification of non-countable taxa and because the video resolution was insufficient to count the organisms individually. Furthermore, it should

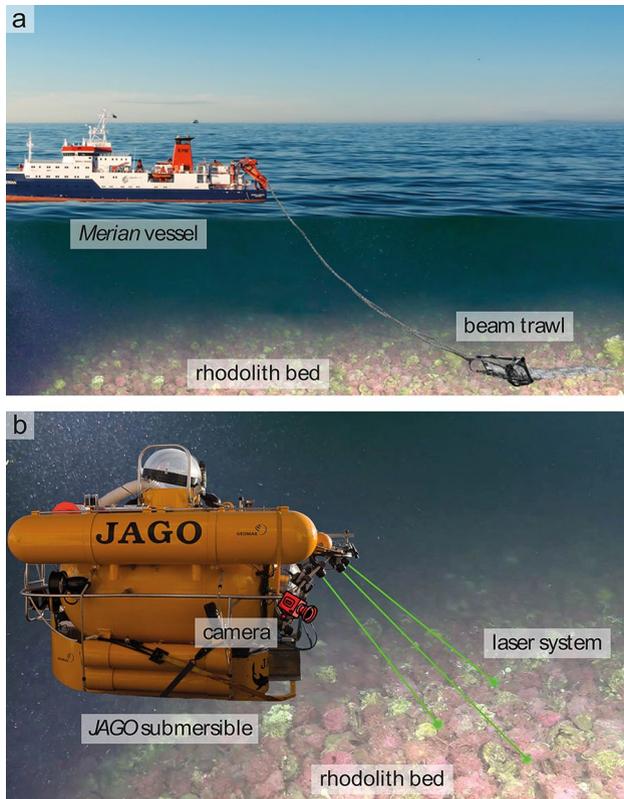


Fig. 2 Visualisation of the implementation of the sampling methods: (a) beam trawl and (b) video transects

be noted that the organism groups used for the assessment of the videos are artificial groups and do not belong to an official taxonomic classification but follow the scheme outlined above. In addition to the organism groups the minimum/maximum grain size and the percentage of the living rhodolith coverage was estimated for each freeze frame. Finally, the data of three freeze frames which belong to one sequence were combined by determining the sum of the counts per organism group and the mean value of the minimum/maximum grain size as well as the rhodolith coverage of all three freeze frames, so that only one value for each category remains for each sequence. Only the summarised values of each sequence were used for further analysis. To ensure that each frame shows a similar area, the results were standardised. The standardisation was based on the area of a laser point triangle which was projected by the submersible during the dive (Fig. 2b). Each sequence was standardised to $17,432 \text{ px}^2$ which corresponds to the median of all calculated triangle areas.

Data analysis

The analysis of the two data sets was carried out separately but based on an identical procedure in the methodology. This means that all calculations were carried out for both data sets and both data sets were analysed with the same statistical models. The models are therefore

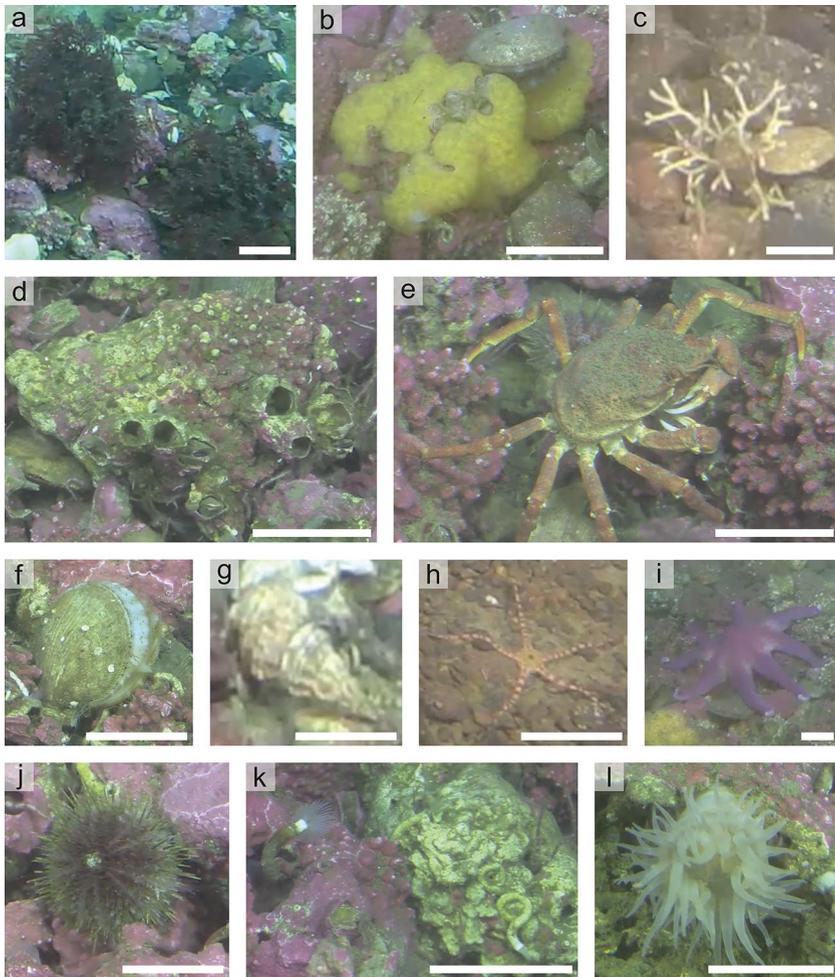


Fig. 3 Exemplary representatives of the organism groups defined for the video analysis. (a) non-calcifying algae, (b) sponges, (c) bryozoans, (d) balanids, (e) crustaceans, (f) bivalves, (g) gastropods, (h) ophiuroids, (i) asteroids, (j) echinoids, (k) serpulids and (l) actinians (Scales: 10 cm)

identical, the only difference is an additional variable in the video models (grain size), which is owing to the sampling method only available for the video data.

The Shannon-Wiener biodiversity index was calculated in the software R based on the standardised values of each beam trawl station and each video sequence using the *diversity()* function of the *vegan* package (Oksanen et al. 2020; R-Core-Team 2020).

The question whether the presence of rhodoliths has an influence on biodiversity was analysed by different statistical models with different structures. Due to the small sample size, Bayesian statistics were used to develop and analyse the models to obtain meaningful results. The general concept behind Bayesian statistics is that it assumes all parameters to be random, which means they have distributions, and the data are fixed. For example, in frequentist statistics the opposite is the case, the data is assumed to be random and the

parameters are fixed (McNeish 2016). In other words, frequentist statistics search for the likelihood to observe the set parameter values in the data, whereas Bayesian statistics search for the values of the parameter with the assumption that the data is collected and there will be no repetition of the experiment (McNeish 2016). Therefore, Bayesian methods do not depend on large samples (McNeish 2016). By using methods such as Markov chain Monte Carlo (MCMC), which are sample-based Bayesian methods that use an iterative approach to estimate the parameters, the quality of the inference is controlled by the number of samples drawn approaching infinity and not by the sample size approaching infinity (Lee and Song 2004; van de Schoot et al. 2014; McNeish 2016). Consequently, considering that MCMC does not rely on asymptotics, as is the case with frequentist methods, it is suggested that MCMC is better suited to model data with small sample sizes. However, when using the MCMC framework for small sample sizes, careful attention should be paid to the selection of the prior distribution (Dunson 2001; Lee and Song 2004; van de Schoot et al. 2014; McNeish 2016). For a better understanding, the general structure of the Bayesian statistic comprises three components: (1) The prior distribution, which is determined by the researcher and includes any prior knowledge before looking at the data; (2) the likelihood, which is determined by the data and indicates the evidence observed (van de Schoot et al. 2014; McNeish 2016); and (3) the posterior distribution, which reflects the new knowledge obtained by weighting the prior knowledge against the observed data. Thus, the posterior distribution represents the combination of prior distribution and likelihood by applying Bayes' theorem (van de Schoot et al. 2014; McNeish 2016). The Bayes' theorem (Bayes and Price 1763) can be described as: "The probability density function $p(\Theta | y)$ of the parameters Θ given the observations y is obtained from the density $p(\Theta)$ of the parameters Θ and the density $p(y | \Theta)$ of the observations y given the parameters Θ by

$$p(\theta | y) \propto p(\theta) p(y | \theta),$$

where \propto denotes proportionality." (p. 4)(Koch 1990).

The application of Bayesian statistics was done in R by using the brms package (Bürkner 2017; R-Core-Team 2020). Before constructing the first model, the variables containing the values for the Shannon-Wiener index were standardised with the *scale()* function of the base R package to achieve a normal distribution of this variable (R-Core-Team 2020). To fit the first model (model 1), a formula had to be defined to characterise the dependent and the independent variables. The formula was determined for the beam trawl data by the Shannon-Wiener index as the dependent variable and rhodoliths and water depth were set as independent variables. In the case of the video data, another independent variable, the grain size, was available and therefore included into the model. In the next step, priors were selected by using the *get_prior()* function of the brms package and after setting the priors, a prior predictive check was performed with the *conditional_effects()* function of the brms package (Bürkner 2017). The prior of the intercept was specified as a normal distribution centred around zero with a small standard deviation of 0.5 as the values were previously standardised. The priors of the coefficients, rhodoliths and water depth, were also defined as normal distributions centred around zero but with a standard deviation of 0.1 to make extreme effect sizes unlikely. Thus, the priors for the coefficients were chosen in a way that no effect is assumed without seeing the data, but it is still possible that an effect will be considered when the data indicate it. The prior of σ was specified as an exponential distribution

centred around 1 to meet the requirements that σ is always positive and theoretically can become very large in rare cases. The chosen prior can accordingly be counted among the group of “weakly informative priors”. This ensures that the analysis is only determined by realistic values, as the parameter range is limited to values that are likely. In the last step, the model was set up by using the *brm()* function of the *brms* package (Bürkner 2017). The *brm()* function uses Stan, which is a programming language for statistical modelling and computation (Stan Development Team 2021), to fit Bayesian generalised linear (or non-linear) multivariate multilevel models to obtain full Bayesian inference (Bürkner 2017). Therefore, the coefficients are determined based on the likelihood by computing HMC (Hamiltonian Monte Carlo). HMC is a variant of MCMC but has a better computational efficiency and a stronger guarantee that the resulting estimates are valid (Betancourt 2018). To set up the *brm* model, the previously determined formula and priors were implemented into the function and the family argument, which reflects the response distribution and link function used in the model, was set to linear gaussian. The arguments “chains” and “iter” were set to default which means the *brm* model used 4 Markov chains with 2000 total iterations per chain (including 1000 warmup iterations per chain) (Bürkner 2017). Finally, a posterior predictive check was performed by using the *pp_check()* function of the *bayesplot* package (Gabry and Mahr 2021). A posterior predictive check is a method used to evaluate whether the model fits the data and if it makes predictions about the reality that are valid and sensible (Gelman and Hill 2007). It simulates replicated data under the fitted model and subsequently compares them with the observed data (Gelman and Hill 2007). Therefore, the posterior predictive check can be used to search for systematic discrepancies between the actual and the simulated data (Gelman et al. 2013).

Furthermore, a second model (model 2) with different variables was set up for both data sets (beam trawl and video) based on the same procedure. In this model, data on various environmental parameters were added to the formula to see if a different structure of the model affects the results. The data on the environmental parameters were taken from Wisshak et al. (2019) and include temperature, salinity, oxygen content and turbidity of the water. These variables were included in the second model, which then for the beam trawl data consisted of the Shannon-Wiener index as the dependent variable and the independent variables rhodoliths, water depth, temperature, salinity, oxygen content and turbidity. The same variables were used for the video data, the only difference again being the additionally added independent variable grain size.

Moreover, the video data were further evaluated by calculating the biodiversity index separately for sessile and vagile organisms by using the *biodiversity()* function of the *vegan* package again (Oksanen et al. 2020). Afterwards, two Bayesian models were set up with the same specifications as for video model 1 but instead of the overall biodiversity, one model contained the biodiversity only of sessile and the other one only of vagile organisms as the dependent variable. The evaluation then followed the same procedure as for the previous models. The aim was to identify if there is a difference between sessile and vagile organism biodiversity regarding their relationship to rhodoliths.

To assess whether the *brm* models worked well and the chains converged, parameters such as \hat{R} , Bulk ESS and Tail ESS were used. The potential scale reduction factor \hat{R} provides a measure for the success of the convergence of the chains by comparing the differences between the different chains (between-chains variability) to the extent of which a chain explores the parameter space (within-chains variability) (Gelman and Rubin 1992;

Nalborczyk et al. 2019). \hat{R} “is computed for each scalar quantity of interest, as the standard deviation of that quantity from all the chains included together, divided by the root mean square of the separate within-chain standard deviations” (p.669) (Vehtari et al. 2021). In this case, the *brm()* function uses the split- \hat{R} , which additionally splits each chain in half and then compares the first and the second half to each other to check for missing convergence within each chain (Gelman et al. 2013). The \hat{R} value should ideally be close to 1 and should not be larger than 1.1 (Nalborczyk et al. 2019). A \hat{R} above 1.1 would commonly indicate that the chains did not converge (McElreath 2015). The effective sample size (ESS) indicates the amount by which within-chain autocorrelation increases uncertainty in estimates (Stan Development Team 2022). ESS values close to the number of iterations (excluding warm-up iterations) of the chains imply that the chains work efficiently (McElreath 2015). Significantly lower values would indicate that the chains work inefficiently (McElreath 2015). Therefore, in general, the higher the ESS values, the better (Vehtari et al. 2021). However, since there is an irregular convergence of the Markov chains across the parameter space it is proposed as useful to also look at the ESS for extreme quantiles (Vehtari et al. 2021). Therefore, a distinction was made into Bulk ESS, which represents the standard ESS estimate in the centre of the posterior distribution, and Tail ESS, which provides the ESS of the whole 95% confidence interval (Vehtari et al. 2021).

For the evaluation of the outcome of all models, the function *hypothesis()* of the *brms* package (Bürkner 2017) was used. The function computes parameters such as an estimate, evidence ratio, a 90% confidence interval and the posterior probability for a given hypothesis and therefore helps to further assess the results of the Bayesian models (Bürkner 2017). The evidence ratio of the function in this case reflects whether the evidence is in favour with the hypothesis or not, whereby values larger than 1 indicate that the evidence is in favour with the hypothesis (Bürkner 2017). Furthermore, the posterior probability indicates the percentage of the posterior distribution that is in favour with the hypothesis and therefore gives an impression of the strength of the discovered relationship. The hypotheses used are indicating either a positive or a negative connection between two variables. A hypothesis > 0 refers to a positive correlation between two variables and implies that as variable 1 increase, variable 2 will also increase to some extent. Accordingly, a hypothesis < 0 reflects a negative correlation and means that with the increase of variable 1, variable 2 will decrease.

Results

Beam trawl data

A total of 56 species were identified in the beam trawl catches. Across all beam trawls, *Balanus balanus* (Linnaeus, 1758) was the most abundant species with 4136 individuals, followed by *Ophiopholis aculeata* (Linnaeus, 1767) with 1105 individuals. The species *Anatoma crispate* (Fleming, 1828) and *Moelleria costulata* (Møller, 1842) were least abundant with only one individual in 10 beam trawls.

Shannon-Wiener biodiversity index for the beam trawl data is in the range from 1.5 to 2 for most stations indicating a relatively similar biodiversity; only three out of ten stations have an index less than 1.5 corresponding to station 468-2 in 24.8 m water depth, station 456-2 in 76.5 m water depth and the deepest station 431-1 in 153.2 m water depth (Fig. 4a).

The highest index value was found at station 443-2 with 1.9 and lowest at station 468-2 with 1.3.

The presence of rhodoliths at the sampling locations could only be determined at three stations (Fig. 4b). These include station 468-2 in 24.8 m water depth, station 468-1 in 27.3 m water depth and station 443-2 in 47.3 m water depth. The number of rhodoliths increased with water depth from 9 rhodoliths at station 468-2 to 27 rhodoliths at station 443-2. The increasing number of rhodoliths corresponds to increasing values of the Shannon-Wiener index with highest values for both at station 443-2.

In the next step, two Bayesian models were used to determine a possible dependency of the local biodiversity on the presence of rhodoliths for the beam trawl data. The outcomes of both models show similar results (Tables 1 and 2). In both models, the comparison of the prior and posterior distribution shows a positive shift of the rhodolith posterior curve. However, the posterior curve is not entirely positive so that a part of the curve remains on the negative side. In summary, around 85% of the curve lies on the positive side (> 0) and 15% plot on zero or the negative side (≤ 0) (Figs. 5 and 6, additional Figs are given in Online Resource 1). A hypothesis test was carried out to further evaluate the results. It also indicates a posterior probability of around 85%. It should be noted, however, that the given estimate value (Tables 1 and 2) cannot be interpreted directly due to the standardisation of the dependent variable of the model. The statistical parameters for both models are within the range

Fig. 4 a) Shannon-Wiener biodiversity index plotted over the water depth of each station of the beam trawl data. The station numbers are indicated in the bars. b) Number of rhodoliths plotted over the water depth of each station of the beam trawl data. The station number is indicated in the bars. The absence of rhodoliths in station 443-1/ 46 m water depth is probably an effect of the patchy distribution of rhodoliths

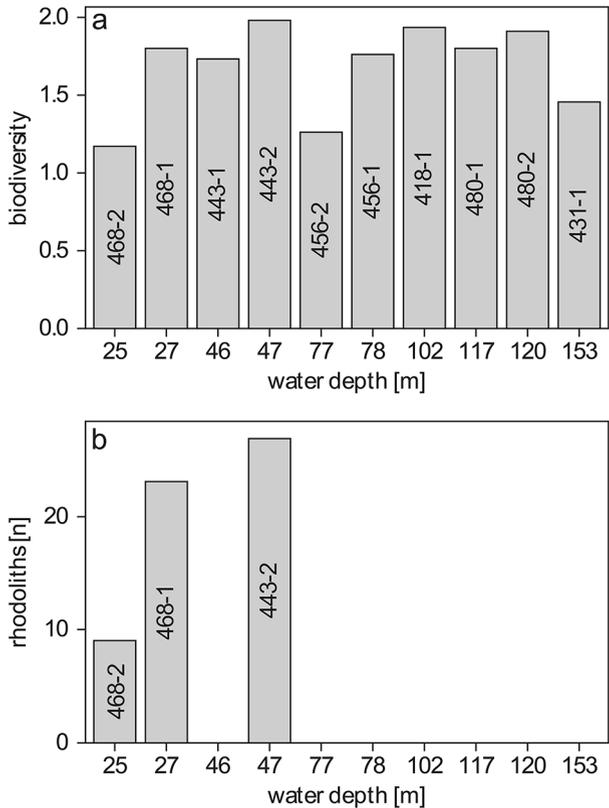


Table 1 Statistical parameters of the beam trawl model 1

beam trawl model 1	Estimate	Est. Error	Lower-95% CI	Upper-95% CI	\hat{R}	Bulk ESS	Tail ESS
Intercept	-0.95	1.02	-2.89	1.10	1	2395	2180
Water depth	0.01	0.01	-0.01	0.03	1	2608	2318
Rhodoliths	0.04	0.04	-0.04	0.12	1	2459	2023
Hypothesis test	Estimate	Est. Error	Lower-90% CI	Upper-90% CI	Evid. Ratio	Post. Prob	
(Rhodoliths) > 0	0.04	0.04	-0.03	0.10	5.54	0.85	

Table 2 Statistical parameters of the beam trawl model 2

beam trawl model 2	Estimate	Est. Error	Lower-95% CI	Upper-95% CI	\hat{R}	Bulk ESS	Tail ESS
Intercept	-0.88	3.80	-8.32	6.64	1	4920	2554
Water depth	0.01	0.01	-0.01	0.03	1	3120	2697
Rhodoliths	0.04	0.04	-0.05	0.12	1	3244	2475
Temperature	-0.01	0.10	-0.20	0.18	1	5653	2779
Oxygen	0.00	0.10	-0.20	0.20	1	6342	3243
Salinity	0.00	0.10	-0.20	0.20	1	5615	2126
Turbidity	0.00	0.10	-0.20	0.20	1	6562	2788
Hypothesis test	Estimate	Est. Error	Lower-90% CI	Upper-90% CI	Evid. Ratio	Post. Prob	
(Rhodoliths) > 0	0.04	0.04	-0.03	0.11	5.86	0.85	

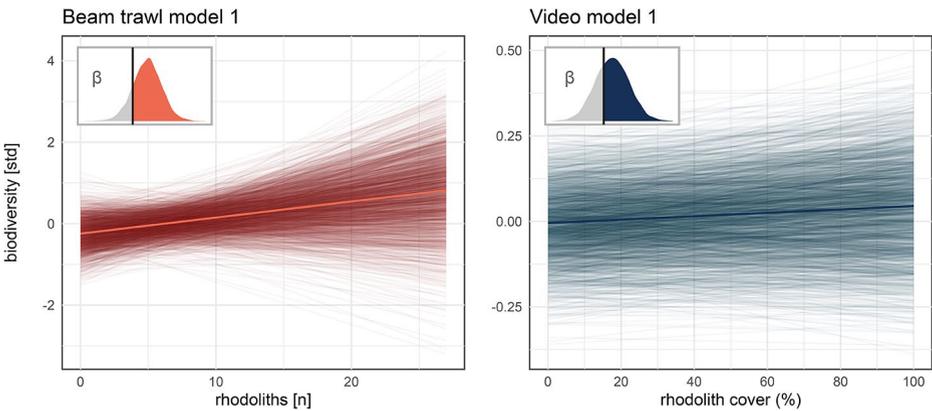


Fig. 5 Correlation plot and posterior curve β (top left) of the Bayesian beam trawl model 1 and video model 1

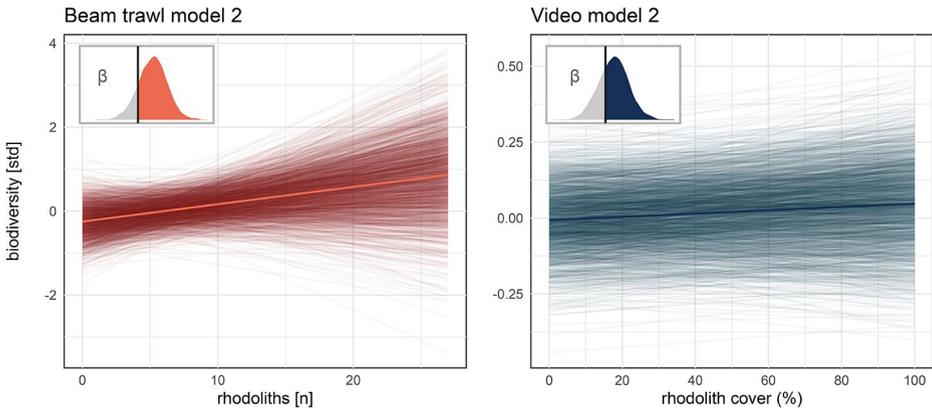


Fig. 6 Correlation plot and posterior curve β (top left) of the Bayesian beam trawl model 2 and video model 2

indicative of a well-functioning model. Accordingly, the models should work correctly from a statistical point of view and can be used for the evaluation of the research question.

Video data

The analyses of video data were done separately, due to the different structure of the data sets. The video data cover a greater depth range and more individual depths compared to the beam trawl data, which increases the amount of information and provides a higher resolution of the results. However, unlike the beam trawl data, the video data could not be analysed at species level, which decreases the resolution of the results in this regard. A comparison of video organism groups present/absent in the beam trawl data set and vice versa can be found in Fig. 7.

A total of 12 taxonomic groups were identified by video analyses. The most abundant groups across all video transects were bivalves and echinoids with more than 900 individuals. The least abundant groups were crustaceans and sea anemones with less than 10 individuals.

The Shannon Wiener index for the video data (Fig. 8c) is similar to the beam trawl data. In the shallower depths between 10 and 28 m, the index was generally below 1.2, with one exception at a depth of 25.7 m. In the depth range between 40 and 51 m, the average index value was around 1.4 with a maximum value of 1.73 at 44 m depth. Only at 40 m water depth, a lower value of 1.3 was found. A small decrease in the values was observed at depths of 55 and 67 m with values of around 1.2. However, the value between these two depths at 57 m was much higher with 1.6 and is therefore comparable to the average of the values in this area. In deeper waters below 60 m, the Shannon Wiener index was always above 1.4 with a maximum value of 1.88 at 125 m. Across all water depths, the highest index was found at 125 m with 1.88. The lowest value with 0.24 was found at 24.5 m water depth.

The occurrence of rhodoliths was mainly limited to low – medium water depths of up to 60 m. However, in shallow water depths of 10 to 12.5 m only a very small proportion of less than 10% rhodolith cover was found. At depths between 21.7 and 27.8 m, the frequency of rhodoliths was mostly around 10%, only in depths from 25.7 to 27.7 m it shows less

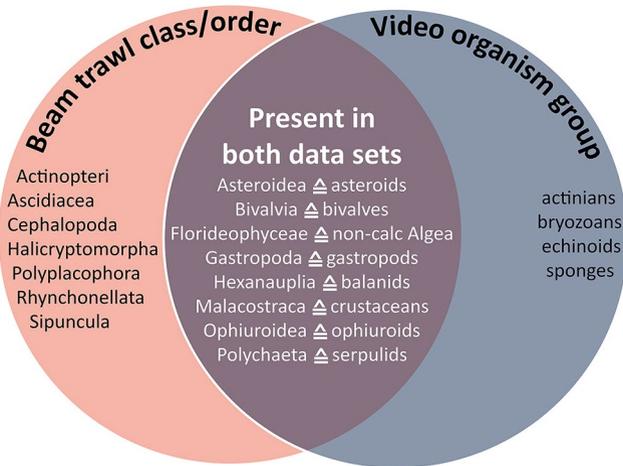


Fig. 7 Comparative overview of the presence, absence or bilateral occurrence of beam trawl classes/orders and video organism groups in the other data set

than or equal 5% rhodolith cover. In a water depth of 40 m, a percentage of 78% rhodolith cover was reached, which is the highest percentage of rhodolith cover in the data set. The subsequent depths of 41 and 44 m showed high coverage values of 57% and 62%. In the depth range of 45 to 46.3 m, the proportion of rhodoliths decreased rapidly, from 46% at 45 m to 7% at 46.3 m. A second increase in rhodolith frequencies was recorded in depths of 47 to 50 m with rhodolith cover percentages between 39% and 25%. From a water depth of 55 m and below, no more rhodoliths were found (Fig. 8b).

The evaluations of the two Bayesian models for the video data revealed similar results (Tables 3 and 4). When comparing the prior and posterior distribution, it was obvious that the posterior distribution positively shifted in both models. Around 70% of the curve plots in the area greater than zero and 30% on zero or in the area less than zero (Figs. 5 and 6 additional Figs are given in Online Resource 1). In order to support these results, a hypothesis test was performed, which also indicated a posterior probability of around 70%.

The last analysis considered to what extent the correlation between biodiversity and rhodoliths changes if the biodiversity is only calculated for sessile or vagile organisms. Here, both models revealed similar outcomes (Fig. 9 additional Figs are given in Online Resource 1, Tables 5 and 6). The hypothesis test, regarding a possible dependency on rhodoliths, revealed a posterior probability of 63% for the model of sessile organisms and 65% for the vagile organisms model.

The statistical parameters for the video data indicated good model performance.

Discussion

Knowledge of biodiversity of a habitat is an important component in understanding the ecological processes in a respective area. One important group in respect to biodiversity in Arctic ecosystems are rhodoliths which supply a habitat for a wide range of organisms by providing a heterogeneous hard substrate for grazers and encrusters and a shelter for mobile

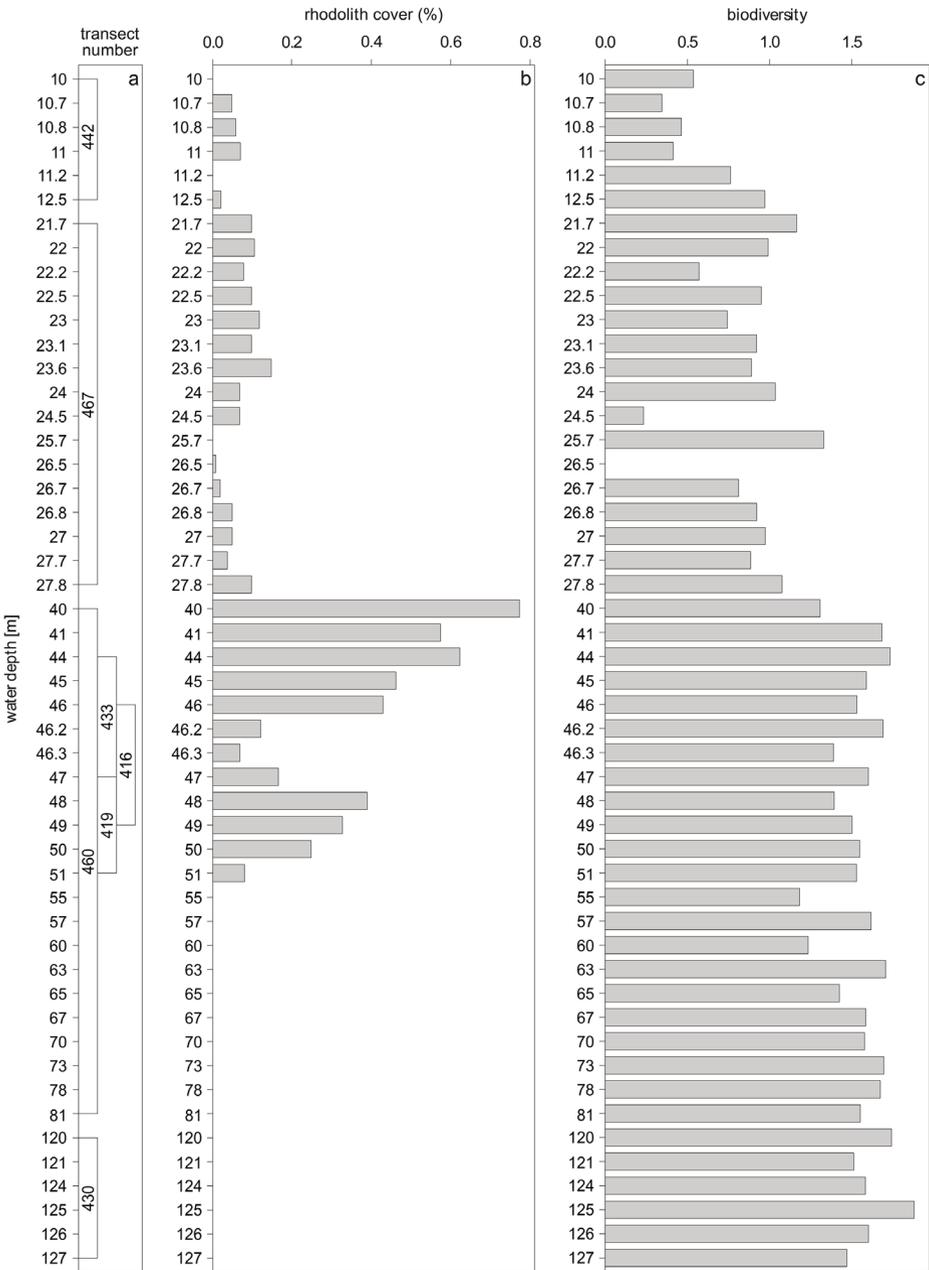


Fig. 8 a) The water depth ranges of the individual video transects. b) The percentage of rhodolith cover plotted over the water depth of each station of the video data. c) Shannon-Wiener biodiversity index plotted over the water depth of each station of the video data. The lack of a biodiversity value for 26.5 m water depth is due to the unfavourable camera angle in this video sequence that led to 0 abundances after standardisation

Table 3 Statistical evaluation parameters for the video model 1

Video model 1	Estimate	Est. Error	Lower-95% CI	Upper-95% CI	\hat{R}	Bulk ESS	Tail ESS
Intercept	-0.91	0.26	-1.41	-0.41	1	4119	3177
Water depth	0.02	0.00	0.01	0.03	1	4595	3270
Rhodoliths	0.05	0.10	-0.14	0.25	1	3077	2020
Grain size	0.00	0.00	0.00	0.00	1	4763	3081
Hypothesis test	Estimate	Est. Error	Lower-90% CI	Upper-90% CI	Evid. Ratio	Post. Prob	
(Rhodoliths) > 0	0.05	0.10	-0.11	0.22	2.35	0.70	

Table 4 Statistical evaluation parameters for the video model 2

Video model 2	Estimate	Est. Error	Lower-95% CI	Upper-95% CI	\hat{R}	Bulk ESS	Tail ESS
Intercept	-1.04	3.57	-7.95	6.18	1	5568	2601
Water depth	0.02	0.00	0.01	0.03	1	5890	3240
Rhodoliths	0.05	0.10	-0.14	0.25	1	5600	2252
Grain size	0.00	0.00	0.00	0.00	1	4157	3125
Temperature	-0.07	0.10	-0.25	0.13	1	4821	3117
Oxygen	0.02	0.10	-0.18	0.21	1	5220	2549
Salinity	0.01	0.10	-0.20	0.20	1	5618	2863
Turbidity	0.01	0.10	-0.19	0.21	1	5167	2456
Hypothesis test	Estimate	Est. Error	Lower-90% CI	Upper-90% CI	Evid. Ratio	Post. Prob	
(Rhodoliths) > 0	0.05	0.10	-0.11	0.21	2.39	0.71	

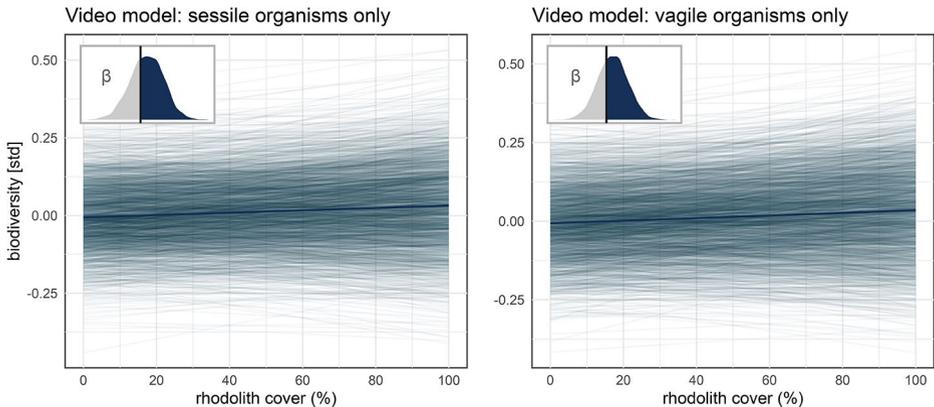


Fig. 9 Correlation plot and posterior curve β (top left) of the Bayesian video model with sessile and video model with vagile organisms only

epibenthos within their partly hollow interior. Therefore, they act as ecosystem engineers in areas that they inhabit (Steller and Foster 1995; Teichert et al. 2014). This relationship was quantitatively investigated in this study by using two data sets obtained by two different sampling methods. The aim was to improve and broaden our understanding of the link

Table 5 Statistical evaluation parameters for the video model only with sessile organisms

Video model sessile	Estimate	Est. Error	Lower-95% CI	Upper-95% CI	\hat{R}	Bulk ESS	Tail ESS
Intercept	-1.09	0.27	-1.62	-0.57	1	3761	2896
Water depth	0.02	0.00	0.01	0.03	1	3850	2414
Rhodoliths	0.04	0.10	-0.17	0.23	1	2704	2262
Grain size	0.00	0.00	0.00	0.00	1	4292	2837
Hypothesis test	Estimate	Est. Error	Lower-90% CI	Upper-90% CI	Evid. Ratio	Post. Prob	
(Rhodoliths) > 0	0.04	0.10	-0.13	0.20	1.74	0.63	

Table 6 Statistical evaluation parameters for the video model only with vagile organisms

Video model vagile	Estimate	Est. Error	Lower-95% CI	Upper-95% CI	\hat{R}	Bulk ESS	Tail ESS
Intercept	-0.75	0.29	-1.32	-0.18	1	3636	2879
Water depth	0.02	0.00	0.01	0.02	1	4049	2835
Rhodoliths	0.04	0.10	-0.15	0.23	1	2444	2344
Grain size	0.00	0.00	0.00	0.00	1	4730	3138
Hypothesis test	Estimate	Est. Error	Lower-90% CI	Upper-90% CI	Evid. Ratio	Post. Prob	
(Rhodoliths) > 0	0.04	0.10	-0.12	0.20	1.84	0.65	

between local biodiversity and the occurrence of rhodoliths as well as to compare the two sampling methods in their effectiveness and functionality.

Biodiversity and rhodolith patterns over water depth

Both data sets provide a similar distribution pattern of biodiversity over depth. The Shannon-Wiener index implies generally lower values in shallow depths of 10 to 40 m and higher values for the interval of 41 to 127 m, with a peak at around 44 to 47 m, coinciding with the peak in rhodolith abundance. Lower biodiversity in shallower depths could be explained by the rather inconsistent environmental conditions, such as salinity fluctuations due to melt water input or temperature fluctuations due to changing currents (Wisshak et al. 2019), which make this habitat less attractive for organisms. Furthermore, a boundary layer in the stratification of the water body at approximately 40 m (Wisshak et al. 2019) reinforces this argument of less stable conditions in shallower water depths, since the stratification boundary correlates well with the onset of the higher biodiversity values below that depth. In general, a higher biodiversity with increasing depth is expected due to the more stable conditions as well as the fact that also the nitrogenous nutrient concentration and the nitrogen/phosphorus ratio in Mosselbukta increases with water depth (Wisshak et al. 2019).

The rhodolith presence and abundance at each water depth was evaluated for both data sets. The results reflect the expected depth range for rhodoliths around the Svalbard archipelago in accordance with the results of Teichert et al. (2014). Most of the rhodoliths were found in 40 to 50 m water depth. The abundance fluctuations within this depth range can be attributed to a generally patchy distribution of rhodoliths. The preference for water depths around 40 to 50 m is presumably due to fast growing competitors, such as green algae, in shallower depths and the general trend of red algae to grow at low light levels even though

they are not specifically restricted to them and could also tolerate euphotic conditions (Gantt 1990). Other factors that influence their depth distribution are water motion and sedimentation (e.g.: Steller and Foster 1995; Otero-Ferrer et al. 2020). The two latter studies implied that the depth distribution of rhodoliths is mainly hampered by high water motion in shallow waters and the sedimentation of fine sediments as well as decreasing light levels in deeper waters. Nevertheless, rhodoliths were also found in shallow water depths between 11 and 28 m but were low in abundance owing to possibly less favourable conditions as outlined above.

Next, Bayesian statistics were used to examine whether the presence of rhodoliths plays a significant role in biodiversity. The models show that rhodoliths appear to have a positive impact on biodiversity with a probability of 85% for the beam trawl data and 70% for the video data. This probability does not change when additional variables such as water temperature, oxygen content, salinity and turbidity are added to the model, suggesting that the probability of an association between biodiversity and rhodoliths is less dependent on the structure of the model and is therefore not influenced by other variables in the model. This dependence of biodiversity on rhodoliths was already determined by Teichert (2014), but the effect has not yet been quantified using a larger data set and Bayesian statistics. The reason why rhodoliths may contribute to a higher biodiversity is that due to their shape a more structured environment and more hard substrate is provided for other organisms to settle or hide (e.g.: Otero-Ferrer et al. 2019; Wisshak et al. 2021). The seafloor in Mosselbukta is generally characterised by glaciogenic pebbles resulting in a low niche diversity (Teichert 2014). Spatial ecosystem structure is increased by rhodoliths, because their irregular 3-dimensional shape with their pronounced protuberances and often hollow interior leads to the creation of new niches for organisms (Teichert 2014). For example, fish have been observed to use hollow rhodoliths as cavities for their eggs and therefore as a nursery ground (Gagnon et al. 2012) and also other organisms, such as ophiuroids or predatory polychaetes, have been found to use the protected space inside the rhodoliths as a hiding place (Teichert 2014). Looking at other components of the local biodiversity, the study of Wisshak et al. (2021), in contrast, found in their long-term settlement experiment, that rhodolith beds show no statistically significant elevation of bioerosion ichnodiversity or encruster biodiversity, compared to aphotic waters. This suggests that the dependency of biodiversity on rhodolith abundance does not universally apply to all functional groups of the macro- and microbenthos.

However, the results of our study still incorporate a small chance (beam trawl = 15%; video = 30%) that there is no positive link between biodiversity and the presence of rhodoliths. To make a more precise statement on the hypothesis, a larger data set would be necessary. Moreover, this study could not independently confirm whether rhodoliths are actually the cause or not just a part of higher biodiversity, which means that other factors could influence biodiversity and/or the occurrence of rhodoliths that would result in a similar correlation but no causation (Maynard et al. 2017). Nevertheless, several aspects such as the structuring of the seafloor and the provision of a food base for grazing organisms as well as the results of the investigations of other studies (Teichert 2014; Teichert et al. 2014), suggest that rhodoliths can support higher biodiversity.

In an additional analysis of the video data, the biodiversity for sessile and vagile organisms was calculated separately and inserted into the Bayesian model instead of the overall biodiversity. This analysis was supposed to show whether the motility of the organisms has an influ-

ence on their relationship to rhodoliths. The results revealed that the dependency on rhodoliths does not change if only sessile or only vagile organisms were considered. Thus, both groups are equally associated with rhodoliths. This might be due to the fact that rhodoliths offer advantages for both sessile and vagile organisms as they provide a surface to settle on but also a hiding spot and a food source (Teichert et al. 2014).

Sampling method comparison

In this study, two fundamentally different methods – beam trawl and video transects – were used to obtain two data sets addressing the same research question. Both methods have been used before in the context of biodiversity surveying studies (Wisshak et al. 2019; Braga-Henriques et al. 2022; Tuya et al. 2023) but each method has its individual clear advantages and disadvantages (Table 7). An obviously negative aspect of beam trawls is the partial destruction of habitat by dragging a net over the seafloor and the fact that some of the trapped organisms die (Mallet and Pelletier 2014). Video transects do not have this disadvantage. However, the correct identification of organisms is challenging with the video technology available today (Flannery and Przeslawski 2015; Esmacili et al. 2021). Artificial organism groups were implemented to overcome this problem and to save time in the classification process to enable the creation of a bigger data set. Data acquisition with beam trawls provide a more precise identification of the organisms as all captured organisms can be inspected by hand and with a binocular in the laboratory. In turn, video transects have the advantage that they depict the ecosystem as a whole, as they are

Table 7 Summary sampling method comparison

Beam Trawl	Video
Taxonomic resolution	
High (species level)	Moderate (organism groups)
Destruction of habitat	
Yes	No
Sampling bias	
Yes: organisms might not get caught because they are too fast, too small, or because unfavourable underground conditions make sampling difficult	Yes: organisms can be overlooked because they are well camouflaged, they hide in or behind something, are too small to be visible from the camera perspective, or because of turbidity
Underestimation of organism groups	
Yes: nekton, infaunal organisms	Yes: nekton, infaunal organisms
Acquisition of the whole ecosystem	
No: Information about habitat structure, organism interaction or sea floor conditions	Yes: provides information on prevailing seafloor conditions, the distribution of organisms, organism behaviour, species associations and interactions
Information on biomass and organism size classes	
Yes	Limited: only estimations of biomass and size classes
Depth resolution	
Low. Depth averaged along trawl	High. Precise depth information along depth transects
Long-term evaluability	
No: samples usually returned to the sea	Yes: re-analysis possible with new methods
Technologically challenging	
No: provided good quality of the trawl and net	Yes: depending on quality of equipment (submersible, video camera, etc.)

able to detect prevailing seafloor conditions, the distribution of organisms, organism behaviour, associations and interactions (Langlois et al. 2010; Mallet and Pelletier 2014). With regard to our research question, it was advantageous to have video data with precise depth information to analyse species depth distributions. This was more difficult to implement with beam trawls, since the net was drawn over a certain distance and only a mean depth could be specified.

The efficiency of sampling is also an important issue differentiating sampling gears. For example, both methods underestimate the abundance of nekton, since most mobile organisms quickly escape through the light and/or noise of the submersible/beam trawl (Mallet and Pelletier 2014). Furthermore, with beam trawls there is a certain proportion of organisms that were not caught, because they are too fast, too small, or unfavourable underground conditions made sampling difficult (Bergman and Van Santbrink 1994; Reiss et al. 2006; Trenkel and Cotter 2009; Mallet and Pelletier 2014). Organisms can also be overlooked in video footage, if they are well camouflaged, hide in or behind something, are too small to be visible from the camera perspective, or because of water turbidity (Cappo et al. 2004; Mallet and Pelletier 2014; McLean et al. 2016). All these factors can lead to differences in the detected species richness and diversity between the data sets. Previous studies showed that trawl sampling revealed a greater diversity and species richness compared to less invasive methods (Langlois et al. 2010; Esmaili et al. 2021; French et al. 2021), but systematically overlooked certain species which are possible to observe with underwater videos (Mérillet et al. 2018). In our study, not all detected taxa in the video footage are also present in the beam trawl data set and vice versa, which largely underpins this conclusion. However, the data sets are only comparable to a limited extent, due to the different taxonomic resolution, nevertheless both were useful in investigating the dependency between the presence of rhodoliths and biodiversity.

Considering long-term evaluability, video data are advantageous because results can be reobtained and improved with new analysing methods later. Beam trawl samples do not offer this advantage, as the catch is usually analysed on board and returned to sea. In addition, video data provide the possibility to revisit and monitor the same transect over several years (Piazza et al. 2019), which is not possible with the impact of beam trawls.

In summary, both methods came to similar results and were useful for addressing our research question. For other studies that require, for example, size classes of species or biomass data, video analysis might not be useful or applicable. However, rhodolith beds are sensitive habitats and it is recommended to avoid destructive sampling gears such as beam trawl whenever possible. We demonstrate that this is possible with the video data.

Conclusion

This study shows the ecological importance of rhodolith beds in supporting biodiversity in the Arctic Svalbard archipelago. With the help of quantitative data evaluation, a high probability that local biodiversity is positively connected to the presence of rhodoliths could be detected. This finding underpins previous assumptions that rhodoliths provide a habitat for other organisms due to their composition and structure. Therefore, more efforts should be made to protect these ecosystem engineers, such as the implementation of more stringent restrictions on bottom trawling, fish farming and extractive industries, to safeguard a habitat for a variety of organisms that depend on them.

Furthermore, our analyses of two data sets offered the ability to compare functionality and effectiveness of the sampling methods. Trawling and video data revealed similar results and were reliable to test the specific research question of this study. Therefore, despite individual advantages and disadvantages, the use of non-invasive video analysis is recommended for future studies rather than destructive beam trawls.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10531-024-02788-y>.

Author contributions The authors Eileen Straube, Sebastian Teichert, Hermann Neumann and Max Wisshak contributed to the study conception and design. The beam trawl and video material was collected during the “Arctic Carbonate Factories” (ARCA) expedition with the research vessel Maria S. Merian in 2016, which Hermann Neumann, Max Wisshak and Sebastian Teichert participated in. The material preparation and analysis were performed by Eileen Straube. The methodological approach to answer the research question was developed and implemented by Eileen Straube, Gregor Mathes, Sebastian Teichert, Hermann Neumann and Max Wisshak. The first draft of the manuscript was written by Eileen Straube and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding Open Access funding enabled and organized by Projekt DEAL. Funding for cruise MSM55 was supplied by the Deutsche Forschungsgemeinschaft (DFG) in concert with the Leitstelle Deutsche Forschungsschiffe.

Data availability All organism counts from the video and beam trawl survey are available through the attached online resources.

Declarations

Competing interests The authors declare no competing interests.

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