Arctic puzzle: Pioneering a northern shrimp (*Pandalus borealis*) habitat model in Disko Bay, West Greenland

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HIGHLIGHTS

- First high-res habitat suitability model for northern shrimp in the Arctic.
- Integrating multi-disciplinary and spatiotemporal factors to predict shrimp habitat.
- Multivariate regression and spatial linear mixed-effect model were key methods.
- Mixed sediments and medium-deep, turbulent waters are key predictors.
- High-res seafloor measurements suit best for northern shrimp distribution maps.

GRAPHICAL ABSTRACT

Arctic puzzle: pioneering a northern shrimp (*Pandalus borealis*) habitat model in Disko Bay, West Greenland
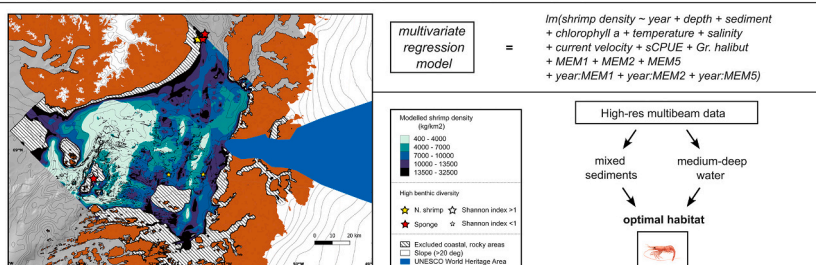
ARTICLE INFO

ABSTRACT

Recent advancements in spatial modelling leverage remote sensing data and statistical species-environment relationships to forecast the distribution of a specific species. Our study focuses on Disko Bay in West Greenland, recognized as a significant marine biodiversity hotspot in the region. We conducted comprehensive analyses using multiple datasets spanning from 2010 to 2019, incorporating shrimp and fish surveys, commercial shrimp fishery catches, high-resolution (25 × 25 m) multibeam bathymetry and backscatter data along with a medium-resolution (200 × 200 m) bathymetric model, measured and modelled oceanographic data, and satellite chlorophyll data. Through multivariate regression analysis, we tested the significance of various physical factors (seafloor depth, sediment class, bottom water temperature, bottom water salinity, bottom current velocity, space, and time), biological factors (chlorophyll *a*, Greenland halibut (*Reinhardtius hippoglossoides*)), and anthropogenic impact (shrimp fishery; standardized catch per unit effort) on the density of northern shrimp in the area. Our results indicate a significant association between northern shrimp density, seafloor depth, and sediment class, explaining 36 % of the variation in shrimp density. Subsequently, we developed a high-resolution (optimized) spatial linear mixed–effect model to map the distribution of northern shrimp across Disko Bay, representing the first model of its kind developed for an Arctic area. The optimal habitat for northern shrimp is characterized by medium-deep waters (approximately 150–350 m), turbulent conditions, and mixed sediments, predominantly located in the northern and southern regions of Disko Bay. Notably, the northern region hosts a relatively diverse

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benthic community, with northern shrimp and sponges as the primary contributors of epibenthic biomass. This novel high-resolution model significantly enhances our understanding of the physical drivers and detailed spatial patterns influencing the distribution of northern shrimp in the Arctic.

1. Introduction

The development of marine spatial models provides the possibility to quantify the impact of environmental factors on a given species (Melo-Merino et al., 2020; Pickens et al., 2021). These models use the statistical relationship between species and their habitat, along with spatial autocorrelations, to predict the spatial distribution of the species (Guisan and Zimmermann, 2000). Over the past decade, numerous spatial models have been developed, focusing on species-habitat association, including commercially important species. Spatial models predicting the distribution of shrimp species have been developed for various regions, such as the North-East Canadian shelf and the West Greenland shelf for northern shrimp (Corre et al., 2020), the Gulf of Maine for northern shrimp (Cao et al., 2017), the Gulf of Mexico for penaeid shrimp (Pickens et al., 2021), the Gulf of California for brown shrimp, blue shrimp, and white shrimp (Cota-Durán et al., 2021), Japanese waters for mantis shrimp (Li et al., 2020), and the Southern Ocean for deep-sea shrimp (Basher and Costello, 2016). These studies quantify the association between shrimp species and specific physical environmental variables, such as seafloor depth, sediment class, water temperature, and salinity. However, these models are characterized by low resolution (i.e. >500 m, often several km) and cover broad-scale areas. The present study is the first to generate a high-resolution spatial model (i.e. ≤50 m) incorporating multivariate factors across different disciplines (geophysics, oceanography, biology, and fishery) for northern shrimp distribution in the Arctic.

Northern shrimp is a circumpolar crustacean, sensitive to changes in environmental conditions, especially during early-life development (Storm and Pedersen, 2003; Ouellet and Chabot, 2005; Cao et al., 2017). Temperature plays a critical role in influencing the survival, growth, and distribution of shrimp, along with many other marine organisms (Li et al., 2020). In the Greenland shelf region, the distribution of northern shrimp has been associated with temperature and seafloor depth (Buch et al., 2005). This species has historically inhabited cold-water conditions over the past 40 years, although it has shown some variations in catch distributions, both geographically and in depth. (Buch et al., 2005; Burmeister and Buch, 2023b). The primary fishing grounds in Greenland are situated along the western continental shelf. In the 1980s, an extremely cold period, influenced by the high positive North Atlantic Oscillation index and other factors, led to a major shift in fishery target species from Atlantic cod (*Gadus morhua*) to northern shrimp and Greenland halibut, resulting in substantial impacts on Greenland's economy (Hamilton et al., 2000). Presently, northern shrimp stands as the most important fishery resource in Greenland (Buch et al., 2005), particularly prevalent in Disko Bay and its adjacent offshore areas (Burmeister and Buch, 2023a, 2023b). Disko Bay is part of the Northwest Atlantic Fisheries Organization (NAFO) statistical area 1 A and up to 26 % of Greenlandic shrimp landings originate from division 1 A alone since 2010 (Burmeister and Riget, 2022). In addition, the nearby Disko Island serves as a larval retention area, facilitated by the westward bifurcation of ocean current promoting the exchange of larvae between the Greenland and Canadian shelves (Corre et al., 2020). This retention area is thought to play a crucial role in the long-term persistence of northern shrimp populations in the Arctic (Fogarty and Botsford, 2007; Cowen and Sponaugle, 2009).

This study presents the first high-resolution spatial model, utilizing data collected from summer shrimp bottom trawl surveys specifically designed for monitoring northern shrimp in West Greenland. Our methodology integrates biological factors (northern shrimp, Greenland halibut, and epibenthic taxa), along with measured and modelled oceanographic data, standardized commercial shrimp fishery catches, geospatial seafloor models (both high- and medium-resolution), and satellite-derived chlorophyll concentration. We aim to test correlations between northern shrimp density and various environmental factors, encompassing temporal and spatial autocorrelations. Building on NAFO reports, literature reviews, and benthic habitat mapping studies, we hypothesize that simple spatial interpolations may prove insufficient in predicting shrimp distributions, given the potentially strong environmental gradients (e.g. high topographic relief). Instead, we propose that accurate predictions of northern shrimp distribution in Disko Bay (Greenland) necessitate the inclusion of detailed seafloor depth and sediment characterization, obtained from high-resolution (multibeam) seafloor measurements.

This paper seeks to delineate the habitat preferences of northern shrimp and predict their suitable habitats within Disko Bay.

2. Study area

2.1. Physiographic setting

Disko Bay (Qeqertarsuup tunua) is a large marine embayment (c. 95 × 85 km) located in central West Greenland (68°30′-69°15′ N and 50°00′-54°00′ W; Fig. 1). It is characterized by a complex geological setting (both onshore and offshore) composed of Precambrian rocks in the southwestern area, Cretaceous sandstone in the central and eastern area, and Paleogene Basalts to the west, as well as more recent (i.e. Holocene) muddy deposits across the area (Krawczyk et al., 2022). Seabed topography is correspondingly complex, with depths generally varying between 300 and 500 m and a large channel system to the west, with depths exceeding 900 m (Fig. 1). This channel system, which is a part of Egedesminde Deep (trough), is a palaeo-ice stream of the Jakobshavn glacier that has discharged across Disko Bay following the last glacial maximum (Long and Roberts, 2003). Such range of sedimentary environments and topographic complexity can harbor a variety of benthic fauna ranging from sessile epifauna associated with hard bottom (rugged) habitats to shrimp and tubeworms linked to soft bottom (floor/flat) habitats (Blicher and Hammeken Arboe, 2021; Boertmann and Mosbech, 2021; Krawczyk et al., 2021, 2022).

2.2. Oceanographic setting

Disko Bay has a polar maritime climate and is typically covered by sea ice from January until March (Buch, 2000; Heide-Jørgensen et al., 2007). Sea ice retreats in April–May until June due to increased insolation. Then, significant meltwater influx leads to the formation of pycnocline (0–20 m; Juul-Pedersen et al., 2006; Heide-Jørgensen et al., 2007). A stratified water column is maintained until September when increased winds and cyclone activity leads to increased mixing (Andersen, 1981). Icebergs originate from calving tidewater glaciers, such as Jakobshavn glacier and Torssukatak (Buch, 2000). Oceanography in the bay is influenced by the inflow of the Subpolar Mode Water (Rignot et al., 2010; Rysgaard et al., 2020). The relatively warm and saline Atlantic-sourced water enters the bay from the south and leaves both to the north (via Vaigat Strait) and south of Disko Island (Söderkvist et al., 2006; Hansen et al., 2012) (Fig. 2A-B). Andersen (1981) identified this Atlantic-sourced water mass as the West Greenland Current (T = 2.5–4 °C, S≥ 34 PSU). Recently referred to as Subpolar Mode Water, this water mass is found below the cold and low-saline Baffin Bay Polar Water, i.e. below the upper c. 200 m (Tang et al., 2004; Rysgaard et al., 2020). Locally, oceanographic conditions can

change due to complex topography, such as steep slopes and high-relief areas transitioning from narrow channels to shallow banks (Krawczyk et al., 2022).

Disko Bay is considered a very productive area, comparable even to temperate areas known as highly productive, e.g. the North Sea (Boertmann and Mosbech, 2021). The sea ice retreat during spring and early summer sets the start of phytoplankton blooms (Jensen, 2003; Juul-Pedersen et al., 2006; Heide-Jørgensen et al., 2007; Krawczyk et al., 2014). Heide-Jørgensen et al. (2007) suggested that the earliest and largest blooms can be observed in southwestern Disko Bay, whereas in eastern Disko Bay, influenced by meltwater influx, phytoplankton blooms accelerate soon after the disappearance of sea ice. A good proxy of phytoplankton biomass is the concentration of chlorophyll *a* in surface waters (Heide-Jørgensen et al., 2007). In the last decade, satellite-derived chlorophyll *a* concentration in Disko Bay for the spring-summer season (i.e. mean and maximum for April–July 2010–2019) showed the highest values in the northeastern part and along southern coasts (Fig. 2D). Export of phytoplankton from the surface to deeper
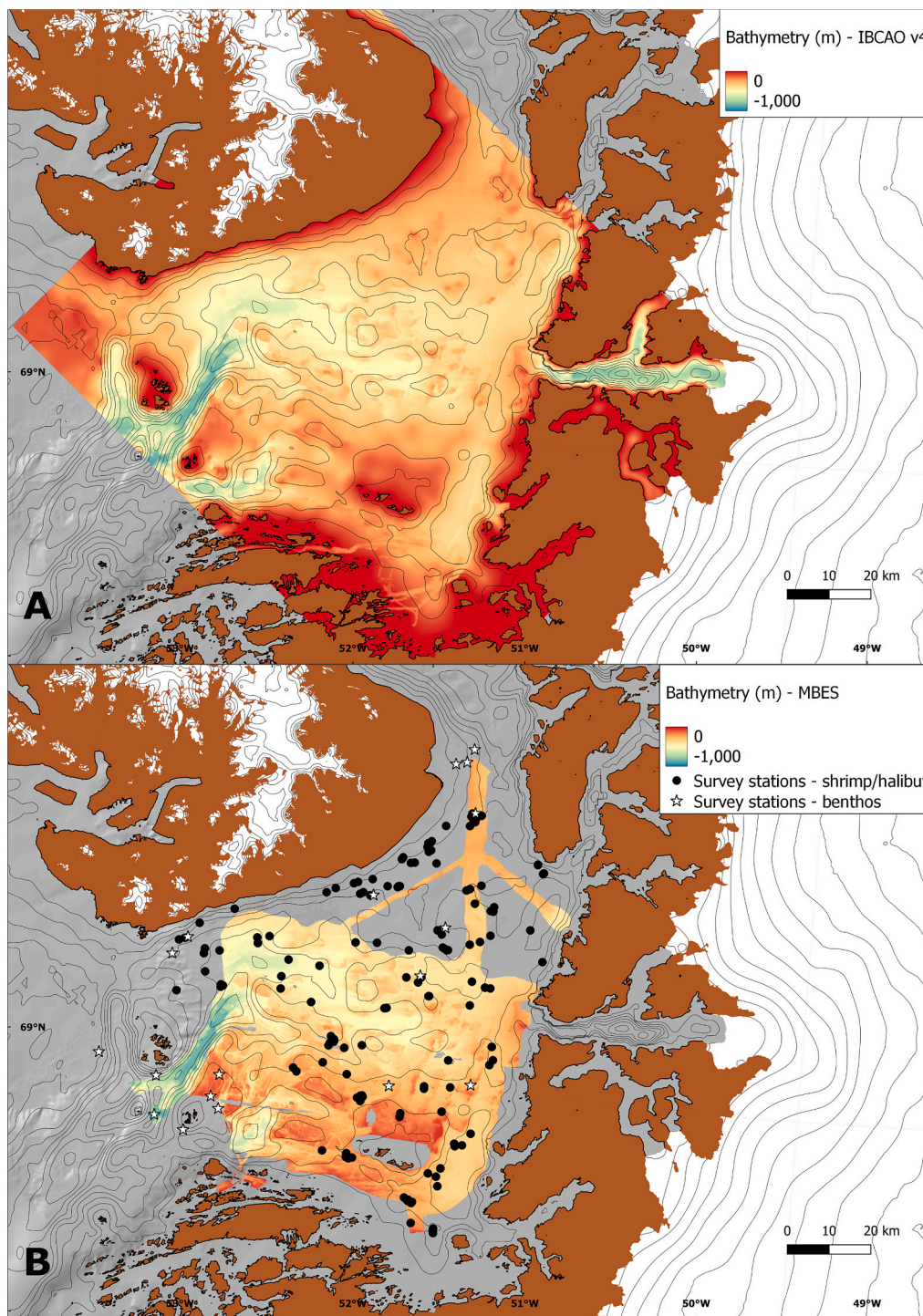

Fig. 1. Maps showing seafloor depths in Disko Bay: (A) medium-resolution IBCAO v4.0 model, i.e. 200 × 200 m (Jakobsson et al., 2020) and (B) high-resolution multibeam data, i.e. 25 × 25 m (Hogan and Ó Cofaigh, 2019; Krawczyk et al., 2022). Locations of survey stations are shown (see legend). Coordinate Reference System (CRS): WGS 84/NSIDC Sea Ice Polar Stereographic North (3413).

waters typically occurs after the peak bloom phase (Nielsen and Hansen, 1995), when water stratification weakens in favor of vertical mixing. However, the efficiency and the process of transport of phytoplankton bloom production to higher trophic levels, including benthos, is not well understood (Heide-Jørgensen et al., 2007).

3. Materials and methods

We compiled different datasets, which are summarized in Table 1: biological survey data (northern shrimp density, Greenland halibut density, benthic diversity), oceanographic survey data (bottom water temperature and salinity), oceanographic modelled data (bottom water salinity, bottom current velocity), shrimp fishery data (standardized catch per unit effort; CPUE), geospatial seafloor data (seafloor depth and sediment class), and satellite chlorophyll data (surface chlorophyll *a*).

3.1. Biological (survey and fishery) data

Survey data were collected during the annual GN assessment surveys, i.e. the annual fish and shrimp trawl surveys carried out in the West Greenland shelf area in late May–July with RV Paamiut, RV Sjudaberg, and RV Helga Maria. In addition to GN trawl data, a sub-set of commercial shrimp fishery data were obtained from logbooks of the Greenland Fisheries License Control Authority. In this study, we focus on

survey data collected in Disko Bay during the recent decade, i.e. 2010–2019.

3.1.1. Northern shrimp and Greenland halibut

The locations of northern shrimp and Greenland halibut (Cosmos) trawl stations in Disko Bay 2010–2019 are shown in Fig. 1B. Survey stations were positioned using 'buffered random' sampling, i.e. placed randomly with the constraint of a minimum distance between the stations, depending on station density within the depth stratum (Kingsley et al., 2004). In addition, every year, 50 % of the stations from the previous year are repeated using the buffered sampling rules (Burmeister and Buch, 2023a). The survey stations covered only the following 4 depth strata: 150–200 m (i.e. medium-deep), 201–300 m (i. e. medium-deep), 301–400 m (i.e. deep) and 401–600 m (i.e. deep). Densities (term consistent with Northwest Atlantic Fisheries Organization) of northern shrimp and Greenland halibut are estimated from the catch and swept area (haul) at each station (kg km^{-2}; Greenland halibut data in Table A1), following the standard procedures described in Burmeister and Buch (2023a) and Nygaard (2023). Shrimp are a known food source for Greenland halibut in Disko Bay (after Wieland et al., 2007), thus halibut density is used as a predation proxy in this study.

3.1.2. Commercial shrimp fishery

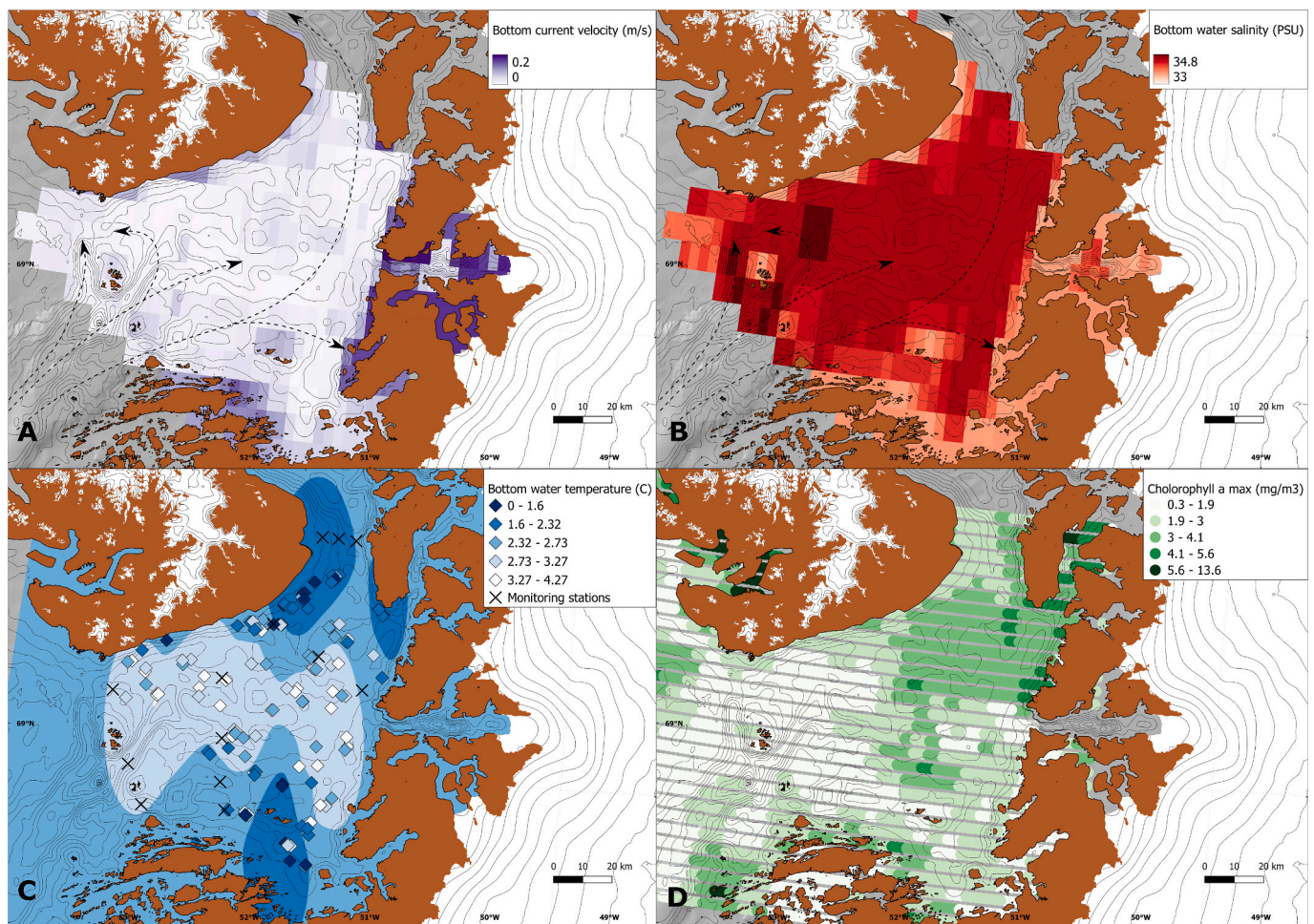Annual shrimp fishery catch (tons) and annual shrimp fishery effort

Fig. 2. Maps showing (A) modelled mean bottom current velocity, (B) modelled mean bottom water salinity (avr 2000–2014; Bio-ORACLE; Assis et al., 2018), (C) measured bottom water temperature (diamond symbol; period: 2010–2019; data in Table A1) superimposed on the interpolated survey data, including locations of the GN monitoring stations (cross symbol; TS data in Fig. A1), and (D) surface chlorophyll *a* concentration (max between April and July 2010–2019 calculated from monthly averaged satellite data OCCCI v5.0). Interpolation of bottom water temperature data was done using kriging technique (see Fig. A2). Dashed arrows indicate the approximate flow of Atlantic-sourced water mass (adapted from Andersen, 1981). CRS: 3413.

Table 1

List of all datasets used in this study with associated information on data type, unit, sampling gear, time frame and area coverage/stations, data resolution and format, data in figures/tables presented in this study, and data source.

Dataset	Data type/variable	Unit	Gear	Time frame	Area coverage/ stations	Data resolution	Data format	Figure/ Table (this study)	Source
Biological (survey) data	Northern shrimp density	kg/ km2	Cosmos trawl	2010–2019	145 stations	N/A	point data	Figs. 4–5	Grønlands Naturinstitut (GN) Assessment
Biological (fishery) data	Northern shrimp fishery catch - standardized catch per unit effort (CPUE)	index	Demersal trawl	2010–2019	Entire area	160 × 160 m	gridded data	confidential	Commercial logbooks; Greenland Fisheries License Control Authority (GFLK)
Biological (survey) data	Greenland halibut density	kg/ km2	Cosmos trawl	2010–2019	145 stations	N/A	point data	Table A1	GN Assessment
Biological (survey) data	Benthic diversity (Taxon richness, Shannon index, community type)	count, index, name	Beam trawl	2015–2017	18 stations	N/A	point data	Fig. 4–5; Table A1	GN
Oceanographic (survey) data	Bottom water temperature	°C	Starmon logger (attached to trawl)	2010–2019	145 stations	N/A	point data	Fig. 2; Table A1	GN Assessment
Oceanographic (survey) data	Bottom water temperature, salinity	°C, PSU	CTD profiler	2010, 2014, 2016, 2018	13 stations	N/A	point data	Fig. A1	GN Monitoring; International Council of the Exploration of the Sea (ICES Data Portal, 2022)
Oceanographic (modelled) data	Bottom water salinity	PSU	Modelled	Present (avr 2000–2014)	Entire area	c. 3 × 9 km	gridded data	Fig. 2; Table A1	Bio-ORACLE; Tyberghein et al., 2012, Assis et al., 2018
Oceanographic (modelled) data	Bottom current velocity	m/s	Modelled	Present (avr 2000–2014)	Entire area	c. 3 × 9 km	gridded data	Fig. 2; Table A1	Bio-ORACLE; Tyberghein et al., 2012, Assis et al., 2018
Seafloor data	Bathymetry (seafloor depth)	meter	Multibeam echo sounder	N/A	Most of the area	25 × 25 m	gridded data	Fig. 1, 4	GN and British Antarctic Survey (BAS); Hogan and Ó Cofaigh, 2019; Krawczyk et al., 2021, 2022
Seafloor data	Bathymetry (seafloor depth)	meter	Various echo sounders	N/A	Entire area	200 × 200 m	gridded data	Fig. 1, 4	International Bathymetric Chart of the Arctic Ocean (IBCAO v4.0); Jakobsson et al., 2020
Seafloor data	Sediment class (bathymetry+backscatter, verified with ground-truthing)	class	Multibeam echo sounder	N/A	Most of the area	25 × 25 m	gridded data	Fig. 3, 4	GN and BAS; Krawczyk et al., 2022
Seafloor data	Sediment class (bathymetry, verified with ground-truthing)	class	Various echo sounders	N/A	Entire area	200 × 200 m	gridded data	Fig. 3, 4	IBCAO v4 clip classified after Krawczyk et al., 2022
Satellite chlorophyll data	Chlorophyll a concentration	mg/m3	MODIS satellite	2010–2019	Entire area	4 × 4 km	point as gridded data	Fig. 2; Table A1	Ocean Color (OCCCI v5.0); Sathyendranath et al., 2019, 2021

(haul time in hours) data were extracted from grids (each grid covers approx. 160 m^2) corresponding to each survey station. Relative fishing pressure on northern shrimp species was calculated from catch and effort data from logbooks with standard linear models to create a standardized CPUE. This was done following the method described in Burmeister and Buch (2023b). Standardized CPUE was further used in statistical analyses together with the survey data and other variables.

3.1.3. Benthic epifauna

Benthic epifauna (animals living on/just above the substrate) were sampled by beam trawl (2.5 m opening) at 18 stations in Disko Bay (Fig. 1B) during 2015–2017. With a mesh size of 10 mm in the cod-end, the beam trawl targeted macrofauna (0.5–50 mm) and megafauna (>50 mm). Hauls lasted 5–10 min (0.1–0.7 km), at a speed of 1–2 knots,

sweeping an area of c. 350–1800 m^2. Epifauna was sorted on board to the lowest-possible taxonomic level and weighed after dripping off excess water (wet mass). Northern shrimp were part of both, Cosmos trawl sampling (see chapter 3.1.1) and beam trawl catch; however, unlike the Cosmos trawl, the beam trawl does not select for northern shrimp, allowing to interpret its abundance in relation to the entire benthic epifauna in the sampled area. The wet mass of epifauna catch was converted to ash-free dry mass (AFDM) using species-specific conversion factors (Maier et al., in prep). Benthic diversity indices, i.e. taxon richness and Shannon index were calculated based on AFDM instead of count data, to include uncountable, e.g. colonial taxa (Roy et al., 2014). This was done using R software (vegan package; Oksanen et al., 2019). For every station, the epifauna community type was described based on the taxonomic group which predominated the AFDM (e.g. sponges,

crustaceans, etc.). Taxon richness, Shannon index, and community type for each station is given in Table A1. Due to the limited number of stations, and to avoid duplicating information (with the Cosmos trawl sampling), we only used epifauna data to discuss northern shrimp densities in relation to the rest of the epifauna community in the area.

3.2. Oceanographic data

During assessment surveys, bottom water temperature (°C) was measured along with trawl deployments (Fig. 2C; Table A1) using Starmon TD temperature loggers in a titanium housing attached to trawl (Star-Oddi, Iceland). In addition, four CTD monitoring transects using a SBE19plus CTD (Seabird) profiler were conducted during the annual surveys (Fig. 2C), measuring water temperature (°C) and salinity (PSU). These monitoring data were available for the years 2010, 2014, 2016, and 2018. Due to the limited number of stations, we only use CTD data for an overview of water mass properties in Disko Bay and to validate survey measurements (Fig. A1). To compensate for the limited oceanographic measurements, we used modelled mean bottom current velocity (m/s) and modelled mean bottom water salinity (PSU) corresponding to the present period (average from 2000 to 2014; Fig. 2A-B) from Bio-ORACLE (Tyberghein et al., 2012; Assis et al., 2018). These modelled data have a grid cell resolution of approx. 3×9 km in Disko Bay. For statistical analyses, information on salinity and current were extracted for each survey station (Table A1) using QGIS software (QGIS Development team, 2022).

3.3. Geospatial seafloor data

3.3.1. Bathymetry

Bathymetry data (seafloor depth; m) combine two published datasets: multibeam measurements (Krawczyk et al., 2022) and an open-source model from the International Bathymetric Chart of the Arctic Ocean (IBCAO v4.0; Jakobsson et al., 2020). The high-resolution gridded multibeam data (25×25 m) cover most of Disko Bay, whereas the medium-resolution IBCAO grid (200×200 m) was interpolated over the entire Disko Bay (Fig. 1). The IBCAO grid was used as a background layer (mainly coastal areas) to fill in data gaps of the high-resolution multibeam data (same for sediment class, below). Detailed information on multibeam surveys, acquisition settings and calibrations can be found in Hogan and Ó Cofaigh (2019) and Krawczyk et al. (2021, 2022). For statistical analyses, information on seafloor depth were extracted for each survey station (Table A1) using QGIS software (QGIS Development team, 2022).

3.3.2. Sediment class

Sediment map was generated in two steps: (1) by reclassifying the existing multibeam-based sediment classes from a previous study in Disko Bay (shown as 'benthic habitats' in Fig. 7 in Krawczyk et al., 2022) and (2) by classifying the IBCAO bathymetry grid into approximate sediment classes. The multibeam-based sediment classification included a number of seafloor variables, i.e. bathymetry and its derivatives (morphology and slope based on Benthic Terrian Modeler), and (partly) backscatter, which were validated with ground-truthing stations. IBCAO bathymetry is highly limited for GIS analyses (e.g. morphology) and lacks information on backscatter, thus detailed sediment classification cannot be performed. To make these datasets comparable, we focused on hard-mixed-soft bottom simplification. (1) The final (multibeam-based) sediment classes are rocky sediments (combining previously identified classes: rocky bank, shallow rocky slope, and rocky/muddy slope), mixed sediments (combining previously identified classes: coarse plain, coarse rugged terrain, and muddy/sandy plain with dropstones), and muddy sediments (combining previously identified classes: muddy plain and muddy trough). In this area, we define 'mixed sediments' as a non-uniform substrate, where patches of mud alternate with patches of coarse sediments and cobbles/boulders, resulting in a high sediment (or

habitat) diversity (in Krawczyk et al., 2021, 2022). This simplified, 3-class sediment map was additionally verified with sediment annotations from the existing ground-truthing stations (Table A1 in Krawczyk et al., 2022). (2) For the IBCAO data, we used seafloor depth (bathymetry) for sediment classification, following the Greenland Ocean floor Classification of Habitats (GOCH) developed for Disko Bay (see Table 2 in Krawczyk et al., 2022). Rocky sediments were based on the GIS slope analysis (i.e. slope $> 20°$) and previously identified rocky banks in SW Disko Bay, whereas mixed sediments generally correspond to the seafloor depths <300 m, and muddy sediments to the seafloor depths >300 m. The IBCAO-based sediment map was also validated with the existing, more precise sediment classes from ground-truthing (see above). A combined sediment map from both geospatial datasets is shown in Fig. 3. The extraction of sediment class information for each survey station (Table A1) and all (re)classification steps were done in QGIS software.

3.4. Satellite chlorophyll data

Surface chlorophyll a (chl a) concentrations (mg m^{-3}) were extracted from the Ocean Color Climate Change Initiative (OCCCI) version 5.0 monthly dataset based on MODIS satellite images (Sathyendranath et al., 2019, 2021). Data were extracted for the entire sampling area in Disko Bay and for the entire sampling period (2010–2019). In this study, we use surface chl a (phytoplankton biomass) as a proxy of food availability in the ecosystem. Phytoplankton is considered one of the food sources for northern shrimp (in Wieland et al., 2007). For each grid cell (4×4 km) and year, maximum surface chl a concentrations (Fig. 2D), and mean surface chl a concentrations were calculated between April and July, i.e. the period of phytoplankton blooms with the highest annual chl a production. For statistical analyses, chl a data closest to the shrimp survey stations were extracted (Table A1).

3.5. Statistical analysis

All data analyzed in this study are listed in Table 1. For statistical analyses, we established a threshold of 15-km radius around the shrimp survey stations for using environmental data (>70 % of data retained). All datasets were first tested for temporal autocorrelation (as data were collected over multiple years) and spatial autocorrelation. Spatial interpolations were done using variogram modelling and kriging interpolations. Further statistical modelling used two different approaches, 1) multivariate regression analysis (MRA) including Moran's Eigenvector Maps (MEMs) to account for spatial autocorrelation and to identify the key environmental, spatial, and temporal factors, and 2) spatial linear mixed-effect model (spaMM) for generating a high-resolution map of northern shrimp distribution. Prior to multivariate regression analyses, variables were transformed to follow a multivariate normal distribution of the residuals and to avoid heteroscedasticity. Shrimp density data were square root transformed, whereas Greenland halibut density, seafloor depth, bottom current velocity, and chl a were log transformed. For the spatial linear mixed-effect model, no transformations were needed, because a non-normal distribution (Gamm distribution) can be defined within the model function. All statistical analyses described below were done in R v 1.3 (R Core Team, 2021).

3.5.1. Autocorrelations

For temporal autocorrelation, the *acf* function was used, for temporal autoregression, the *pacf* function, and for trend over time, the *mann kendall* test (kendall package; McLeod, 2022). Autocorrelation and autoregression are considered significant if a lagged response exceeds the 95 % confidence intervals (Holmes et al., 2020). A trend is considered significant at *p* value <0.05. For spatial autocorrelation, *moran's I* test was performed using the *moran.mc* function.

Table 2

Table showing the importance of different explanatory variables for northern shrimp density in full and optimized multivariate regression model, including variance partitioning (variation explained), effect size (estimate), standard error, T value, and *p* values. Statistical significance is marked with asterisk, i.e. ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$.

| Explanatory variable	Variation explained	Estimate	Std error	T value	P (>|t|)	Significance
Full model						
Seafloor depth	23 %	−45.533	12.377	−3.679	0.000	***
Sediment class	13 %	−32.161	8.721	−3.688	0.000	***
Chlorophyll a (mean Apr-Jul)	0 %	−6.578	7.204	−0.913	0.364	
Bottom water temperature	0 %	−2.368	5.425	−0.436	0.664	
standardized catch per unit effort (CPUE)	2 %	−1.739	6.854	−0.254	0.800	
Greenland halibut	0 %	−1.012	2.011	−0.503	0.616	
Bottom current velocity	1 %	−16.069	8.999	−1.786	0.078	.
Bottom water salinity	1 %	−35.056	22.898	−1.531	0.129	
Year	15 %	−6.150	1.411	−4.360	0.000	***
Moran Eigenvector Map (MEM) 1	0 %	9451.945	1887.455	5.008	0.000	***
MEM2	0 %	2584.800	2301.030	1.123	0.264	
MEM5	0 %	4134.334	2424.312	1.705	0.092	.
Year:MEM1	9 %	−4.692	0.937	−5.008	0.000	***
Year:MEM2	0 %	−1.282	1.141	−1.124	0.264	
Year:MEM5	1 %	−2.052	1.204	−1.705	0.092	.
Optimized model						
Seafloor depth	23 %	−33.930	14.400	−2.356	0.021	*
Sediment class	13 %	−38.390	9.677	−3.967	0.000	***
Bottom water salinity	1 %	−30.790	25.930	−1.187	0.238	
Bottom current velocity	1 %	8.957	9.009	0.994	0.323	
Year:MEM1	0 %	0.001	0.002	0.382	0.704	
Year:MEM5	0 %	0.001	0.002	0.585	0.560	
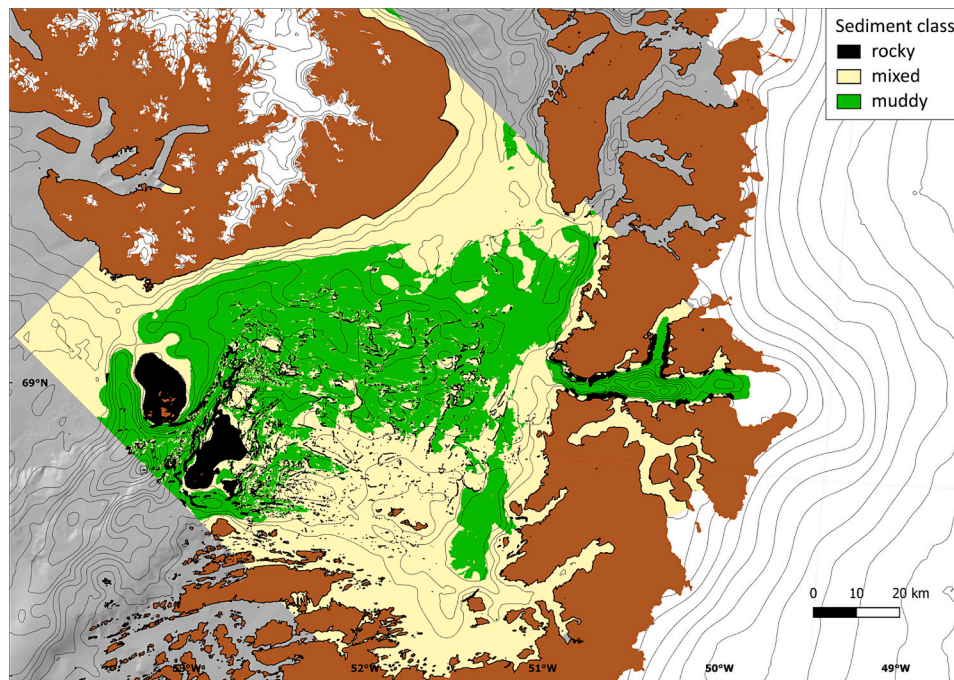
Fig. 3. Map showing modelled sediment classes (rocky, mixed, and muddy) using the combined multibeam dataset (modified Fig. 7 from Krawczyk et al., 2022) and the IBCAO v4 model. CRS: 3413.

3.5.2. Geostatistical interpolation

Variogram modelling, utilized as input for kriging interpolation, was conducted on all point data, i.e. northern shrimp density, Greenland halibut density, benthic diversity (Shannon index), standardized CPUE, and bottom water temperature. Variograms were calculated using the *variogram* function (gstst package) and fitted using the *fit.variogram* function. For this process, a linear approximation was used for the Shannon index, whereas a spherical approximation was used for the other variables in the *vgm* function. The kriging approximations were subsequently calculated using the *krige* function (gstat package), with the variogram fit serving as the model input.

3.5.3. Multivariate regression analysis (MRA)

MRA was calculated to test the significance of temporal (year), spatial (MEMs), and environmental (seafloor depth, sediment class, bottom water temperature, salinity and current velocity, Greenland halibut, standardized CPUE, and chl *a*) factors. The MRA allowed variance partitioning of potential predictors of northern shrimp distribution

to determine the significance (p value) and importance (explained variance) of tested variables and account for spatial scale using MEMs. MEMs extract different directional spatial configurations (e.g., MEM1 follows a North-South direction) as separate covariates that were included in regression analyses together with other potential predictors (Blanchet et al., 2008; Dray et al., 2012). MEMs were created to identify spatial scales that significantly explain shrimp density variations (i.e. spatial predictors). The MEMs are based on a connectivity matrix calculated from the shrimp density (survey) data and their spatial position along a cartesian coordinate system. First, a distance matrix between all survey stations was calculated using the *dist* function (stats package; R Core Team, 2021). Secondly, a minimal spanning tree was calculated using the *mstree* function (spdep package; Pebesma and Bivand, 2023), which was then used to calculate a broad-scale connectivity matrix from 0 to 48 km distance using the *dnearneigh* function (spdep package). Spatial weights for the connectivity matrix were added using the *nb2listw* function (spdep package). The matrix was then used to calculate MEMs (*mem* function) and the associated eigenvalues (*attr* function) (adespatial package; Dray et al., 2023). Only MEMs with positive eigenvalues (positive spatial correlations) and significant contributions to *moran's I* test (*moran.randtest* function with 999 permutations) were kept for further analyses. The remaining MEMs were further reduced to MEMs that contribute significantly to explaining the variation in shrimp densities using a redundancy analysis (*RDA* function) and automated forward selection (*forward.sel* function with 9999 permutations). MRA with variance partitioning was done using the *lm* function. The significant MEMs (i.e. MEM1, MEM2, and MEM5) were included as spatial predictors in the full multivariate regression model, together with year as temporal scale, year:MEMs as spatiotemporal interaction, and other potential environmental predictors, i.e. bottom water temperature, salinity and current velocity, seafloor depth (total depth), sediment class, chl *a*, Greenland halibut, and standardized CPUE (Table 2). These factors were applied to the transformed shrimp density data. Only two sediment classes, i.e. mixed and muddy sediments were included in the modelling; rocky sediments were excluded as rocky areas were not sampled for northern shrimp and Greenland halibut, thus the final model cannot be validated with in situ survey stations. Benthic diversity (i.e. taxon richness, Shannon index) and bottom water salinity from the GN monitoring (see Table 1) were not included in the analysis due to insufficient number of sampling stations in the area. The full multivariate regression model is defined as:

$$
\begin{aligned}
\text{model} = \text{lm}(\text{density} &\sim \text{year} + \text{depth} + \text{sediment} + \text{chl a} + \text{temp} \\
&+ \text{salinity} + \text{botCurrvel} + \text{sCPUE} + \text{halibut} + \text{MEM1} \\
&+ \text{MEM2} + \text{MEM5}) + \text{year} : \text{MEM1} + \text{year} : \text{MEM2} + \text{year} : \text{MEM5}
\end{aligned}
$$

In addition to this, full MRA with time lags of t-1 year, t-2 years, and t-3 years were computed for chl *a*, standardized CPUE, and Greenland halibut data (see Table A2) to test lagged environmental effects.

Subsequently, the full MRA without time lags was optimized by minimizing the Akaike information criterion (AIC) in a stepwise algorithm using the *step* function (stats package) (Table 2). The optimized model is defined as:

$$
\begin{aligned}
\text{model} = \text{lm}(\text{density} &\sim \text{depth} + \text{sediment} + \text{salinity} + \text{botCurrvel} + \text{year} \\
&: \text{MEM1} + \text{year} : \text{MEM5})
\end{aligned}
$$

3.5.4. Spatial linear mixed-effect model (spaMM)

SpaMM was used to generate a high-resolution spatial distribution model and describe northern shrimp habitat. SpaMM fits a non-directional variance-covariance matrix of the spatial observations (Dormann et al., 2007), which makes it more suitable for predictive modelling than the MRA. Shrimp density data were fitted to the statistically significant predictors identified via the optimized MRA (in Table 2). The spaMM was fitted using *fitme* function of the spaMM package and the machine learning method. Due to the non-normal

distribution of shrimp density and seafloor depth data a Gamm(loglink) distribution was used, which also resulted in the best model fit (i.e. lowest AIC). The optimized spaMM was employed to predict northern shrimp densities by utilizing high-resolution maps of the statistically significant predictors.

4. Results

4.1. Statistical predictors

While no statistically significant temporal autocorrelation, autoregression, or trend over time have been found, the Moran's I test shows a significant spatial autocorrelation (Fig. A3). Variogram modelling indicates that the semivariance of northern shrimp densities increases up to a distance of 0.3° latitude/longitude, suggesting a spatial autocorrelation up to approx. 33 km (Fig. A2). Analysis of Moran's Eigenvector Maps (MEMs) show that various directional gradients (MEM1, MEM2, MEM5) contribute to shrimp distribution, with the strongest spatial predictor following a North-South direction (MEM1) across Disko Bay (Table 2). MEMs in the full multivariate regression analysis (MRA) explain 10 % of the total variation in northern shrimp density when interacting with the year (i.e. year:MEMs; Table 2). In particular, the interaction year:MEM1 explains 9 % of the variation in full model and is also retained in the optimized model (Table 2). Year alone is significant only in the full model, explaining 15 % of the variation in northern shrimp density (Table 2). However, the variogram-based kriging interpolations reveal broad spatial patterns in shrimp densities that do not align well with the estimated survey data, or the bathymetry and sediment distribution in the area (see Fig. 4).

Of all the potential predictors used in multivariate regression model (see Table 2), only seafloor depth and sediment class have significant ($p < 0.05$) relationship with shrimp density in both, the full and optimized MRA. The most important variable is seafloor depth (23 % variation explained), followed by sediment class (13 % variation explained). Shrimp densities are lower in muddy sediments and deeper waters (negative estimate values in Table 2). While bottom water salinity and current velocity each explained 1 % of variation in shrimp density in the full and in the optimized model, these effects were not statistically significant ($p > 0.05$; Table 2). Moreover, chlorophyll *a* (chl *a*), Greenland halibut, and bottom water temperature appear unrelated to shrimp density in the full model (0 % variation explained). Standardized CPUE, Greenland halibut, and chl *a*, remained non-significant factors in full MRA, even with time lags of one to two years (Table A2). The final optimized MRA includes seafloor depth, sediment class, bottom water salinity, bottom current velocity, and the interactions year:MEM1 and year:MEM5 (Table 2).

For developing the spaMM for northern shrimp habitat suitability in Disko Bay, only the most significant predictors (p < 0.05), i.e. seafloor depth and sediment class were used. The spaMM demonstrates that shrimp density is higher in mixed sediments and medium-deep waters, i.e. between c. 150–350 m (see Fig. A4). The combined spaMM using high- and medium-resolution geospatial grids is presented in the discussion.

4.2. Northern shrimp and Greenland halibut

The distribution of northern shrimp in Disko Bay is described in relation to statistically significant environmental factors, i.e. seafloor depth and sediment class (Fig. 4). Estimated shrimp densities in the area range from 523 kg km^{-2} to 50,436 kg km^{-2}, with the highest densities (>13,551 kg km^{-2}) recorded in the northern and southern regions of Disko Bay (Fig. 4A). These areas of high density are predominantly characterized by mixed sediments and seafloor depths less than c. 300–350 m (Figs. 4). In contrast, lower densities (<3787 kg km^{-2}) were observed in central and south-western Disko Bay. Low shrimp densities were found across all depth strata, but mainly in seafloor depths >400 m
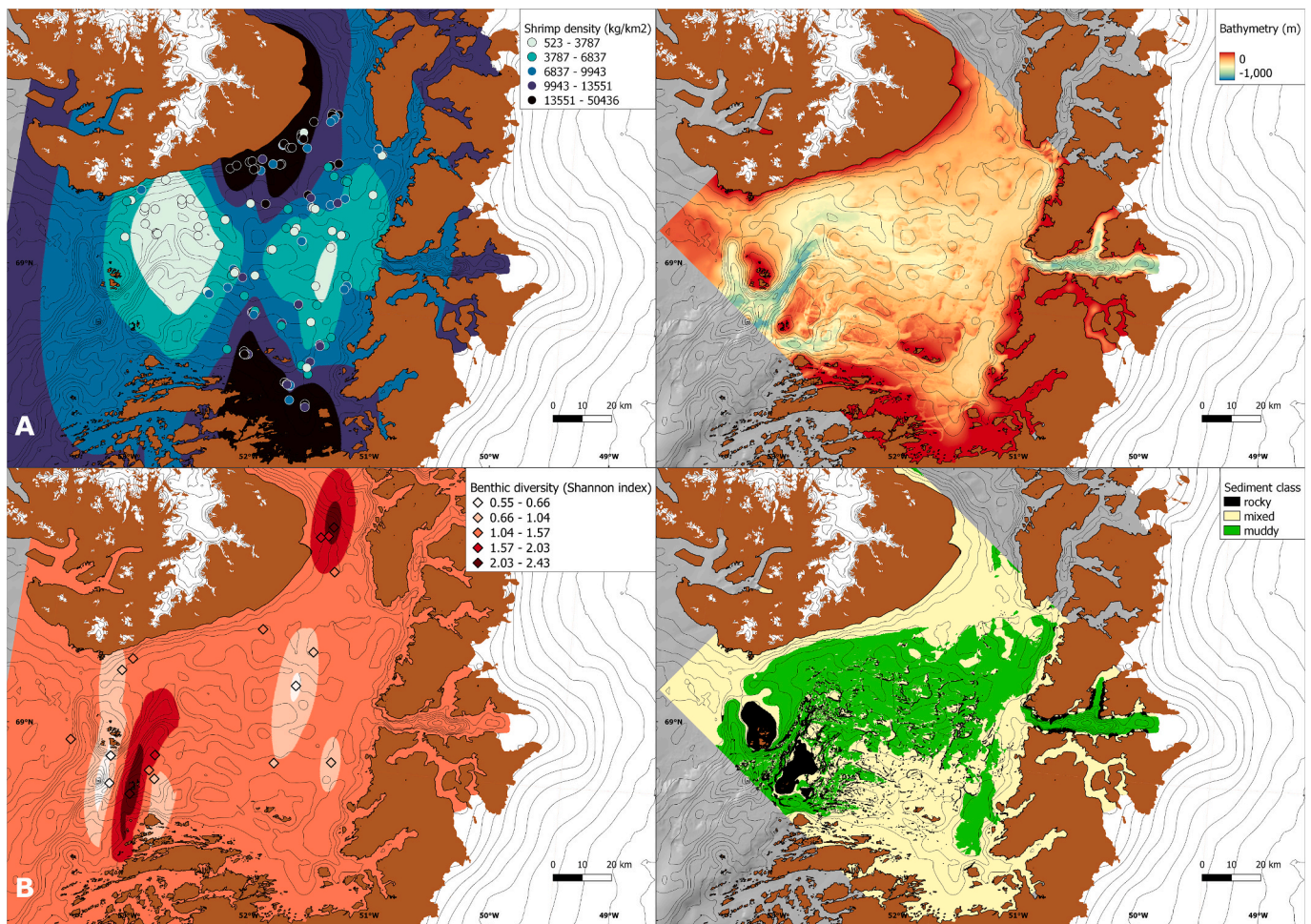
Fig. 4. Maps showing (A) estimated northern shrimp density (circle symbol; period: 2010–2019) superimposed on the interpolated survey data and (B) estimated benthic diversity, i.e. Shannon index (diamond symbol; period: 2015–2017; data in Table A1) superimposed on the interpolated survey benthic data. Interpolations were done using kriging technique (see Fig. A2). Combined bathymetry and sediment maps are displayed to the right, for reference (source maps in Figs. 1 and 3). CRS: 3413.

and in muddy sediments (Figs. 4). Greenland halibut densities show no significant correlation with northern shrimp density (see Table 2).

4.3. Benthic diversity

The highest benthic diversity (taxon richness >29, Shannon index >1.6; Fig. 4B) was observed in shallow and medium-deep areas (<300 m seafloor depth) and in mixed sediments found in the northern and south-western regions of Disko Bay (Fig. 4 and Table A1). On the other hand, lower benthic diversity (taxon richness <29, Shannon index <1.6) was observed in seafloor depths ranging from c. 200 to 900 m, primarily within deep channels and muddy waters of central Disko Bay (Fig. 4 and Table A1). Throughout the area, benthic communities were predominantly composed of various broad taxonomic groups, i.e. (in descending order of importance) crustaceans (Malacostraca), mostly represented by snow crab (*Chionocetes opilio*) and northern shrimp (*Pandalus borealis*); sea stars (Asteroidea), sponges (Porifera), sea squirts (Ascidiacea), anemones (Anthozoa), and tube worms (Annelida) dominated by the species *Spiochaetopterus* sp. In general, sponge- and sea squirt-dominated communities showed relatively high diversity (Shannon index >1.6 for sponges and > 1.4 for sea squirts), whereas anemone-dominated communities displayed low diversity (Shannon index <0.6). The remaining community types demonstrated mixed diversity patterns (Table A1).

5. Discussion

In this study, we utilized a range of datasets (detailed in Table 1) to develop a habitat suitability model for northern shrimp in Disko Bay. This model considers spatial and temporal variability, autocorrelation, and factors related to the physical environment, biological components, and anthropogenic influences.

5.1. Spatial variability

Spatial variability is an important factor in statistical analyses for species distribution models, although it often remains inadequately addressed (Cao et al., 2017). Our study demonstrates strong spatial autocorrelations observed in northern shrimp densities across Disko Bay, extending up to approx. 33 km, particularly evident along the latitudinal axis (i.e. North-South orientation; MEM1 in Table 2). Notably, the southern region of Disko Bay exhibits high topographic complexity, characterized by large gradients in seafloor depth and sediment composition (Fig. 4) (Krawczyk et al., 2022). Furthermore, simple spatial maps of northern shrimp density and benthic diversity (Shannon index) using kriging interpolation reveal broad-scale patterns; however, they fall short of capturing the variability at smaller scales (Fig. 4). Hence, we suggest that additional environmental predictors (which show high gradients at finer spatial scales) are necessary for high-resolution habitat modelling. Indeed, our full multivariate regression

model highlights that seafloor depth and sediment class exert significantly more influence on northern shrimp distribution than the spatial autocorrelation (MEMs; Table 2).

5.2. Optimal shrimp habitat

The distribution pattern of northern shrimp in Disko Bay is primarily associated with static habitat factors, namely sediment class and seafloor depth (Table 2). The optimal shrimp habitat within our study region is characterized by mixed sediments in medium-deep waters (c. 150–350 m) (Fig. 4). These favorable seafloor conditions were predominantly found in the northern and southern regions of Disko Bay, where we recorded maximum shrimp densities (both modelled and estimated) exceeding 10,000 kg km^{-2} (Fig. 5). Additionally, our model predicts a potentially high-density shrimp habitat in the non-surveyed area located in the north-western part of (offshore) Disko Bay (Fig. 5). It should be noted that our (shrimp) survey samples were collected from depths >150 m. This implies that in our model, the northern shrimp density will generally decrease beyond the depth of 150 m, although this may not apply to shallower areas (<150 m), i.e. the non-surveyed peripheral regions, along with rocky banks and the coastal zone (marked as the excluded area in Fig. 5). Consequently, we were unable to validate the modelled shallow areas to determine whether the patterns of shrimp density are associated with specific combination of covariates.

The identified static habitat predictors likely represent an environment suitable for a combination and interaction of functional drivers, such as food availability, water temperature, and currents. For instance, coarser sediments (grain size >0.2 mm) in Disko Bay may indicate stronger local current activity and the deposition of ice-rafted debris (e. g. Perner et al., 2013). However, our study did not find a significant effect of bottom water temperature, salinity, current velocity, surface chlorophyll *a* (food source), or Greenland halibut (predator) on northern shrimp density (Table 2). This lack of significance could be due to the absence of accurate seasonal measurements and data caused by the seasonal sea ice cover in Disko Bay, coupled with the limited spatial range. In the West Greenland region, northern shrimp are typically found in waters ranging from 1 to 6 °C (Buch et al., 2005), a temperature range consistent with the bottom water temperature measured in our surveys (see Fig. 2C). This suggests that our temperature data may not have shown enough variation to significantly impact shrimp distribution. While northern shrimp generally thrive in a broad temperature range (from below 0 to 10–12 °C) (Shumway et al., 1985), local stocks are assumed to be adapted to narrower temperature ranges (Jorde et al., 2015). Interestingly, despite the weak significance, bottom water salinity and current velocity did show some effect on shrimp density (Table 2). Our findings suggest that northern shrimp may prefer a less saline environment with higher current velocity, likely corresponding to more turbulent water conditions in Disko Bay. This preference is not directly linked to the saline Atlantic water mass properties (see details in chapter 2.2). Therefore, the northern shrimp habitat in Disko Bay seems to correspond to relatively deep waters with turbulent oceanic conditions, set within a complex topographic setting characterized by mixed sediments (Fig. 4). These conditions likely support water column mixing above the seafloor and facilitate the seasonal transport of organic-rich (phytoplankton) surface water towards the seafloor (cf. White et al., 2005). Northern shrimp primarily feed on phytoplankton, small zooplankton, benthic prey, such as polychaetes, nematodes, foraminiferans, molluscans, and echinoderms, as well as detritus. However, our study did not find a significant relationship between remotely sensed surface chl *a* and shrimp density. This lack of correlation may be due to the seasonal variability in phytoplankton export to deeper waters; surface chl *a* typically corresponds to spring-summer phytoplankton blooms when water column is stratified (see chapter 2.2), possibly limiting pelagic-benthic coupling. Furthermore, satellites do not detect sub-surface phytoplankton blooms, which could potentially occur in this area. Other food sources for northern shrimp, such as small benthic

epifauna and zooplankton, were not sampled in this study. Further studies aiming for a more accurate representation of food availability for northern shrimp in Disko Bay should include the quantification of all potential food sources. Northern shrimp, in turn, serves as prey for various fish species (Hopkins et al., 1993; Wieland et al., 2007), with Greenland halibut considered one of their primary predators in West Greenland (Wieland et al., 2007; Wieland and Siegstad, 2012). The presence and abundance of predatory fish can influence the distribution of shrimp populations, as shrimp may avoid areas with high predation pressure to minimize the risk of predation. This can lead to spatial patterns in shrimp distribution, with higher densities in areas with lower predation risk. Unsurprisingly, low northern shrimp densities are observed in deep waters of Disko Bay, where Greenland halibut is more abundant (>2000 kg km^{-2} at depths >300 m; Table A1). The lack of seasonal variability in the distribution and migrations of Greenland halibut, similar to other dynamic habitat factors mentioned earlier, results in no statistically significant effect on shrimp densities in this study.

The optimal habitat for northern shrimp in the northern Disko Bay exhibits a notably high benthic diversity, as indicated by the Shannon index (Fig. 5B). The prevalence of northern shrimp in the epifaunal biomass at several stations (Table A1) underscores the significance of this species in the northern Disko Bay, aligning with both model predictions and estimated data (Fig. 5). This observation suggests that the presence of mixed sediments in turbulent medium-deep waters supports diverse benthic communities characterized by a high density of shrimp. Moreover, the high benthic diversity likely promotes a complex food web (e.g. Sokołowski et al., 2012), providing a rich diet for opportunistic feeding behavior of northern shrimp (it's worth noting that epifauna smaller than 10 mm were not sampled by beam trawl). The overall high benthic diversity in northern Disko Bay may be linked to the high biomass of habitat-forming sponges found in this area (Fig. 5B). Ecosystems dominated by sponges in the deep-sea environments typically support high biodiversity, biomass, and carbon turnover due to their role in providing habitat for a wide array of associated species (Klitgaard and Tendal, 2004; Kutti et al., 2013; Blicher and Hammeken Arboe, 2021).

5.2.1. Sediment association

In Disko Bay, areas with high modelled shrimp density are distributed across various morphological structures and geological units, including Cretaceous sandstone to the north, Precambrian Gneiss to the south, and Paleogene basalts to the west (Krawczyk et al., 2022). Thus, it seems that topographic complexity and sediment origin may have less influence on predicting shrimp distribution in the area, with sediment hardness and diversity as more significant predictors (Fig. 3).

The association of northern shrimp with mixed sediments in Disko Bay, despite their typical occurrence in medium-deep waters on the broader West Greenland shelf (Buch et al., 2005; Burmeister and Buch, 2023a), presents a surprising finding. A previous study on benthic habitat mapping in Disko Bay suggested that northern shrimp, along with tube worms, were dominant in muddy sediments (Krawczyk et al., 2021). However, the previous study was conducted on a smaller scale (approx. 30 × 20 km) and lacked trawl data. In contrast to our results, studies in other North Atlantic regions, such as the Gulf of Maine, indicated that northern shrimp are primarily found in fine-grained sediments at intermediate depths (<300 m), likely due to increased availability of soft-bottom benthic invertebrates (Cao et al., 2017). In northern Norway, shrimp are commonly associated with soft, muddy substrates with high organic content (Shumway et al., 1985; Zimmermann et al., 2019). Similarly, pink shrimp in the Gulf of Mexico prefer sandy substrate (Pickens et al., 2021), while brown shrimp favor mud and silty sediments (Montero et al., 2016). Japanese mantis shrimp also show a preference for sediments with a high silt and clay content (Li et al., 2020). These divergent findings may stem from the substrate annotations specific to each study, which are often gears-specific, and the limited coverage of the ground-truth station, making direct
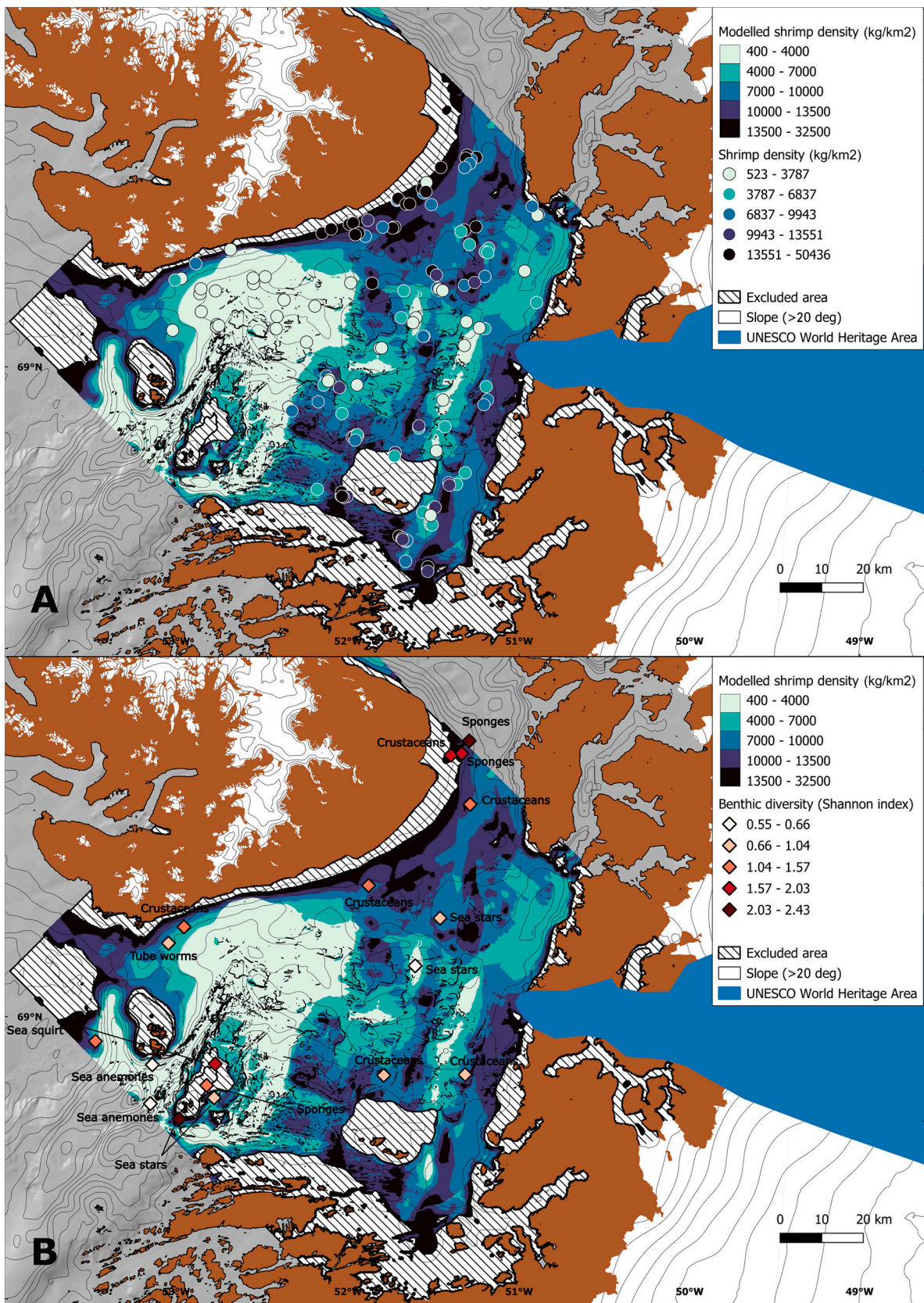
Fig. 5. High-resolution habitat suitability model for northern shrimp with (A) survey stations showing estimated northern shrimp density (circle symbol) and (B) survey stations showing benthic diversity, i.e. Shannon index (diamond symbol; data in Table A1). The benthic community type is labeled for each station. Hatched area (excluded from the model) consists of coastal zone (<150 m seafloor depth) and rocky banks surrounding islands. Steep slopes (>20°) are also marked. CRS: 3413.

comparisons across different studies and areas challenging. Typically, grab samples enable detailed grain-size analysis, whereas benthic camera footage provides more general information with a limited ability to distinguish sediment classes within the mixed sediment range (e.g. sand from mud). A reliable approach to validate these sampling procedures involves collecting multibeam backscatter data, which represent seafloor reflectivity and allow for seafloor characterization on a continuous spatial scale (e.g. Kostylev et al., 2001; Krawczyk et al., 2021).

5.3. Less favorable habitat

The less suitable habitat for northern shrimp in Disko Bay is characterized by muddy sediments in deep waters (>350 m) (Fig. 4). One plausible explanation for such an unfavorable habitat is the limited supply of food to the deeper muddy waters, where reduced water turbulence hampers nutrient transport. The greater seafloor depths result in fewer phytoplankton and other essential food sources reaching the bottom due to grazing and/or microbial degradation in the water column during sinking (e.g. Lee et al., 2004). Additionally, the deep waters of Disko Bay pose a higher predation risk by Greenland halibut (as discussed earlier). We observed low modelled shrimp densities (<7000 kg km^{-2}) in the deep channels of the south-western part of Disko Bay, and central plains (Fig. 5). These areas typically host low-diversity (Shannon index) epibenthic communities, primarily composed of sea anemones (Fig. 5B). It is worth noting that the beam trawl used for collecting benthic taxa samples is designed to sample only epibenthic animals, not infauna, thus our conclusions are limited to epibenthic diversity. Nevertheless, the muddy areas of Disko Bay are known to support a rich diversity of infauna species (Boertmann and Mosbech, 2021).

5.4. Arctic environment – limitations

Our survey and fishery data (see Table 1) are limited to the summer seasons, due to the winter sea ice cover in Disko Bay. This constraint allows for detecting interannual changes but does not capture shifts in seasonal patterns. The small-scale spatial and temporal dynamics in oceanographic and biological drivers may have limited their statistical significance and predictive power in our models (Table 2), thereby limiting our understanding of the seasonal variability in northern shrimp distribution within Disko Bay (refer to chapter 5.2). Additionally, modelled parameters, such as bottom water salinity, current velocity, and satellite chl *a* data would benefit from higher spatial resolution beyond several kilometers, as well as improved temporal resolution, to better illustrate their impacts on northern shrimp density in the area. However, it is noteworthy that we observed a strong correlation between bottom water temperature and salinity in our in-situ monitoring data across the entire Disko Bay (R^2 = 0.89; Fig. A1), indicating that higher resolution of salinity data may not significantly alter the modelling outcomes.

Changes in water masses across seasons and years can significantly influence the distribution of northern shrimp, attributed to larval dispersal via ocean currents (Corre et al., 2020) and the advection of food sources. Water circulation patterns in the area may disperse phytoplankton in various directions, expanding its coverage over a larger area. Furthermore, the distribution of motile demersal fauna, such as northern shrimp and Greenland halibut, is influenced by seasonal migrations during different life stages (Storm and Pedersen, 2003; Li et al., 2020; Nygaard, 2023). However, this study did not evaluate the specific characteristics of the life cycle of northern shrimp. The impact of both food availability and predation by Greenland halibut is likely to be limited on adult shrimp densities in the same year but may have a more substantial effect on their reproductive output, larval survival, and, subsequent recruitment success in the following year(s) (e.g. Wieland et al., 2007; Corre et al., 2020; Nygaard, 2023). While our analysis did not reveal a significant correlation between chl *a*, predation, and

northern shrimp densities at a time lag up to 3 years (Table A2), longer time series data may reveal a significant relationship.

Disko Bay has been a target for commercial fishing by coastal vessels, with an estimated overall exploitation rate of approximately 20–30 % (Burmeister and Riget, 2022; Burmeister and Buch, 2023b). Fishing activities in Disko Bay and offshore areas north of 66° latitude along the West Greenland coast are typically constrained by sea ice cover and heavy drift ice from February to April (Burmeister and Buch, 2023b). Over the recent decade, there has been a relatively consistent distribution of northern shrimp catches in West Greenland, regardless of the fishing season (Burmeister and Buch, 2023b). However, the decline and subsequent increase in abundance of northern shrimp stocks in the West Greenland region over the past two decades (Burmeister and Buch, 2023a) may be related to historical and present-day fishing activities. While our shrimp distribution model for Disko Bay is based on data from 2010 to 2019 (Fig. 5), past and ongoing fishing practices could have influenced the observed distribution. Similar to food and predation proxies, the impact of shrimp fishery effort on northern shrimp density is likely to be more significant with a longer time lag than the tested 3 years (Table A2). A more accurate habitat suitability model for northern shrimp could be derived from an area that remains unexploited. Ideally, integrating fisher's knowledge with rigorous scientific methodologies and predictive modelling will lead to a more comprehensive understanding of shrimp habitats.

Considering our findings and the discussed limitations, the most accurate maps predicting species distribution can be derived from high-resolution, temporally stable habitat characteristics, such as seafloor depth and sediment class. Although we did not find temporal autocorrelation, interannual variability does influence shrimp densities in our study (as seen in the year variable in the full model; Table 2). Hence, caution is necessary when generating predictive distribution maps of northern shrimp in the Arctic region.

6. Conclusions

Various physical, biological, and anthropogenic factors were examined to characterize the environment of northern shrimp in Disko Bay and generate a predictive model of their distribution. Spatial interpolations alone represented broad-scale patterns but failed to capture small-scale variability due to the strong environmental gradients in the area. Among these factors, sediment class and seafloor depth emerged as the strongest predictors, representing static habitat factors, that likely interlink with other dynamic and temporal factors. The association of sediment class with northern shrimp density has received limited documentation in the Greenland shelf area, which suggests that our study may offer valuable insights in this aspect.

Our study presents the first high-resolution habitat suitability model for northern shrimp in the Arctic, revealing that optimal shrimp habitat features mixed sediments in medium-deep turbulent water and is associated with a high epibenthic diversity. The main challenge in high-resolution modelling was the spatiotemporal variability in environmental factors, constrained by the seasonal sea ice cover and sampling limitations in the Arctic region.

This study underlines the importance of collecting high-quality and high-resolution seafloor measurements using multibeam systems for generating accurate habitat maps of northern shrimp and other benthic species. This is especially relevant for commercially fished species, such as northern shrimp, which are a key export product in Greenland. Furthermore, we recommend testing the species distribution models in unexploited areas, where shrimp have not been commercially fished, to provide reliable habitat suitability maps.

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CRediT authorship contribution statement

D.W. Krawczyk: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **T. Vonnahme:** Validation, Methodology, Formal analysis. **A.D. Burmeister:** Validation, Methodology, Data curation. **S.R. Maier:** Validation, Methodology, Data curation. **M.E. Blicher:** Validation, Data curation. **L. Meire:** Validation, Data curation. **R. Nygaard:** Validation, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability Northern shrimp data are subject to the annual stock assessments and used directly in the advice to the Government of Greenland; these data can only be used with the permission of the researchers from the Grønlands Naturinstitut (contact GN: info@natur.gl, and/or the authors). Shrimp fishery catch data are the property of Greenland Fisheries License Control Authority (GFLK) and due to client protection, this sub-set of data is confidential. All other survey data, measurements, modelled and satellite data used in this study are provided in Table A1. Geospatial grids are available as published material (Hogan and Ó Cofaigh, 2019; Jakobsson et al., 2020; Krawczyk et al., 2022) and in public repositories, i.e. PANGAEA (https://doi.pangaea.de/10.1594/PANGAEA.935642) and IBCAO (https://www.gebco.net/data_and_products/gridded_bathymetry_data/arctic_ocean/). The R scripts for all statistical analyses are available in github under Tobivnnhm/Disko-Bay-shrimp-modelling-GIT (github.com).

Northern shrimp data are subject to the annual stock assessments and used directly in the advice to the Government of Greenland; these data can only be used with the permission of the researchers from the Grønlands Naturinstitut (contact GN: info@natur.gl, and/or the authors). Shrimp fishery catch data are the property of Greenland Fisheries License Control Authority (GFLK) and due to client protection, this sub-set of data is confidential. All other survey data, measurements, modelled and satellite data used in this study are provided in Table A1. Geospatial grids are available as published material (Hogan and Ó Cofaigh, 2019; Jakobsson et al., 2020; Krawczyk et al., 2022) and in public repositories, i.e. PANGAEA (https://doi.pangaea.de/10.1594/PANGAEA.935642) and IBCAO (https://www.gebco.net/data_and_products/gridded_bathymetry_data/arctic_ocean/). The R scripts for all statistical analyses are available in github under Tobivnnhm/Disko-Bay-shrimp-modelling-GIT (github.com).

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