



Functional Pattern of Benthic Epifauna in the Chukchi Borderland, Arctic Deep Sea

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Assessment of Arctic deep-sea ecosystem functioning is currently an urgent task considering that ongoing sea-ice reduction opens opportunities for resource exploitation of yet understudied deep-sea regions. We used Biological Trait Analysis to evaluate ecosystem functioning and test if common paradigms for deep-sea fauna apply to benthic epifauna of the deep-sea Arctic Chukchi Borderland (CBL). We also investigated the influence of environmental factors on the functional structure of the epifauna. The analysis was performed for 106 taxa collected with a beam trawl and a Remotely Operated Vehicle from 486 to 2610 m depth. The most common trait modalities were small-medium size, mobile, benthic direct and lecithotrophic larval development, and predatory feeding, which mostly supports the current view of epifauna in the global deep sea. Functional composition of epifauna differed between two depth strata (486–1059 m and 1882–2610 m), with depth and sediment carbon content explaining most of the functional variability. Proportional abundances of the modalities free-living, swimming, suspension feeders, opportunists/scavengers, internal fertilization and globulose were higher at deep stations. Functional redundancy (FR) was also higher there compared to the mid-depth stations, suggesting adaptation of fauna to the more homogeneous deep environment by fewer and shared traits. Mid-depth stations represented higher functional variability in terms of both trait modality composition and functional diversity, indicating more variable resource use in the more heterogeneous habitat. Food input correlated positively with the proportional abundance of the modalities tube-dwelling, sessile and deposit feeding. Areas with drop stones were associated with higher proportional abundance of the modalities attached, upright, and predators. Comparatively low FR may render the heterogeneous mid-depth area of the CBL vulnerable to disturbance through the risk of loss of functions. Across the study area, high occurrence of taxa with low dispersal ability among adult and larval life stages may prevent rapid adaptation to changes, reduce ability to recolonize and escape perturbation.

Keywords: Arctic deep sea, benthic epifauna, biological trait analysis, functional composition, ROV

Abbreviations: CBL, Chukchi Borderland; FD, functional diversity; FR, functional redundancy.

INTRODUCTION

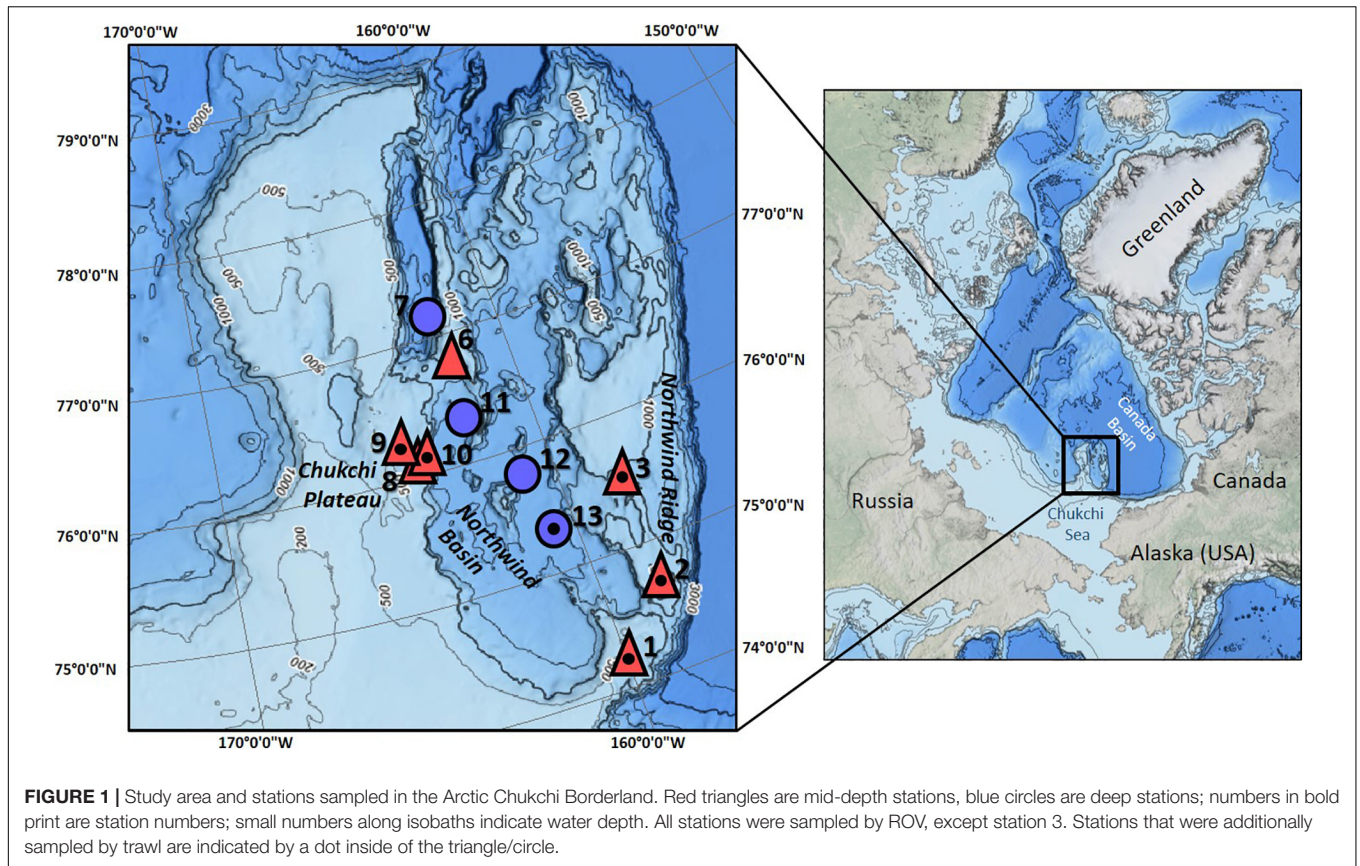
The deep ocean floor covers around 65% of the surface of the earth, yet it is the least explored ocean habitat. While we have begun to identify trends in deep-sea biodiversity patterns such as mid-depth peaks and latitudinal declines in diversity, and a generally higher level of rarity and endemism compared to shelf communities (Levin et al., 2001; Stuart et al., 2003; Renaud et al., 2006; Rex and Etter, 2010; Bluhm et al., 2011), still little is known about functional characteristics of deep-sea ecosystems. This is a serious gap, because deep-sea regions experience increasing anthropogenic influences (e.g., deep-sea fisheries, oil and gas exploration, mining, marine debris), and are at the same time subjected to the influences of climate change, in particular in polar regions (Smith et al., 2008; Ramirez-Llodra et al., 2011; Levin and Le Bris, 2015; Tekman et al., 2017). These impacts may bring changes in environmental properties, biodiversity and functioning of deep-sea ecosystems (Danovaro et al., 2008; Levin and Le Bris, 2015; Sweetman et al., 2017). Understanding of the current state of deep-sea ecosystem functioning and assessing its potential vulnerability to human impact and climatic changes is, thus, essential.

In contrast to shallower marine ecosystems, the deep sea is generally thought to be a more stable environment with constantly low bottom water temperature (typically, 0.01–4°C, but down to sub-zero values in the Arctic), high pressure, and low current velocity and resuspension (e.g., Gage and Tyler, 1991; Thistle, 2003; Tyler, 2003; Sweetman et al., 2017). More than 75% of the sea floor is covered by visually homogeneous abyssal plains, interrupted by geological structures such as ridges, canyons, hydrothermal vents, and cold seeps that add substantial heterogeneity to the habitat, biota and processes (Ramirez-Llodra et al., 2010; Levin and Le Bris, 2015). Deep-sea benthic communities are driven to a large extent by the amount of energy provided to the system from surface production (Iken et al., 2001, 2005). Only ~0.5–2% of the surface production typically reaches the deep-sea floor and by that time is dominated by heavily reworked detrital organic material (Fischer et al., 2000; Ramirez-Llodra et al., 2010). Food limitation is particularly extreme in the central Arctic basins where the high latitude and seasonal or permanent sea ice control light penetration into the upper water column, and stratification limits the availability of nutrients during the short productive seasons (Leu et al., 2015; Randelhoff and Guthrie, 2016). Consequently, primary production in the oligotrophic Arctic basins is low (typically 1–15 g C m⁻² year⁻¹) with low levels of vertical flux of generally ≤1 g C m⁻² year⁻¹ below 120 m depth, and often less than half of that reaching the deep-sea floor (Wiedmann et al., 2020). These levels are considerably lower than other deep-sea areas, where pelagic primary production is highly variable, but often exceeds 20–50 g C m⁻² year⁻¹ (Karl et al., 1996; Levin and Gooday, 2003; Emerson, 2014).

Environmental conditions shape the biological characteristics of deep-sea benthic communities. Early studies suggested that benthic “associations governed by constantly limited food availability are composed of small individuals on the average” (size-structure hypothesis, Thiel, 1975). Indeed, recent studies

confirmed that organisms of comparatively smaller size dominate at greater depth (Rex et al., 2006; Wei et al., 2010), though organisms of all sizes can inhabit the benthic environment in the deep sea (e.g., Billett et al., 2001; Ruhl and Smith, 2004; Bluhm et al., 2011; Rybakova et al., 2019). Low food availability and quality on the deep-sea seafloor, and low ambient current velocity are typically reflected in high proportions of deposit-feeding fauna (Iken et al., 2001, 2005; Bergmann et al., 2009). While suspension feeders, predators and scavengers are also represented in the deep sea (e.g., Premke et al., 2006; Cartes et al., 2008; Bergmann et al., 2009; Zhulay et al., 2019), suspension feeders tend to be less frequent due to the generally low currents and thus low amount of suspended material (Thistle, 2003), and low frequency of predators likely is due to low densities of prey (e.g., Thistle, 2003; Bluhm et al., 2011). In addition, scarce food may result in a dominance of mobile taxa that are more efficient in finding food (Iken et al., 2001; Thistle, 2003; Boetius et al., 2013) than sessile taxa that can only be supported in regions with enough particle flux and stronger currents (Degen, 2015). Both pioneering and recent studies suggested that deep-sea benthic fauna present a rich assortment of reproductive modes and life-history traits, including direct development, brooding, lecithotrophic, and planktotrophic larvae (Mosely, 1880; Thorson, 1950; Pearse and Lockhart, 2004; Arellano and Young, 2009; Bennett et al., 2012; Berecovechea et al., 2017; Martinez and Penchaszadeh, 2017; Lauretta et al., 2020; Rivadeneira et al., 2020).

In summary, based on the current literature, the general view of the typical deep-sea fauna is one of taxa of small size, non-sessile, often deposit feeding and developing either directly or indirectly. These and other biological characteristics of species, also referred to as traits (Bremner et al., 2005), can be used to assess ecosystem functioning, that is the maintenance and regulation of ecosystem processes (Naeem et al., 1999), including organism-environment interaction (Bremner et al., 2006; Degen et al., 2018). Seafloor fauna are heavily involved in ecosystem processes such as consumption and transfer of organic matter to higher trophic levels, organic matter decomposition, nutrient renewal, productivity and habitat provision (e.g., Danovaro et al., 2008; Loreau, 2008; Thurber et al., 2014). These processes depend, directly or indirectly, on morphological, behavioral and life history traits that species exhibit in a community (Usseglio-Polatera et al., 2000; Bremner et al., 2003; Oug et al., 2012). Thus, an assessment of these traits can provide a deeper insight into functional structure and variation than is possible with a taxonomic description of a community alone (Bremner et al., 2003; Petchey and Gaston, 2006; van der Linden et al., 2012; Pomerleau et al., 2015). Biological trait analysis (BTA) (cf. Bremner et al., 2003) can assess functional characteristics of a given community as well as ecosystem vulnerability through metrics such as functional diversity (FD) (i.e., diversity of trait categories called modalities), and functional redundancy (FR) (i.e., a measure of the degree to which species exhibiting the same trait modalities (Bremner et al., 2003; Petchey and Gaston, 2006; van der Linden et al., 2012). Studies investigating Arctic ecosystem function using the BTA approach have advanced our understanding of functional structure of benthic communities



mostly on the shelves and for macrofauna (i.e., mostly infaunal taxa ≥ 0.5 or 1 mm) (Cochrane et al., 2012; Krumhansl et al., 2016; Kokarev et al., 2017; Rand et al., 2018), while few studies have so far focused on biological traits of epifaunal megafauna (i.e., invertebrates and demersal fish on top of the sediment and typically \geq ca. 5 mm) (Sutton et al., 2020) or deep ecosystems (Degen, 2015; Liu et al., 2019). Functional patterns have not been examined for epifaunal communities anywhere in the Arctic deep sea.

The goal of this study was, therefore, to characterize Arctic deep-sea epifauna using a biological traits approach in the Chukchi Borderland (CBL) in the Amerasian Arctic deep sea, an area of complex habitats created by plateau and ridge areas at mid-depths, surrounding or bordering deeper basins (Jakobsson et al., 2008). Specifically, the objectives of the present study were to: (1) identify dominant trait modalities represented in the epifauna of the study area; (2) describe variability in functional structure of epifaunal communities between mid-depth (plateau and ridge) and deeper (basin) areas; and (3) identify environmental factors influencing the functional structure of epifaunal communities in the study area. We tested the following hypotheses: (1) current deep-sea paradigms suggesting that deep-sea benthic communities are dominated by small-sized, non-sessile deposit-feeders or scavengers, with equal representation of direct and indirect development, hold true for the epifauna in the CBL; and (2) given that environmental conditions change with depth, there is a difference in functional

structure between mid-depth and deep communities. Specifically, we proposed that (a) trait-modality composition changes with depth strata; (b) the more heterogeneous mid-depth habitats provide higher diversity of niches reflected in higher FD, while the more homogeneous deep-basin stations are likely to have lower FD but higher FR; and (c) depth, food availability and food quality strongly influence distribution of trait modalities across the study area.

MATERIALS AND METHODS

Study Area and Field Sampling

The community composition data underlying this study were collected in the CBL, north of Alaska ($7\text{--}78^\circ\text{N}$, $158\text{--}165^\circ\text{W}$) onboard USCGC *Healy* in July–August 2016 (Figure 1). The CBL extends from the Chukchi shelf into the Canada Basin, covering a depth gradient from ~ 300 to 3000 m. It consists of the Northwind Ridge and Chukchi Plateau where stations were grouped as “mid-depth” (486–1059 m), and of the isolated Northwind Basin where stations were grouped as “deep” (1882–2610 m) (Figure 1 and Table 1; Jakobsson et al., 2008; Mayer et al., 2010). Waters of Arctic, Atlantic, and Pacific origins interact in the CBL study area with Pacific-origin water comprising the Polar Mixed Layer and upper halocline (McLaughlin et al., 2004; Steele et al., 2004; Woodgate, 2013). The lower halocline is of Atlantic origin, arriving from Fram Strait and the

TABLE 1 | Station information for ROV images and beam trawl samples collected in the Arctic Chukchi Borderland.

Stations group/ station number	Depth, m	Latitude, °N	Longitude, °W	Temperature, °C	Bottom salinity, PSU	Mean sediment Phaeo, µg pigment/g dry sediment	Mean sediment Chl, µg pigment/g dry sediment	Sediment organic carbon, %	Mean C/N ratio	Mud, %	Gear	Number of images analyzed	
Mid-depth*	6	486	77.06	-161.82	0.70	34.84	0.15	0.02	0.63	3.90	97	ROV	98
	9	508	76.59	-163.98	0.48	34.85	0.20	0.02	0.78	5.51	99	ROV, Trawl	180
	8	557	76.63	-164.06	0.41	34.86	0.19	0.02	0.98	6.52	99	ROV	39
	3	746	75.64	-158.82	0.28	34.86	0.09	0.01	0.81	6.92	96	Trawl	
	1	853	74.32	-159.42	0.07	34.87	0.77	0.10	1.26	7.98	93	ROV, Trawl	100
	10	873	76.43	-163.47	0.06	34.84	0.24	0.03	0.88	5.90	95	ROV, Trawl	69
Deep**	2	1059	74.71	-158.48	-0.05	34.88	0.30	0.04	1.14	8.11	96	ROV, Trawl	80
	11	1882	76.40	-162.26	-0.29	34.92	0.19	0.02	1.09	6.81	98	ROV	79
	13	2091	75.40	-160.73	-0.29	34.92	0.27	0.03	1.25	8.05	100	ROV, Trawl	80
	12	2107	75.93	-161.45	-0.28	34.92	0.19	0.02	1.13	7.15	99	ROV	80
	7	2610	77.07	-162.53	-0.30	34.93	0.12	0.01	0.77	4.85	98	ROV	99

Stations are listed by increasing depth. Note the low number of images for station 8 was due to limited bottom time. The high number of images for station 9 is due to two stations (9a and 9b) being combined.

*Mid-depth stations are within the Atlantic Water layer (salinity 33.5–34.9 PSU) and range in depth between 486 and 1059 m.

**Deep stations are within Deep Water layer (salinity \geq 34.9 PSU) and range in depth between 1882 and 2610 m.

Barents Sea (Woodgate and Aagaard, 2005). Underneath it and characterizing the “mid-depth” stations is the Atlantic water layer (McLaughlin et al., 2004; Woodgate et al., 2007; Bluhm et al., 2015), while “deep” stations are in the Arctic Ocean deep-water layer originating from the Greenland Sea and spreading across the Eurasian Basin to the Canada Basin (Bluhm et al., 2015).

Epifauna (including invertebrates and demersal fishes) was sampled with the ROV Global Explorer (Oceanering International), which performed a photographic survey of the seafloor at ten stations (Table 1), as described in Zhulay et al. (2019). 24-megapixel still images were collected with a downward-looking DSSI DPC-8800 digital camera along transects every 5–8 s. Four digital laser pointers, one located at each corner of a fixed distance of a 10-cm square, served as a size reference for the imaged area and size of organisms at four stations (stations 1, 6, 7, and 8), after which they stopped functioning. In addition, epifauna was sampled with a single trawl sample at six stations (stations 1, 2, 3, 9, 10, and 13, Table 1) using a 3.05 m modified plumb staff beam trawl (Abookire and Rose, 2005) equipped with a 7 mm mesh net with 4 mm in the cod end. Ca. 30 min hauls at \sim 1.5 knots speed over ground were taken with bottom time estimated from a time depth recorder (Star Oddi) affixed to the net. Organisms were sorted, identified to the lowest possible taxonomic level, and counted. Select taxonomic vouchers were further identified by expert taxonomists (see section “Acknowledgments”) and taxon names were verified using WoRMS (<http://www.marinespecies.org/>, on September 10, 2020). The proportional abundance of each taxon was then calculated for each trawl station.

At each station, near-bottom water temperature and salinity were measured with a SBE9/11 + CTD at \sim 20 m above the bottom. Sediment surface samples (0–1 cm) from box core samples were taken and frozen at -20°C for later determination of grain size composition, carbon and nitrogen content, and concentration of sediment chlorophyll *a* and phaeopigments

(Zhulay et al., 2019). Sediment grain size was analyzed from samples pre-treated with HCl and H_2O_2 , to remove calcium carbonate and organic material, on a Beckman Coulter Particle Size Analyzer LS 13320 at the Geology Laboratory of UiT The Arctic University of Norway in Tromsø. Sediment organic carbon and nitrogen (%) were determined on a Costech ESC 4010 elemental analyzer at the stable isotope facility at the University of Alaska Fairbanks (UAF). The C/N ratio, an indicator of food quality with higher values indicating lower food quality (e.g., Dorgelo and Leonards, 2001; Iken et al., 2010), was then calculated for each station. Concentrations of sediment chlorophyll *a* and phaeopigments (μg pigment/g dry sediment) were measured on a Turner Designs TD-700 fluorometer after pigment extraction with 5 ml of 100% acetone for 24 h in the dark at -20°C at UAF. The fluorescence of the sample was read before and after acidification with HCl (final concentration of HCl was 0.003 N) for determination of phaeopigments (Arar and Collins, 1997; Jeffrey and Welschmeyer, 1997).

Image Analysis

A subset of the useable ROV images of the sea floor were manually analyzed from each station (39–180 per station, 940 images in total) (Table 1, Zhulay et al., 2019). Image processing and analyses were performed with the ImageJ¹ (Rasband, 2009). Taxa were identified to the lowest possible level based on a combination of morphological features visible on the ROV imagery, the voucher collection from trawls, and additional identifications by taxonomic experts (see acknowledgments). Taxa that could not be identify were excluded from this analysis due to difficulties related to assigning trait modalities to these organisms. All taxa present on the images were counted per image and proportional abundance of taxa per station was calculated. Rocks larger than two cm were counted and the average number

¹<https://imagej.nih.gov/ij/>

of rocks per picture was included in the statistical analyses as an environmental factor.

Biological Traits

Nine commonly used traits represented by a total of 39 modalities were chosen for the present analysis following established definitions by Bremner et al. (2006), Costello et al. (2015), Degen et al. (2018), and Sutton et al. (2020) (**Table 2**). The traits reflected morphology (adult size, body form), behavior (living habitat, mobility, adult movement, feeding habit, substrate affinity) and life-cycle characteristics (larval development and reproduction) (**Table 2**; reviewed by Martini et al., 2020a). For the purpose of this study, modalities of larval development trait were based on the published concept for Arctic traits analysis (Degen and Faulwetter, 2019) that assumes that planktotrophs disperse farther than lecithotrophs although many exceptions are known to occur in the deep sea (Young, 2003). Every trait was coded for every taxon identified based on: (1) observations made from trawl-collected material during the cruise and/or from ROV images (i.e., traits directly measured *in situ*, also referred as realized traits, c.f. Martini et al., 2020a) for size, body form, adult movement, living habit, and substrate affinity or (2) information inferred from published literature (referenced in **Supplementary Table 1**), online traits databases (e.g., polytraits, Faulwetter et al., 2014; the Arctic Traits Database, Degen and Faulwetter, 2019) and relevant web pages (e.g., FishBase², Sea Life Base³) (i.e., traits acquired from other sources, also referred as potential traits, c.f. Martini et al., 2020a) for the rest of the traits. The size of organisms was measured on board from specimens collected at each station in the trawl samples or from the ROV images with the ImageJ software (Rasband, 2009). Size measurements from ROV images were possible at the four stations where the digital laser pointers were functioning and where the positioning of a given organism was suitable for those measurements. The average adult size of a given species across all stations was used for the analysis. As information about biology and behavior of many epifaunal taxa in the Arctic deep sea remains limited or is at times non-existent at the species level, coding of these taxa was conducted based on information available for closely related species in the same genus or family (following, e.g., Faulwetter et al., 2015; Rand et al., 2018; Sutton et al., 2020). In a few cases, modalities common at even higher taxonomic rank (such as direct development in Peracarida) were applied. For coding a “fuzzy coding” procedure (Chevenet et al., 1994) was used, resulting in a “traits by taxon” matrix (**Supplementary Table 2**). The “fuzzy coding” procedure allows taxa to be coded with multiple modalities to different degrees using a 0–3 code, with 0 indicating no affinity, 1 and 2 indicating partial affinity, and 3 indicating the highest affinity for a given modality. This approach was proposed to account for variation encountered within a species (Chevenet et al., 1994) and when incorporating information from species in the same genus or family (Charvet et al., 2000). While including higher taxonomic levels may introduce uncertainty to the results, their suitability has been

documented for biological traits analysis as well as taxonomic community analysis, especially in multivariate analyses that showed that the functional structure of communities could be conserved (Bournaud et al., 1996; Bowman and Bailey, 1997; Dolédec et al., 1998). To give the same weight to each taxon and trait, the fuzzy codes (0–3) were converted to proportions for each trait modality totaling to 1 (e.g., Bolam et al., 2017).

A total of 106 invertebrate and fish taxa were used for BTA, of which 53 taxa occurred in the ROV images and 77 taxa in trawls with 26 taxa common to both sampling gears. In addition to the “traits by taxon” matrix, “taxa by stations” (i.e., presence/absence of taxa or proportional abundances of taxa at each station) and “traits by stations” (i.e., trait composition at each station, obtained by multiplying the “taxa by stations” and “traits by stations” matrices and indicated by presence/absence or proportional abundance weighted scores) matrices were generated (following Beauchard et al., 2017; Degen et al., 2018). Three “taxa by stations” (**Supplementary Tables 3–5**) and three “traits by stations” (**Supplementary Tables 6–8**) matrices were compiled for subsequent analysis: presence/absence of taxa based on ROV and trawl samples combined across all stations, and one each with proportional abundances acquired from either ROV or trawl samples. Proportional abundance was chosen over absolute abundance due to the above-mentioned failure of the laser pointers that made it impossible to calculate absolute abundances for all ROV stations. Proportional abundance was also used for trawl samples for consistency.

Data Analysis

To test our first hypothesis, namely that epifaunal organisms in the CBL are predominantly small-sized, non-sessile deposit-feeders or scavengers with equal representation of direct and indirect development, we included the four traits: size, larval development, adult movement and feeding habit. The “traits by stations” matrix was used to test this hypothesis; it was based on presence/absence data of taxa collected with both the ROV and the trawl (**Supplementary Table 6**).

To test the second hypothesis, namely that a difference in functional structure exists between mid-depth and deep communities, all nine traits were used. To investigate differences in the overall functional composition of epifauna and visualize potential differences between these two depth strata, we applied a fuzzy correspondence analysis (FCA, Chevenet et al., 1994). FCA is an extension of a regular correspondence analysis that is suitable for fuzzy coded traits data of discrete variables (Chevenet et al., 1994). FCA is based on the “traits by stations” matrix (**Supplementary Tables 7, 8**) and identifies and visualizes traits and their modalities contributing most to the difference in the functional structure among stations (Bremner et al., 2006), and provides correlation ratios of each trait along the fuzzy principal axes, representing the amount of variance of a certain trait modality explained by a given axis (Chevenet et al., 1994). Correlation ratios greater than 10% were considered as the traits contributing most to variation among the stations following Conti et al. (2014). A Kruskal–Wallis test was used to test for significant differences in proportional abundance of trait modalities between mid-depth and deep stations using

²www.fishbase.org

³http://www.sealifebase.org

TABLE 2 | Overview of traits and their modalities used in the present paper.

Trait	Modality	Modality code	Definition
Size	Small (<10 mm)	S1	<10 mm
	Small-medium (10–50 mm)	S2	10–50 mm
	Medium (50–100 mm)	S3	50–100 mm
	Medium-large (100–300 mm)	S4	100–300 mm
	Large (>300 mm)	S5	>300 mm
Body Form	Globulose	BF1	Round or oval
	Vermiform	BF2	Worm-like or thin, elongate body form
	Dorsoventrally compressed	BF3	Flattened from dorsal and ventral sides
	Laterally compressed	BF4	Flattened from side to side
	Upright	BF5	Upstanding, vertical
Reproduction	Asexual	R1	Budding and fission
	Sexual-external fertilization	R2	External fertilization, eggs and sperm deposited on substrate or released into water (broadcast spawners)
	Sexual-internal fertilization	R3	Internal fertilization, but no brooding, eggs deposited on substrate, indirect or direct development
Larval development	Sexual-brooding	R4	Internal or external fertilization, eggs or larvae are brooded, indirect or direct development
	Planktotrophic	LD1	Generally pelagic for several weeks, larvae feed and grow in water column
	Lecithotrophic	LD2	Shorter larval period, larvae with yolk sac pelagic or benthic
Living habit	Direct	LD3	Direct development (i.e., no larva), benthic ¹
	Free-living	LH1	Not limited to any restrictive structure at any time. Able to move freely within and/or on the sediments
	Crevice dwelling	LH2	Inhabit crevices in coarse/rock substrate and/or biogenic substrate
Adult movement	Tube dwelling	LH3	Inhabit tubes
	Burrowing	LH4	Inhabit permanent or temporary burrows in the sediment, or burrow in the sediment
	Epizoic	LH5	Live on or in other organisms
	Attached	LH6	Adherent to a substratum
	Sessile/none	MV1	No movement as adult
	Burrower	MV2	Movement in the sediment
Mobility	Crawler	MV3	Movement along on the substratum via movements of its legs, appendages or muscles
	Swimmer	MV4	Movement above the sediment
	None	MO1	No movement as adult
	Low	MO2	Slow movement
Feeding habit	Medium	MO3	Medium movement
	High	MO4	High movement, swimmer or fast crawler
	Surface deposit feeder	FH1	Active removal of detrital material from the sediment surface
	Subsurface deposit feeder	FH2	Removal of detrital material from within the sediment matrix
	Filter/suspension feeder	FH3	Capture and ingestion of food particles suspended in water
	Opportunist/scavenger	FH4	Use different types of food sources/feeds on dead organic material
Substrate affinity	Predator	FH5	Preying (hunting or killing) upon other organisms
	Parasite/commensal/symbiotic	FH6	Obtain nourishment and shelter on or in another organism (a host) with a harm to the host/without significant harm to a host/with mutual benefit from an interaction
Substrate affinity	Soft	SA1	Sand or mud
	Hard	SA2	Rocks, gravel
	Biological	SA3	Epizoic or epiphytic life style
	None	SA4	Hyper-benthos

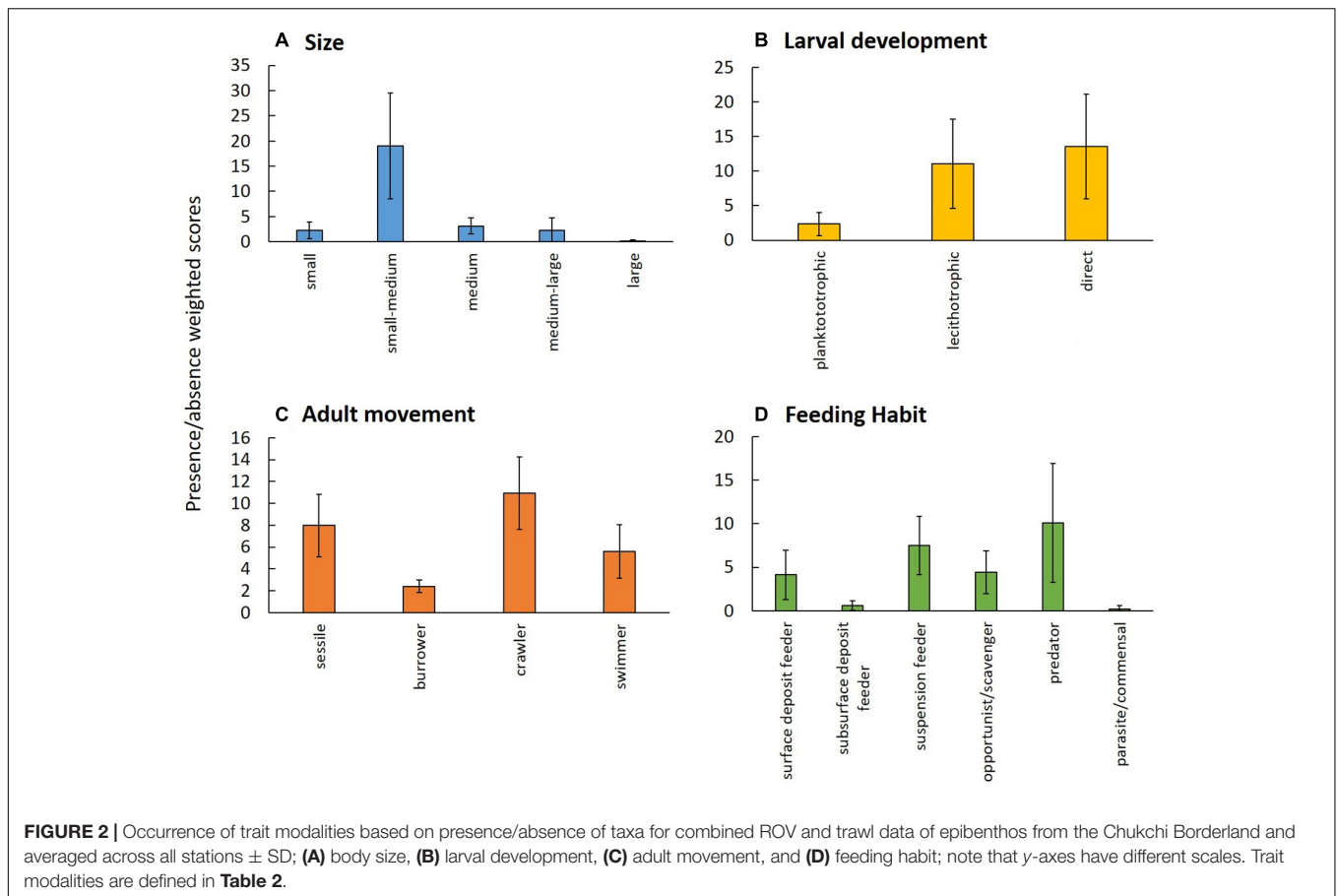
Slightly adjusted from Bremner et al. (2006), Degen et al. (2018), Costello et al. (2015), and Sutton et al. (2020).

¹Brooders of juveniles are included here.

the “traits by stations” matrix from ROV data (**Supplementary Table 7**). Only one trawl sample was available from deep stations preventing statistical comparisons.

We then visualized which of the available environmental variables explained most of the variation in the functional structure of the epifaunal communities using a canonical

correspondence analysis (CCA) performed on the “traits by stations” matrices for ROV (**Supplementary Table 7**) and trawl (**Supplementary Table 8**) samples. For environmental data, we included water depth, bottom water salinity and temperature, grain size composition, number of rocks in ROV images, concentration of benthic pigments in sediment (phaeopigments



and Chl *a*), carbon content in sediment, and C/N ratio. A forward selection procedure was used to identify environmental variables explaining most of the variability in the trait-by-station data. These variables were then used in the model, whereas other factors were overlaid on the plots as passive factors. The significance of the models and environmental variables were tested with Monte Carlo permutation tests (Oksanen et al., 2013).

As part of hypothesis two, we tested for differences in functional diversity and redundancy between depth strata for both ROV and trawl-based data. FD was estimated using Rao's quadratic entropy (Rao's *Q*), which is a measure of trait dissimilarity (Rao, 1982; Botta-Dukát, 2005). Rao's *Q* ranges from 0 to 1, where 0 means low FD (i.e., communities are the same in their biological trait profiles) and 1 means high FD (i.e., communities are unique in their biological trait profiles) (Van der Linden et al., 2016). FD was calculated based on the "traits by taxon" (**Supplementary Table 2**) and "taxa by stations" (**Supplementary Tables 4, 5**) matrices.

FR is the relationship between FD and species diversity (Ricotta et al., 2016), and was calculated as the ratio of FD to the taxonomically based Simpson index (*D*, calculated using equation (1)).

$$D = 1 - ((\sum n(n-1)/N(N-1)), \quad (1)$$

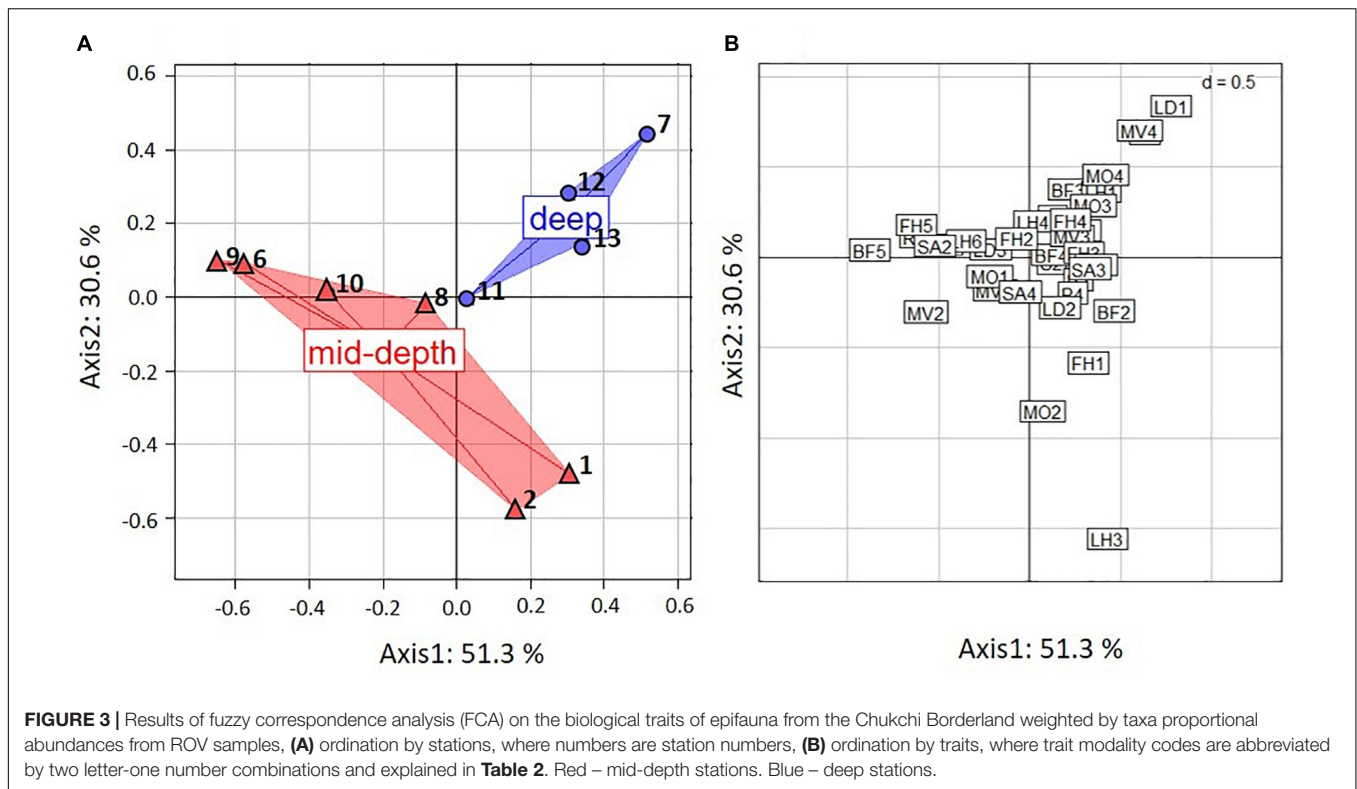
where *n* is the total number of organisms of a particular species, and *N* is the total number of organisms of all species. In order to obtain a regularly increasing index, the formula was converted to: $1 - (FD/D)$ (Van der Linden et al., 2016). FR defines to which degree different species represent the same ecosystem functions (Petchey and Gaston, 2006; de Bello et al., 2007) and ranges from 0, where all species have different trait-categories, to 1, meaning all species display the same trait-categories (de Bello et al., 2007). A Kruskal–Wallis test was used to check for significant differences in FD and FR between mid-depth and deep ROV stations.

All statistical analyses were performed using the software R (R Core Team, 2017) with the package *ade4* (Dray and Dufour, 2007) for the FCA and calculation of FD index, and the package *vegan* (Oksanen et al., 2013) for the CCA analyses. A schematic representation of the hypotheses tested and methods used to test the hypotheses, along with figure and table numbers representing results of the tests, is given in the **Supplementary Figure 1**.

RESULTS

Trait Modality Composition

The body size modality "small-medium" was the most frequent in the epifauna across the study area, while size "large" was rarest



(**Figure 2A**). The most frequent larval development was “direct” followed by “lecithotrophic,” while the occurrence of the modality “planktotrophic” was much lower (**Figure 2B**). Non-sessile adult movement modalities combined were more frequent than sessile forms. Individually, “crawlers” were dominant, though “sessile” was second most frequent and since this study focused on epifauna, “burrowers” were expectedly least frequent in the data set (**Figure 2C**). Feeding habit “predators” was most frequent, followed by “suspension feeder.” The least frequent modalities of feeding habit were “parasite/commensal” and “subsurface deposit feeder” (**Figure 2D**).

Functional Structure of Epifaunal Communities

The FCA showed substantial variation in functional composition across all stations. The first two axes of the FCA accounted for 81.9% of the variability in distribution of trait modalities, with 51.3% for the first and 30.6% for the second axis (**Figure 3A**). Most of the variation along the first axis was explained by body form (BF) (31%), reproduction (R) (20%), living habit (LH) (14%), feeding habit (FH) (18%), and substrate affinity (SA) (19%) (**Table 3**).

Trait modality composition generally differed between mid-depth and deep stations (**Figure 3A**). Deep stations 7, 12, and 13 were located on the upper right hand side of the FCA plot and corresponded to higher proportional abundance of modalities “swimming” (MV4), “sexual-internal fertilization” (R3) and “planktotrophic larval development” (LD1) (**Figures 3A,B**). Mid-depth stations 6, 9, and 10, located on the lower left

hand side of the FCA plot, were characterized by higher proportional abundance of “upright body form” (BF5), affinity for hard substrate (SA2) and “predators” (FH5) (**Figures 3A,B**). Variation along the second axis was driven mostly by living habit (LH) (32%) and mobility (MO) (10%) (**Table 3**). These traits separated mid-depth stations 1 and 2 from the rest of the stations (**Figure 3A**), and the two stations were characterized by higher proportional abundance of modalities “low mobility” (MO2), “sessile” (MV1), “deposit feeding” (FH1), and “tube-dwelling” (LH3) (**Figure 3B**). Deep station 11 and mid-depth station 8 were not differentiated from the remaining stations based on the traits used. In general, results for the trawl

TABLE 3 | Correlation ratios of each biological trait on the first two axes of the fuzzy correspondence analysis for ROV samples of epibenthos in the Chukchi Borderland.

Traits	Axis 1	Axis 2
Size	0.06	<0.01
Body form	0.31	0.06
Reproduction	0.20	0.06
Larval development	0.09	0.09
Living habit	0.14	0.32
Adult movement	0.09	0.09
Mobility	0.08	0.10
Feeding habit	0.18	0.07
Substrate affinity	0.19	<0.01

Correlation coefficients higher than 10% are in bold.

TABLE 4 | Results of Kruskal–Wallis test comparing proportional abundance of modalities at deep and mid-depth stations for ROV data of epibenthos in the Arctic Chukchi Borderland.

Trait modalities	p-value	Trait modalities	p-value
S1	0.20	MV1	0.06
S2	0.20	MV2	–
S3	0.21	MV3	0.06
S4	0.83	MV4	0.03*
S5	–	MO1	0.14
BF1	0.03*	MO2	0.03*
BF2	0.39	MO3	0.06
BF3	0.39	MO4	0.03*
BF4	0.52	FH1	1
BF5	0.02*	FH2	0.67
R1	0.14	FH3	0.03*
R2	0.67	FH4	0.03*
R3	0.01*	FH5	0.14
R4	0.67	FH6	–
LD1	0.06	SA1	0.20
LD2	0.83	SA2	0.13
LD3	0.09	SA3	0.45
LH1	0.03*	SA4	0.64
LH2	–		
LH3	0.01*		
LH4	0.29		
LH5	–		
LH6	0.39		

Asterisks indicate significant results ($p \leq 0.05$). Trait modalities are defined in Table 2.

data supported those from the ROV (Supplementary Figure 2 and Supplementary Table 9). The difference was that higher proportional abundance of modalities “sessile” (MV1) and “small size” (S1) was observed at the single deep trawl station, while mid-depth trawl stations were characterized by high proportional abundance of modalities “free-living” (LH1), “crawlers” (MV3), “dorsoventrally compressed” (BF3), and “medium size” (S3) (Supplementary Figure 2).

Results of the Kruskal–Wallis test indicated significant differences between mid-depth and deep stations for body form (BF), feeding habit (FH), reproduction (R), and lifestyle and mobility traits [adult movement (AM), living habit (LH), and mobility (MO)]. Deep stations were characterized by significantly higher proportional abundance of the body form “globulose” (BF1), feeding habits “suspension feeder” (FH3) and “opportunist/scavenger” (FH4), reproduction “sexual-internal fertilization” (R3), and higher proportional abundance of “free-living” (LH1), “highly mobile” (MO4), and “swimmer” (MV4) modalities (Kruskal–Wallis test; Table 4 and Figure 4). Mid-depth stations had significantly higher proportional abundance of the body form “upright” (BF5), living habit “tube-dwelling” (LH3), and mobility “slow movement” (MO2) (Kruskal–Wallis test; Table 4 and Figure 4). The Kruskal–Wallis test was not run on trawl data because only one deep station was sampled by trawl, but boxplots for the trawl data indicated generally similar patterns to those from the ROV data. Differences

included higher proportional abundance of modalities “attached” and “sessile” at the single deep trawl station than at deep ROV stations, and higher proportional abundance of modalities “free-living” and “crawling” at the mid-depth trawl stations (Supplementary Figure 3).

Significantly lower FD and higher FR were found for deep ROV stations compared with mid-depth stations ($p = 0.03$ for both, Figure 5). Though the lack of station replication prevented statistical analysis for the trawl samples, the trends in FD and FR were similar to the ROV results, though the difference in FD and FR between the two depth strata was less distinct (Supplementary Figure 4).

Environmental Factors Influencing Functional Structure of Epifaunal Communities

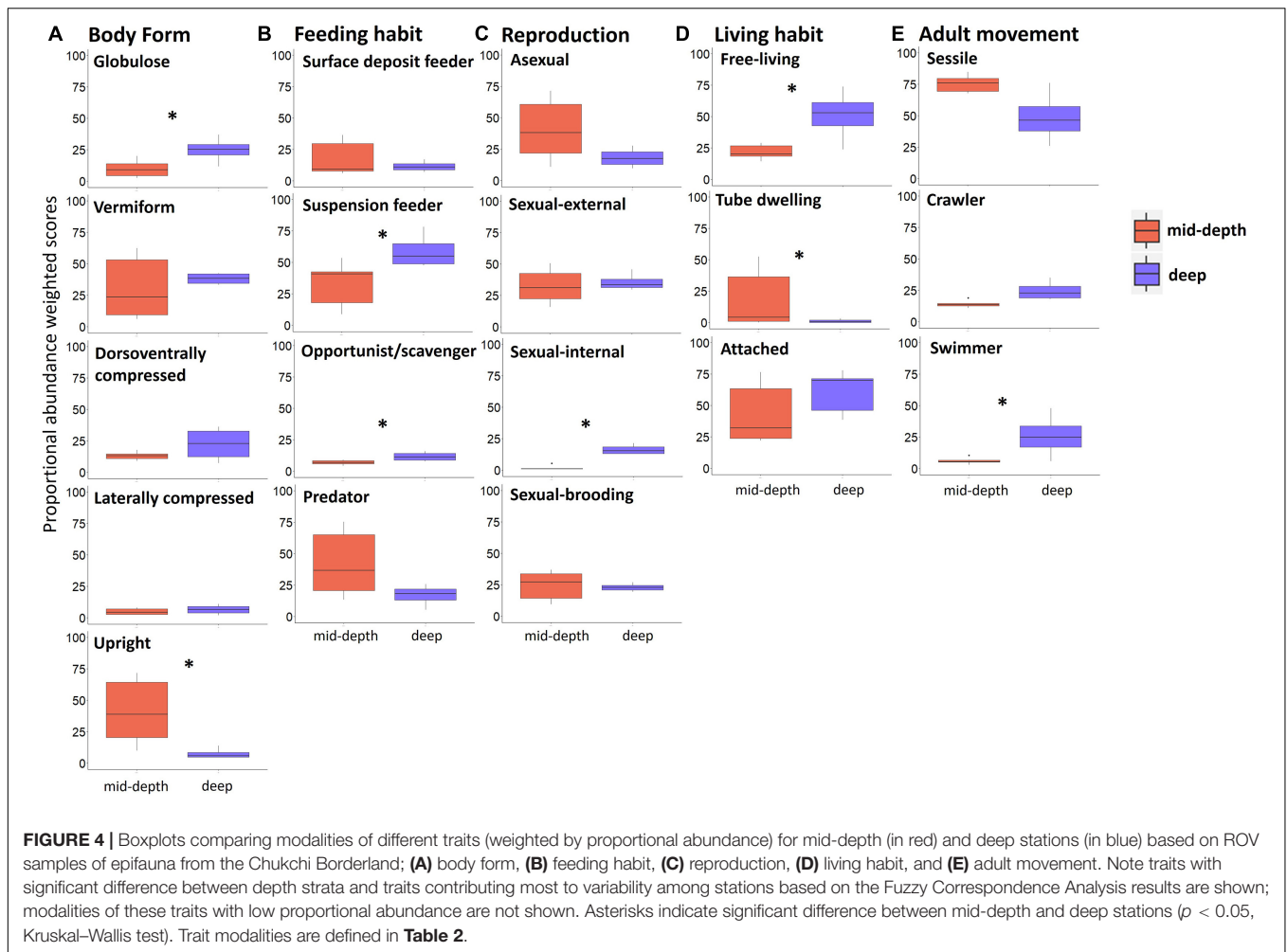
Results of the CCA for the ROV samples showed that depth and sediment organic carbon content were the most important factors explaining variability in the distribution of trait modalities (Table 5). These environmental factors explained 64% of the total variation. Depth was positively associated with “dorsoventrally” compressed (BF3) and “globulose” (BF1), “internal fertilization” (R3), “free-living” (LH1), “swimming” (MV4), and “suspension-feeding” (FH3), modalities (Figure 6). High carbon content was positively associated with the modalities “vermiform” (BF2), “sexual-external fertilization” (R2), “sexual-brooding” (R4), “tube-dwelling” (LH3), and “surface deposit-feeding” (FH1) (Figure 6).

Results of the CCA for trawl samples also indicated depth as the most important factor influencing the functional composition of epifaunal communities, with temperature also being a significant factor (Supplementary Table 10). Both factors were used to constrain the CCA, resulting in 92.9% of the total variation explained. In contrast to the ROV data, depth was positively associated with “sessile” (MV1) and “attached” (LH6), and substrate affinity “hard” (SA2). Temperature was positively associated with “predators” (FH5) and “opportunist/scavenger” (FH4) modalities, and substrate affinity “biological” (SA3) (Supplementary Figure 5).

DISCUSSION

Trait Modalities Composition Across the Deep-Sea CBL

Body size of organisms affects many ecological functions including energy and nutrient cycling, and secondary production (Degen et al., 2018). One of the most common characteristics of deep-sea benthos is the small size of most species (Rex and Etter, 1998). Our study results are consistent with this paradigm and hence with our hypothesis, in that the second smallest (small-medium size, 10–50 mm) organism category had the highest occurrence, while large organisms (≥ 50 mm) had the lowest occurrence in epifaunal communities across the CBL. Low occurrence of the smallest size category is unsurprising given that we targeted epibenthic megafauna (typically ≥ 10 mm).



A series of studies reporting reduced average body size with depth for deep-sea meiofauna (Soltwedel et al., 1996; Soetaert et al., 2002; Kaariainen and Bett, 2006) and macrofauna (Rex et al., 1999; Kaariainen and Bett, 2006) generally support Thiel's size-structure hypothesis (Thiel, 1975) for these groups. This decrease in body size with depth has also been found for epifauna (Rex et al., 2006; Wei et al., 2010). Opposite to this trend, some deep-sea taxa with larger body sizes than in shallow areas have also been documented (Rex and Etter, 1998), in some cases resulting in gigantism. This phenomenon, often attributed to low temperature and high oxygen availability that causes slow growth rate and longevity (Shirayama and Horikoshi, 1989), has been found for deep-sea isopods, amphipods, pycnogonids, ostracods, and anemones (Timofeev, 2001; Danovaro et al., 2014) but in our study, only the very large pycnogonid *Colossendeis proboscidea* could fit this concept.

Overall, we confirm our hypothesis that the majority of epifauna found in our study was non-sessile; most were crawlers but swimmers were also found. Not unexpectedly, burrowers were less common, given the focus of the study was epifauna. As a consequence of the ability to move organisms can escape from disturbance (natural or anthropogenic), disperse or migrate

(Beauchard et al., 2017; Degen and Faulwetter, 2019) and increases the chance of finding scarce and patchy food compared to sessile or less mobile organisms. Still, movement rates of epibenthic megafauna are generally lower in the deep sea compared to shelves (Thistle, 2003; Ruhl, 2007). For example, deep-sea brittle stars and holothurians move at $1\text{--}3\text{ cm min}^{-1}$ and $1\text{--}2\text{ cm min}^{-1}$, respectively, compared with $15\text{--}45\text{ cm min}^{-1}$ and 7 cm min^{-1} , respectively, in shallow waters (summarized in Thistle, 2003). When stimulated, for example by food, however, many deep-sea animals can move faster (Premke et al., 2006; MacDonald et al., 2010; Taylor et al., 2016). For example, we observed unusual swimming behavior in the brittle star *Ophiostriatius striatus*, perhaps an adaptation to access patchy food falls (Boetius et al., 2013). ROV observations such as ours, hence, increase our often scarce knowledge of traits of deep-sea taxa. Besides mobile taxa, we did also find an unexpectedly high occurrence of the modality sessile in our study, especially obvious in ROV imagery. Sessile taxa in our study area, including ascidians, sponges, stalked cirripedes and crinoids, and zoanthid and nephtyid cnidarians were in part present on the numerous drop stones providing hard substrate for these organisms (Zhulay et al., 2019).

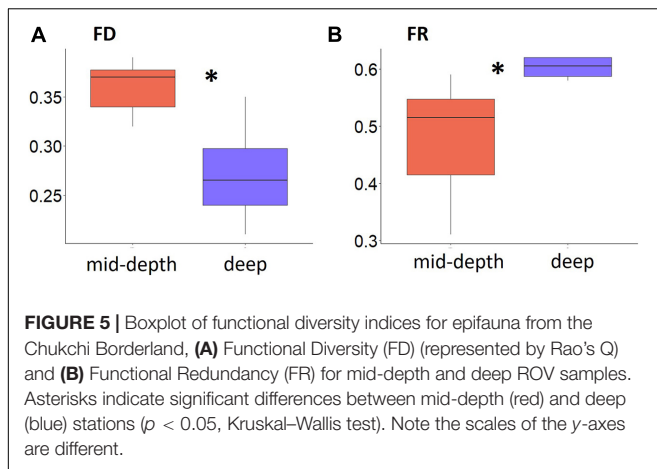


TABLE 5 | Results of canonical correspondence analysis using Monte-Carlo permutation test, performed on a traits by stations matrix for ROV samples of epibenthos in the Arctic Chukchi Borderland.

	p-value	F-value
Full model (depth + carbon)	0.001***	6.10
Depth	0.001***	7.40
Carbon	0.002**	4.79

Asterisks indicate statistical significance (** $p \leq 0.01$, *** $p \leq 0.001$).

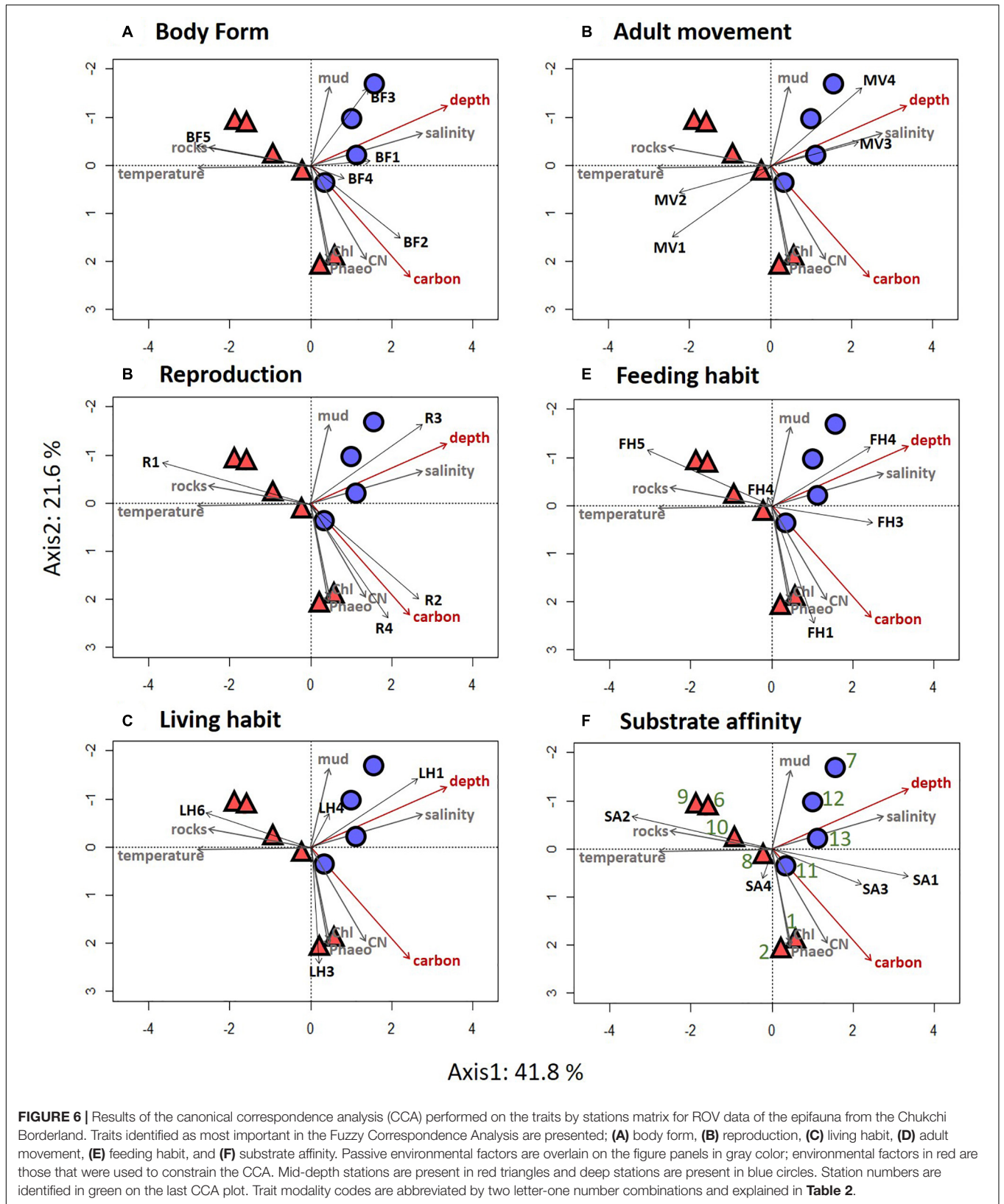
Trophic structure of the Arctic benthic deep-sea communities is poorly studied (but see Iken et al., 2005), though feeding habits influence energy flow, nutrient cycling, secondary production, organic matter decomposition, and nutrient regeneration (Bremner, 2008; Degen et al., 2018). We do know that the major food source is organic detritus originating mostly from the upper productive zone (Fabiano et al., 2001; Thistle, 2003). This organic material often undergoes strong transformation while sinking, decreasing nutritional value and particle size (Thistle, 2003). The paradigm that deposit feeding is among the best strategies to collect and process this organic detritus efficiently (Thistle, 2003) has indeed been supported for both macrofaunal and megafaunal deep-sea communities (Kröncke, 1998; Iken et al., 2005; Rex and Etter, 2010). The deposit feeders were also common yet not dominant in our study area, only partly confirming our hypothesis. Predators and suspension-feeders, however, were more common among our epifaunal taxa. This is contrary to a trend of decreasing proportions of predatory asteroid and gastropod species with depth (Carey, 1972; Rex et al., 1990). Our findings, however, are in agreement with other studies that found that predation is in fact common in oligotrophic seas or in areas with little food input (Kröncke and Türkay, 2003; Wieking and Kröncke, 2003; Vacelet, 2008), and are supported by high nitrogen isotope values in certain taxa of our study area (Iken et al., 2005). One theory states that prey can be more easily detected in the deep sea compared to shallow water environments, as “flow in the benthic boundary layer is slow and thus chemical gradients and pressure waves produced by prey should be more persistent and provide better information for prey location” (Thistle, 2003). Facultative predation is even

known for specific deep-sea species of, for example, sponges (Vacelet, 2006; Godefroy et al., 2019; Martini et al., 2020b), and bivalves (Morton, 2016; Morton and Machado, 2019), suggesting feeding modes may be unusual, highly plastic and require more study. A stable isotope-based assessment for the study area is ongoing and will provide more clarification of the species' feeding modes and trophic levels.

The high occurrence of suspension feeding taxa among the CBL epifauna was initially surprising. Higher current and particle fluxes, proving food for suspension feeders, tend to occur on elevations and slopes (Clark et al., 2010) including the Chukchi Slope Current in the CBL (Corlett and Pickart, 2017) and were suggested to provide food for suspension feeders from the nearby Chukchi shelf to the Northwind Ridge (Bluhm et al., 2005). In addition, suspension feeders on the above-mentioned drop stones can extend above the substrate and into the benthic boundary layer, where the currents are slightly faster and carry food particles (Vogel, 1996). Besides on stones, some taxa (in particular anthozoans) were elevated above the seafloor in other ways, namely either on stalks of crinoids or polychaete tubes or, in the case of most hormathiid anemones (*Hormathia* spp., *Allantactis parasitica*) on gastropod shells (usually *Colus* spp.).

Scavengers were also represented in the study area, although not as highly occurring as reported in some deep-sea areas including the Eurasian Arctic (Klages et al., 2001; Premke et al., 2006). It is unsurprising that parasites/commensals were the least occurring feeding type in the study area given our study focused on epifaunal megafauna of which few are parasitic. Smaller external and internal parasites are in fact occurring in Arctic megafauna, especially in demersal fish (Klimpel et al., 2006), but were invisible on the ROV images. We did encounter taxa such as ribbon worms, isopods and sea leeches, which generally contain parasitic forms on fishes and arthropods (Køie, 2000; Mantelatto et al., 2003; Ravichandran et al., 2009), but we did not observe them on a potential host. Commensalism was encountered for some hormathiid anemones attached to shells of gastropods, a widespread strategy increasing probability of contact with food particles, while providing protection to the host (Buhl-Mortensen et al., 2015). Similar commensal relationships were observed for other anthozoans and the amphipod *Amathillopsis spinigera* that were often found in association with sessile tubeworms and stalked crinoids. Clearly, more research is needed on parasitic and commensal biotic interactions in the deep-sea.

Little is known about larval development in the Arctic Ocean in general. Recent molecular studies, however, have documented the presence of pelagic larvae of more species than previously acknowledged for the Arctic (Ershova et al., 2019) and the deep sea (Kersten et al., 2019), and detailed studies in the deep sea have added species-specific observations (e.g., Mercier and Hamel, 2008; Martinez and Penchaszadeh, 2017; Montgomery et al., 2017). This trait is important for ecological functions such as dispersal, recolonization, recovery, tolerance to stress, and link between pelagic and benthic realms (Degen and Faulwetter, 2019). In the present study, direct development dominated as a single modality, yet given the sparse species-specific literature, generalizing this conclusion



for the Arctic is premature. Nevertheless, advantages of this development type include, for example, protection from various unfavorable environmental conditions in the pelagic realm and settling on unfavorable substrate, and experiencing little planktonic predation. Most important for the deep sea, juveniles are less dependent on either limited or variable food availability (Mileikovsky, 1971). Yet indirect development, including planktotrophic and lecithotrophic larvae, was almost equally prevalent in the epifaunal taxa of our study area, which, in general, supports our hypothesis. This finding is consistent with a growing number of studies documenting the occurrence of pelagic larvae in both polar waters (Schlüter and Rachor, 2001; Fetzer and Arntz, 2008; Kuklinski et al., 2013; Brandner et al., 2017; Ershova et al., 2019) and deep-sea areas (Scheltema and Williams, 2009; Kersten et al., 2019). Among larval development types, lecithotrophs were most common in our study area. This is similar to findings in the NE Greenland, the deep-sea of the NE Atlantic, and Antarctica, where more than 70% of echinoderms were found to reproduce with pelagic larvae, the majority of which were lecithotrophs (Pearse, 1994). Development with pelagic larvae allowing dispersal over broader areas is an advantage, in particular for species with limited mobility (Fetzer and Arntz, 2008; Stübner et al., 2016), which were found in high numbers in our study area. In a work by Mercier and Hamel (2008), depth-related shifts in life history strategies and a simultaneous combination of brooding and broadcast-spawning with lecithotrophic larvae were reported in a deep-sea asteroid. This finding also stresses the need to species- and habitat-specific work to help close many knowledge gaps that currently limit final conclusions on true diversity and plasticity of life-history traits in deep-sea benthos.

In summary, our investigation of functional traits of deep-sea epifauna from the CBL area generally supported our first hypothesis that small, non-sessile organisms are the most common, with a relatively equal proportion of direct and indirect (mostly through lecithotrophic larvae) development. The hypothesized predominance of deposit feeding, however, was not found in the observed species pool, though that feeding mode was more prominent in the proportional abundance-weighted data set. That modality is common in infaunal taxa, which we did not cover here (Gage and Tyler, 1991; Iken et al., 2001; Mamouridis et al., 2011). Our analysis of trait modalities highlights instead that there is no single way to live successfully under deep-sea conditions, but rather that, similar to shallower areas, multiple strategies are in fact viable.

Functional Differences Between Epifauna at Deep and Mid-Depth Stations

Trait Modality Composition at Mid-Depth and Deep Stations

Our hypothesis that functional traits of epibenthic communities would change with increasing depth in the CBL was generally

confirmed. In particular, epifauna of deep stations reflecting more homogeneous habitat (Zhulay et al., 2019) had significantly higher proportional abundance of the modalities free-living, swimming, suspension feeders, opportunists/scavengers, internal fertilization and globulose compared to the mid-depth stations, which were characterized by complex habitat structure including ridges, a plateau with pockmarks, and rocks. In addition, our data also suggest that the increasing distance from the productive Chukchi shelf corresponded with spatial patterns of functionality in addition to the depth-related patterns.

The higher proportional abundance of modalities free-living and mobile/swimming at greater depths is consistent with generally decreasing food availability with increasing depth in deep-sea areas, both globally and in the Arctic (Thistle, 2003; Wiedmann et al., 2020). In the study region, this decrease is reflected in an annual POC flux on the adjacent Chukchi Sea shelf being at least an order of magnitude higher ($4\text{--}166\text{ g C m}^{-2}\text{ year}^{-1}$; Grebmeier et al., 2006) than in the Northwind Abyssal plain ($0.24\text{--}0.32\text{ g C m}^{-2}\text{ year}^{-1}$; Watanabe et al., 2014). Indeed, the deepest and most food limited basin station (station 7) had the highest proportional abundance of the modality swimming. Conversely, lower proportional abundance of free-living and mobile/swimming (i.e., more sessile, attached) modalities at mid-depth stations coincided with higher food availability at lower depths in general. This pattern was, however, not robust as trawl samples in fact showed a higher proportional abundance of the modality mobile at the mid-depth stations compared to the ROV data, where the modality crawling was most abundant. Mobile fauna is often caught with trawls (Brandt et al., 2016), while trawls can be less reliable in assessing density of some sessile fauna compared to ROV approach (Chimienti et al., 2018). The combination of both tools, thus, allowed us to get more comprehensive insights into the functional structure of benthic communities.

Suspension feeding was surprisingly more abundant at deeper stations in our study, where numerous persisting lebensspuren confirmed low bottom current velocity (Zhulay et al., 2019). The question arises as to what and how these organisms eat. In fact, suspension feeders are able to feed on a wide range of food items, ranging in size (from bacteria to zooplankton) and quality (Gili et al., 2001). Bacterial abundance and biomass do not decline with depth in the global ocean, thus becoming relatively more important in deeper layers (Rex et al., 2006; Wei et al., 2010) and, potentially, serving as food for benthic organisms in our study area. In addition, deep-water zooplankton communities in the Arctic Deep Water may provide a food source, though their abundances are low (less than 1 ind m^{-3}) (Kosobokova and Hirche, 2000; Kosobokova et al., 2011). Adaptations that allow suspension feeders to maximize food capture even at slow current velocity might also play a role including generating feeding currents and associations with microbial communities (Gili et al., 2001; Siegl et al., 2008; Weisz et al., 2008). Finally, little maintenance energy was documented for Antarctic deep-water sponges (Gatti, 2002). Besides suspension-feeding, proportional abundance of

opportunists/scavengers was also significantly higher at greater depths. These feeding strategies become increasingly more useful with depth as scavengers have an ability to detect sparse carrion across large distances (Premke et al., 2006), while opportunists can take advantage of almost whatever they come across in the food-poor environment (Drazen and Sutton, 2017). In turn, predation and deposit feeding were more common at the mid-depth stations, with deposit feeding being the dominant modality in the trawl samples. This might point to higher availability of deposited organic matter or prey at these mid-depth stations.

Proportional abundance of the modality internal fertilization was significantly higher in the deep compared to mid-depth stations. This pattern is consistent with previous studies where internal fertilization was common (Young, 2003). In an environment where chances of finding a mate are low, internal fertilization may have a higher success rate than external fertilization once a mate has indeed been found.

In addition to the depth pattern, substantial variability found in trait modality patterns was likely related to variable distance to the productive shelf rather than to depth alone. Evidence for this effect is for example the high proportional abundance of modalities tube-dwelling, sessile and deposit feeding at mid-depths stations at Northwind Ridge (stations 1, 2), which were associated with higher food input, likely from productive waters from the Chukchi shelf, as indicated by sediment pigment values and carbon content. In the same mid-depth range, higher proportional abundance of the modality predators farther north in the study area (stations 6, 9, and 10) was associated with a high amount of drop stones, where attached and upright predators took advantage of the presence of stones and elevated themselves to increase capture of prey. Additionally, mobile predators were occasionally observed in the vicinity to the stones, likely attracted by the enhanced amount of prey attached to the stones (Zhulay et al., 2019).

Functional Metrics and Ecosystem Vulnerability at Mid-Depth and Deep Stations

Both FD and FR indices showed changes with depth, where deep stations had lower FD and higher FR compared to the mid-depth stations, supporting our hypothesis. The depth-related FD trend was in agreement with results from the Arctic Nansen Basin (Degen, 2015), but contrary to a study from the Bering Sea (Liu et al., 2019), although the direct comparison of values obtained in different studies is not appropriate due to different authors using different traits or different numbers of traits in their calculations. Since FD indicates “the range of things organisms do in an ecosystem” (Petchey and Gaston, 2006; van der Linden et al., 2012), higher FD at the mid-depth stations indicates that these communities support more diverse ecological functions than those at greater depths. It seems likely that this pattern is linked to the more heterogeneous habitat structure at mid-depth stations providing more functional niche space for epifaunal organisms compared to the more homogeneous deeper abyssal plain. In contrast, higher FR at the deeper stations is, in turn,

likely related to the homogeneity of the abyssal environment to which epifauna appear to have adapted by fewer and shared trait modalities. Low FR at mid-depth stations may render these areas less resilient to ongoing and future change and potential human use as functions may be lost when species loss occurs (Loreau, 2008; Van der Linden et al., 2016), a conclusion consistent with studies on Arctic benthic macrofauna (Kokarev et al., 2017; Liu et al., 2019; Sutton et al., 2020). In addition, modalities such as sessile, attached, and upright body form at these stations point to higher vulnerability of mid-depth epifauna to predation, disturbances or decreases in food availability (Degen and Faulwetter, 2019). The higher FR at deeper stations in addition to high proportional abundance of modalities mobile/swimming might indicate lower vulnerability to disturbances, higher flexibility to perturbation, and higher ability for dispersal after disturbance (Degen and Faulwetter, 2019). It is important to note, however, this conclusion is potentially biased by low faunal densities and low sampling effort. It is, therefore, premature to conclude that deeper communities in the CBL are resilient.

In support of our second hypothesis, data indicated an overall difference in functional structure of epifauna between mid-depth and deep stations in terms of trait composition, FD, and FR. In addition, depth, carbon content in sediments (reflecting food availability), and bottom temperature (reflecting difference in water masses) were the main predictors of the functional structure of epifaunal communities, which generally supported our second hypothesis.

PERSPECTIVE AND OUTLOOK

Currently, we have limited ecological information on structure and function of deep-sea ecosystems in general, and in the Arctic Ocean in particular. Despite this lack, exploitation of Arctic deep-sea resources is now discussed widely in light of sea-ice cover decline. It is important to gain sufficient knowledge prior to any potential exploitation to assess and understand potential risk of human impacts and develop sustainable management strategies for possible resource use. The results generated in this study are, thus, very timely and can directly serve current assessments of biological and ecosystem resources and functions in the Central Arctic Ocean (CAO) by Scientific Experts on Fish Stocks of the Central Arctic Ocean (FisCAO) (fish stock assessment, Dupuis et al., 2019), the Working Group for Integrated Assessment of the Central Arctic Ocean (WGICA) (fisheries, ICES, 2020), and the International Union for Conservation of Nature (IUCN) (deep-sea mining plans and threats) (Cuyvers et al., 2018). Within FisCAO, the CBL is categorized as having fishable depth. In many places across the world's oceans the documented negative effects from seabed fishing include reduced biodiversity, body size and biomass and particularly strong effects on fragile, upright and epifaunal taxa (Wassenberg et al., 2002; Blanchard et al., 2004; Jørgensen et al., 2019; Tiano et al., 2020), and shifts toward opportunistic species (Blanchard et al., 2004). Recovery from

such and other impacts can be slow (Bergman et al., 2015), especially in high latitudes where recolonization is depressed by low temperature, long life cycles and high longevity (Al-Hababeh et al., 2020). Indeed, the presence of upright body forms in the mostly sessile species visible in our imagery, in particular at the northern mid-depth stations, indicated a vulnerability of the system to trawling, as was also suggested for example for the Barents Sea shelf (Jørgensen et al., 2019). In addition, oil and gas reserves have also been quantified in this area (Bird et al., 2008). It has been made clear that the onset of such multiple pressures in deep sea habitats results in an urgent need for biodiversity and trait-based characterization of deep-sea fauna (Costa et al., 2020), a need we directly address in the present study. Our trait-based evaluation of CBL epifauna points to potentially high sensitivity of benthic community function to disturbances especially at mid-depths as indicated by high FD and low FR. In addition, rapid climate change may have a greater impact on sessile taxa reproducing with larvae of low dispersal ability than mobile species or species with high larval dispersal (Young et al., 1997). Thus, traits analysis can offer insight into resilience and recovery capacity of taxa after disturbance.

Our study forms the first step toward filling research gaps of Arctic deep-sea system functioning and vulnerability, though study limitations include the poorly known biology of many of the taxa encountered, as well as spatially limited sampling in a heterogeneous area. We strongly recommend further study that: (a) enhances spatial and temporal coverage; (b) uses traits generated from the actual species in question, as higher taxonomic levels contain different species, which may have distinctive trait modalities (Cochrane et al., 2012; van der Linden et al., 2012); (c) includes more traits, in particular those that might be helpful to indicate potential effects of direct human impact such as trawling or climate-change related impacts such as warming and acidification on organisms (e.g., fragility, temperature tolerance, life span, skeleton); and (d) generates trait information from the area of interest as, due to plasticity of organisms, modalities can change in response to local environmental settings (Bremner, 2005).

DATA AVAILABILITY STATEMENT

The datasets generated and analyzed for this study can be found in the DataverseNO <https://doi.org/10.18710/OGOAWN>.

AUTHOR CONTRIBUTIONS

KI and BB conceived the study idea. KI obtained the funding for fieldwork. KI and IZ conducted the fieldwork. IZ conducted the image analysis with input by BB, PR, and KI. IZ and RD compiled biological trait information with the input by BB and KI, and conducted the statistical analysis. IZ and BB conducted most writing with all authors participating in data interpretation and article preparation. All authors have approved the final article.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2021.609956/full#supplementary-material>

Supplementary Figure 1 | Schematic representation of the hypotheses, methods used to test the hypotheses and number of figures/tables representing results. Trait modality codes are abbreviated by two letter-one number combinations and explained in **Table 2**.

Supplementary Figure 2 | Results of the fuzzy correspondence analysis on the biological traits of epifauna from the Chukchi Borderland weighted by taxa proportional abundances from trawl samples, **(A)** ordination by stations, where numbers are station numbers, **(B)** ordination by traits, where trait modality codes are abbreviated by two letter-one number combinations and explained in **Table 2**. Red – mid-depth stations. Blue – deep stations.

Supplementary Figure 3 | Boxplots comparing modalities of different traits (weighted by proportional abundance) for mid-depth (in red) and the single deep station (grey line) based on trawl samples of epifauna from the Chukchi Borderland; **(A)** body form, **(B)** feeding habit, **(C)** reproduction, **(D)** living habit, and **(E)** adult movement. Note traits contributing most to variability among stations based on the Fuzzy Correspondence Analysis results are shown; modalities of these traits with low proportional abundance are not shown. Asterisks indicate significant difference between mid-depth and deep stations ($p < 0.05$, Kruskal–Wallis test). Trait modalities are defined in **Table 2**.

Supplementary Figure 4 | Boxplot of functional diversity indices for epifauna from the Chukchi Borderland, **(A)** Functional Diversity (FD) (represented by Rao's Q) and **(B)** Functional Redundancy (FR) for mid-depth (red) and deep trawl samples of epifauna from the Chukchi Borderland. Note the scales of the y-axes are different.

Supplementary Figure 5 | Results of canonical correspondence analysis performed on the traits by stations matrix for trawl data of the epifauna from the Chukchi Borderland. Traits identified as most important in the FCA analysis are presented; **(A)** body form, **(B)** reproduction, **(C)** living habit, **(D)** adult movement, **(E)** feeding habit, and **(F)** substrate affinity. Passive environmental factors are overlain on the figure panels in gray color; environmental factors in red are those that were used to constrain the CCA. Mid-depth stations are present in red triangles and deep station is present in blue circles. Station numbers are identified in green on the last CCA plot. Trait modality codes are abbreviated by two letter-one number combinations and explained in **Table 2**.

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Supplementary Table 1 | Literature and other sources used to collect trait information for epifauna sampled in the Arctic deep Chukchi Borderland (also available at Arctic Trait Database: <https://www.univie.ac.at/arctictraits/index.php>).

Supplementary Table 2 | Traits by taxon matrix for epifauna sampled in the Arctic deep Chukchi Borderland using fuzzy coding.

Supplementary Table 3 | Presence and absence of epifaunal taxa at each station sampled in the Arctic deep-sea Chukchi Borderland with a remotely operated vehicle and a beam trawl.

Supplementary Table 4 | Proportional abundance of epifaunal taxa at each station sampled in the Arctic deep-sea Chukchi Borderland with a remotely operated vehicle.

Supplementary Table 5 | Proportional abundance of epifaunal taxa at each station sampled in the Arctic deep-sea Chukchi Borderland with a beam trawl.

Supplementary Table 6 | Traits by stations matrix based on presence/absence of epifaunal taxa sampled in the Arctic deep-sea Chukchi Borderland with a remotely operated vehicle and a beam trawl.

Supplementary Table 7 | Traits by stations matrix based on proportional abundance of epifaunal taxa sampled in the Arctic deep-sea Chukchi Borderland with a remotely operated vehicle.

Supplementary Table 8 | Traits by stations matrix based on proportional abundance of epifaunal taxa sampled in the Arctic deep-sea Chukchi Borderland with a beam trawl.

Supplementary Table 9 | Correlation ratios of each biological trait of epibenthos in the Arctic Chukchi Borderland with the first two axes of the fuzzy correspondence analysis for trawl samples ($n = 6$). Correlation ratios higher than 10% are in bold.

Supplementary Table 10 | Results of canonical correspondence analysis using Monte–Carlo permutation test, performed on a trait by station matrix for trawl samples of epibenthos in the Arctic Chukchi Borderland. Asterisks indicate significant results ($p \leq 0.05$).

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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