



First trait-based characterization of Arctic ice meiofauna taxa

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Abstract

Trait-based approaches connect the traits of species to ecosystem functions to estimate the functional diversity of communities and how they may respond to environmental change. For the first time, we compiled a traits matrix across 11 traits for 28 species of Arctic ice meiofauna, including Copepoda (Subclass), Nematoda (Phylum), Acoela (Order), Rotifera (Phylum), and Cnidaria (Phylum). Over 50 years of pan-Arctic literature were manually reviewed, and trait categories were assigned to enable future trait–function connections within the threatened ice-associated ecosystem. Approximately two-thirds of the traits data were found at the genus or species level, ranging from 44% for Nematoda to 100% for Cnidaria. Ice meiofauna were shown to possess advantageous adaptations to the brine channel network within sea ice, including a majority with small body widths < 200 µm, high body flexibility, and high temperature and salinity tolerance. Diets were found to be diverse outside of the algal bloom season, with most organisms transitioning to ciliate-, omnivore-, or detritus-based diets. Eight species of the studied taxa have only been recorded within sea ice, while the rest are found in a mixture of sympagic–pelagic–benthic habitats. Twelve of the ice meiofauna species have been found with all life stages present in sea ice. Body width, temperature tolerance, and salinity tolerance were identified as traits with the largest research gaps and suffered from low-resolution taxonomic data. Overall, the compiled data show the degree to which ice meiofauna are adapted to spending all or portions of their lives within the ice.

Keywords Functional traits · Arctic sea ice · Sea ice meiofauna · Trait database

Introduction

Arctic sea ice contains an extensive brine channel network that serves as habitat for both protozoans and metazoans (Horner et al. 1992). Those metazoans which range from ~ 20 to ~ 500 µm in size are grouped into a category called sea ice, or sympagic, meiofauna. The most common taxa found in sea ice are species from Copepoda (Subclass), Nematoda (Phylum), Acoela (Order), and Rotifera (Phylum), but other taxa like Cnidaria (Phylum) were also found (Marquardt et al. 2011; Bluhm et al. 2017). Some ice meiofauna species also live in the benthic or pelagic zones and are believed to settle within the ice via active migration, incorporation during ice formation, or through sediment incorporation on shelves (Carey and Montagna 1982; Gradinger et al. 2009; Kiko et al. 2017). Other species may

be endemic and colonize new ice from summer multi-year ice refuges (Bluhm et al. 2017). Ice meiofauna are considered one of the most poorly studied groups in the Arctic with large knowledge gaps related to their diversity, abundance, and ecological functions (Bluhm et al. 2018).

The sea ice brine channel network forms during the freezing of sea water (Assur 1958). Ice crystals, being pure fresh-water, expel all sea salts and concentrate them into the liquid in between, called brine because of its often high salinity. This interstitial environment serves as the in-ice habitat for meiofauna (Bluhm et al. 2017) and its volume within the ice varies with temperature and salinity, ranging from 5 to 25% of the total sea ice volume (Golden et al. 1998). The ice crystal matrix itself is impenetrable for meiofauna.

All types of sea ice contain this narrow brine channel network, which is characterized by large vertical gradients within the ice cover. In its upper layers, ice in situ temperatures can fall below -10 °C and brine salinities may soar above 150 (Assur 1958; Gradinger and Schnack-Schiel 1998). These values become less extreme toward the ice–water interface, where brine temperatures and

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salinities are typically close to the freezing point of sea water ($-1.8\text{ }^{\circ}\text{C}$) and full marine salinity around 35, respectively (Gradinger and Schnack-Schiel 1998). Ice conditions are highly seasonal and in winter months ice in situ temperatures are typically lower and brine salinities higher, with more concentrated brine than in summer (Assur 1958; Gradinger et al. 2009). During summer melt the ice–water interface can become brackish or even fresh (Spindler 1994; Hop et al. 2000), and ice meiofauna must be well adapted to these extreme and variable conditions to survive. The brine volume fraction differs with age of ice, driven by the gravitational loss of dense brine and a resulting smaller brine volume fraction with increasing age of ice floes. For example, the surface decimeters of multi-year sea ice are essentially freshwater and in winter are devoid of a brine channel network in contrast to saltier and younger first-year ice. In summer, warming then creates brine channels in multi-year ice, allowing meiofauna to inhabit the interior and upper parts of the ice (Friedrich 1997). Overall, all ice types possess the largest brine volume fraction in their bottom 10–30 cm where the brine channel network is generally more open to the underlying seawater (Petrich and Eicken 2017).

Arctic sea ice is rapidly disappearing and strongly reducing in area and volume (Barber et al. 2015; Meredith et al. 2019; Meier et al. 2021), which will have consequences for sympagic meiofauna that depend on ice for grazing, refuge, and reproduction (Bluhm et al. 2018). The survival and colonization ability of endemic fauna may also be impacted (Kiko et al. 2017). With conditions in the Arctic changing so quickly, scientists are searching for efficient and accurate methods of assessing ecosystem health and the impacts of anthropogenic stressors. Traditional studies use taxonomic richness, species composition, and the abundance of organisms to gauge the status of ecosystems (Cifoni et al. 2021). However, all species can directly influence ecosystem functions such as nutrient and energy fluxes via their quantitative (i.e., measurable) and qualitative (i.e., categorical) traits (e.g., body size or feeding habits, respectively) (Chapin et al. 1996; Naeem 2002; Hooper et al. 2005). Some studies have also shown that observed responses to ecosystem fluctuations are due more to patterns of trait diversity than to the richness or abundance of species (Gagic et al. 2015; Martini et al. 2020). Communities with low functional diversity are also generally believed to be less resilient (Naeem et al. 1994; Naeem and Li 1997). Therefore, trait-based approaches are increasingly used to catalogue the functional diversity of communities, based on the concept that ecosystem resistance and resilience can be quantitatively assessed through the functional redundancy of response traits (Hooper et al. 2005; McGill et al. 2006; Martini et al. 2020). Spatially mapping functional diversity can also aid in conservation and management strategies (Degen et al. 2018).

Only a few trait-based studies from the Arctic have been published, possessing a clear focus on benthic invertebrates and fish or targeting few traits (see Degen et al. (2018) for a synopsis of existing papers). Trait information from the polar regions in general is still very scarce. The Arctic Traits Database (see Degen and Faulwetter 2019) is focused on larger benthic species and, hence, several of its trait categories are not applicable to the unique environment of the sea ice brine channel network. Our goal was, therefore, to (1) compile a first traits matrix for common Arctic sea ice meiofauna taxa to provide data for subsequent studies on the functional response of sea ice biota to ice variability and change and (2) characterize the adaptations of taxa that may be well suited for inhabiting sea ice brine channels. We hypothesized that sea ice meiofauna would be dominated by morphological traits that allow them to fit into and move through the narrow brine channel system and tolerate the extreme environmental conditions of their habitat. To our knowledge, the present study serves as the first comprehensive synthesis of ice meiofaunal traits and is hoped to provide a solid base for future use in forming trait–function connections within the ice-associated ecosystem. Trait–function connections are key elements in establishing a deeper understanding of ecosystem responses to environmental stressors and presently represent a large gap in Arctic community studies (Beauchard et al. 2017; Degen et al. 2018).

Methods

Compilation of ice meiofauna species analyzed

The traits of 28 species and/or morphotypes of sympagic meiofauna were used for this study: nine copepods, six nematodes, three acoels, nine rotifers, and the cnidarian *Sympagohydra tuuli* (Table 1). The species were chosen based on a literature survey that established considerable evidence of presence in ice (sources given in Table 1), not based on any abundance parameters. The taxa of this study have overall been recorded throughout the Arctic, including the Beaufort Sea (Gradinger et al. 2005), Greenland (Gradinger et al. 1999), the Canadian Arctic Archipelago and Hudson Bay (Grainger et al. 1985), Svalbard (Schünnemann and Werner 2005), the Siberian shelves (Tchesunov and Riemann 1995), and the Transpolar Drift (Friedrich and De Smet 2000). We combined information from across the Arctic into one analysis, as most taxa have pan-Arctic wide distributions that result from large-scale ice drift patterns (Beaufort Gyre, Transpolar Drift) that connect various Arctic regions on annual to decadal time scales. On a coarse taxonomic level, the pan-Arctic distribution of these taxa is well recorded in Bluhm et al. (2018), recognizing, however, that not all studies report species or genus level for all groups.

Table 1 List of sea ice meiofauna taxa used in the present study

Taxonomic group	Species/genus/morphotype	Source for observation in sea ice
Copepoda		
Harpacticoida	<i>Halectinosoma neglectum</i>	Carey and Montagna (1982)
	* <i>Halectinosoma elongatum</i>	Arndt and Swadling (2006)
	<i>Harpacticus superflexus</i>	Arndt and Swadling (2006)
	<i>Tisbe furcata</i>	Grainger (1991)
	<i>Pseudobradya</i> sp.	Carey and Montagna (1982)
Cyclopoida		
	<i>Cyclopina schneideri</i>	Grainger (1991)
	<i>Cyclopina gracilis</i>	Carey and Montagna (1982)
	<i>Arctocyclopina pagonasta</i>	Mohammed and Neuhof (1985)
Calanoida		
	<i>Pseudocalanus</i> sp.	Grainger and Mohammed (1990)
Nematoda		
	<i>Theristus melnikovi</i>	Riemann and Sime-Ngando (1997)
	<i>Theristus</i> sp.	Pitusi (2021)
	<i>Cryonema tenue</i>	Riemann and Sime-Ngando (1997)
	<i>Cryonema crassum</i>	Riemann and Sime-Ngando (1997)
	<i>Hieminema obliquorum</i>	Tchesunov and Portnova (2005)
	<i>Halomonhystera</i> sp.	Pitusi (2021)
Acoela		
	Red morphotype	Friedrich and Hendelberg (2001)
	White morphotype	Friedrich and Hendelberg (2001)
	Orange morphotype	Janssen and Gradinger (1999)
Rotifera		
	<i>Encentrum graingeri</i>	Friedrich and De Smet (2000)
	<i>Proales reinhardti</i>	Friedrich and De Smet (2000)
	<i>Synchaeta bacillifera</i>	Friedrich and De Smet (2000)
	<i>Synchaeta cecilia</i>	Friedrich and De Smet (2000)
	<i>Synchaeta glacialis</i>	Friedrich and De Smet (2000)
	<i>Synchaeta hyperborea</i>	Friedrich and De Smet (2000)
	<i>Synchaeta tamara</i>	Friedrich and De Smet (2000)
	<i>Synchaeta</i> sp. A	Friedrich and De Smet (2000)
	<i>Cephalodella</i> sp. A	Chengalath (1985)
Cnidaria		
	<i>Sympagohydra tuuli</i>	Bluhm et al. (2007)

*Previously *Halectinosoma finmarchicum*

*Meroplankton was deliberately excluded from this list

Species rarely mentioned in the literature were not included in the trait table but still recorded (see Online Resource #1). Meroplankton larvae, common inhabitants of the brine channel network that peak in abundance in spring and summer (Gradinger et al. 2009; Michelsen et al. 2016; Bluhm et al. 2018; Descôteaux et al. 2021), were also excluded from the species list due to taxonomic identification challenges and brief time spent within the ice. The Acoela were divided into ‘morpho-species’ based on coloration consistently mentioned in several sources. Though distinct, the exact taxonomy of these sea ice inhabiting taxa is still unknown (Oliver

and Beatty 1996; Friedrich and Hendelberg 2001; Derraik et al. 2010) and a topic of current research. The ‘white’ acoel morphotype may possibly instead be a platyhelminth but given the evolving research on the relationship of Acoela and Platyhelminthes we have here grouped them together, recognizing a separation may be likely (Achatz et al. 2013).

The literature survey was composed of both relatively early observations of Arctic sea ice fauna (Carey and Montagna 1982; Chengalath 1985) and more recent comprehensive lists (Riemann and Sime-Ngando 1997; Friedrich and De Smet 2000; Arndt and Swadling 2006; Pitusi 2021).

Halectinosoma finmarchicum, appearing most recently in Arndt and Swadling (2006), had been reclassified as *H. elongatum* in Clément and Moore (2000). Therefore, species data for both *H. finmarchicum* and *H. elongatum* were used in this study and are grouped under the latter. There were two instances where data on a species identified to genus level were considered species-level information, these are the Rotifera *Synchaeta* sp. A (Friedrich and De Smet 2000) and *Cephalodella* sp. A (Chengalath 1985). In both cases these organisms were observed in sea ice and identified as distinct from all other Rotifera in their respective samples.

Analysis and organization of data

A literature survey comprising over fifty years of research on Arctic ice meiofauna was conducted to gather trait information. Search terms for adequate literature included, for example, ‘sea ice meiofauna,’ ‘sympagic fauna,’ and ‘sea ice biota’ in addition to certain taxa names listed in overview articles and book chapters, such as Arndt and Swadling (2006) and Bluhm et al. (2017). Reference lists to insightful articles often pointed to additional sources. Occasionally, early taxonomic papers would also be searched for to fill in basic morphological data. When information pertaining to a trait (e.g., body size) was identified, the source was directly quoted or summarized and the taxonomic level of the material was recorded in a trait table for that particular species and trait. Based on this available evidence, a trait category of best fit (e.g., small, large) and the degree to which the trait is exhibited, known as a ‘fuzzy code’ (see ‘Fuzzy Coding Procedure’ in *Methods*), was then assigned. Species-level data were considered the most specific available information and was always searched for first, but the decision to assign a trait category often depended on material from multiple taxonomic levels and sources. If no information could be found at the species level, genus-level data were then searched for, continuing to the next highest taxonomic level until evidence for every species-trait combination was found, an approach used in earlier studies (Brun et al. 2017). A common caveat of traits coding is that not all trait modalities are provided in every record of a given taxon, hence limiting insights into trait plasticity among regions. The trait-by-taxon table was organized by taxonomic group (Copepoda, Nematoda, etc.) and provided a column for species name, the assigned trait category, a fuzzy code, sources and quotes, and the taxonomic level of information. This trait table can be found in Online Resource #2.

Selection of traits

Before compiling a list of traits and trait categories, existing databases were consulted to gain a broader idea of

relevant traits commonly used in literature (Costello et al. 2015; Degen et al. 2018; Degen and Faulwetter 2019; Martini et al. 2020; Cifoni et al. 2021). Eleven traits considered especially applicable to fauna which spend at least part of their life cycle in ice and encounter the extreme conditions found within were chosen. These traits were grouped into four broad categories as in Litchman et al. (2013) and Degen et al. (2018): *morphological*, which here included body length, body width, body shape, and flexibility; *physiological*, which included temperature and salinity tolerance; *life history*, here consisting of habitat occurrence and if all life stages are found in sea ice; and *behavioral*, which here included feeding mode while in ice, diet while in ice, and mobility. These 11 traits were further divided into trait categories and are summarized in Table 2.

“**Body length**” and “**body width**” were coded as the range of adult body sizes of both males and females. “**Body shape**” describes the form of an organism and can be a combination of elongate, globulose, fusiform, or compressed. All are relevant for determining which part of the brine channel system a species can inhabit. “**Flexibility**” describes how easily an organism can flex or manipulate its body shape and is a proxy for rigidity, a trait relevant for moving around tight brine channels. “**Salinity tolerance**” describes if an organism can survive fresh, brackish, marine, or briny water and minimum tolerance is here assumed to be 25–40 by default for marine organisms. Note that we used the salinity definition of the practical salinity scale (PSS) (Lewis, 1980), as most literature we cite utilizes this scale. Because it is based on the ratio of the conductivity of a water sample to a standard, it does not have a unit. “**Temperature tolerance**” describes the degree to which an organism can survive above- and/or below-zero conditions and is here assumed to be at least -2 to 0 by default for Arctic organisms. The combination of temperature and salinity tolerance would determine whether and at what time of year organisms can inhabit the ice interior.

The “**habitat occurrence**” trait is intended to reflect the degree a species relies on the sea ice (‘sympagic’ being most extreme) and its likely origin through its co-occurrence in other realms (‘pelagic’ and/or ‘benthic’). “All stages found in sea ice” likewise infers how reliant a species is on the sea ice habitat throughout its life cycle, although which life history stages are found in sea ice are not always known or published. “Feeding mode while in ice” describes the main method of ingestion of ice organisms and “diet while in ice” characterizes their known food sources during one or more seasons in sea ice. Both traits are important for understanding sea ice nutrient and energy fluxes. “**Mobility**” describes the various modes of transport an organism uses and is relevant to ice colonization.

Table 2 List of traits and trait categories chosen to characterize sea ice meiofauna

Trait	Trait category
Morphological	
Body length (adult forms) [μm]	Small (< 200 μm); Small-Medium (200–400 μm); Medium (400–700 μm); Medium-Large (700–1000 μm); Large (> 1000 μm)
Body width (adult forms) [μm]	Small (< 25 μm); Small-Medium (25–50 μm); Medium (50–100 μm); Medium-Large (100–200 μm); Large (> 200 μm)
Body shape	Elongate (worm-like); Globulose (round); Fusiform (spindle-like); Compressed (laterally – copepods, dorso-ventrally – flatworms)
Flexibility	Rigid (hard skeleton); Semi-Flexible (no skeleton but protective structure); Flexible (no form of protective structure)
Physiological	
Salinity tolerance [unitless]	Tolerant: 0–25; 25–40; 40–60; 60+
Temperature tolerance [$^{\circ}\text{C}$]	Tolerant: < – 4; – 4 to – 2; – 2 to 0; 0 <
Life history	
Habitat occurrence	Sympagic only; Sympagic–pelagic; Sympagic–benthic; Sympagic–pelagic–benthic
All stages found in sea ice	Yes; No
Behavioral	
Feeding mode while in sea ice	Filter/Suspension feeder; Scavenger/Predation; Grazer; Absorption; Non-Feeding
Diet while in sea ice	Herbivore; Carnivore; Omnivore; Osmotrophic; Bacterio-/Ciliivore; Detritivore
Mobility	Attached; Swimmer; Crawler; Immobile

Table 3 Fuzzy coding explanation after Degen and Faulwetter (2019)

Code	Explanation
3	Taxon has total and exclusive affinity for a certain trait category
2	Taxon has a high affinity for a certain trait category, but other categories can occur with equal (2) or lower (1) affinity
1	Taxon has a low affinity for a certain trait category
0	Taxon has no affinity for a certain trait category

Fuzzy coding procedure

Fuzzy coding is a procedure that assigns a trait category to an organism based on the degree to which it exhibits that trait category. The procedure reflects the existence of biological plasticity, uncertainty, and the combination of multiple categories within one organism (Chevenet et al. 1994). Fuzzy coding establishes a common code that enables a comparison of data from multiple sources on a per-category basis (Degen et al. 2018) and can also represent qualitative data in a quantitative way. This analysis utilizes a code from 0 to 3 and follows the system of the Arctic Traits Database (Table 3) (Degen and Faulwetter 2019). While this procedure is not without shortcomings and introduces some subjectivity into trait-based analyses, Degen et al. (2018) found in an experiment that participants coded 83% of the trait categories of three common Arctic benthic invertebrates identically. This suggests that the introduced subjectivity remains low and will likely be

reduced as more experts are involved in the fuzzy coding process (Degen et al. 2018).

For one coding example, all Copepoda possess rigid, chitinous frames (Reid and Williamson 2001). Additionally, Krembs et al. (2000) found that harpacticoid copepods could only fit through ice capillaries that were 100% their body width, confirming the rigidity of the exoskeleton. This exclusive rigidity means all species of Copepoda are coded as a “3” for the flexibility category “rigid.” As a more difficult example: white Acoela are described as “slender and drop-shaped” in literature (Janssen and Gradinger 1999), which does not fit directly into any of the available body shape categories and must therefore be a combination of them (Table 2). With “drop-shaped” considered analogous to a mixture of “globulose” and “fusiform”, and “slender” synonymous with “elongate”, white acoels are here coded as “2” in the fusiform, globulose, and elongate categories.

A specific coding procedure was followed for the temperature and salinity tolerance traits, as ranges were involved. If the tolerance of a species was fully within a single category it was coded “3.” If it fully or mostly covered multiple categories, these were coded “2.” However, if the range only covered a small portion of a category, this category was coded “1.” For example, *Halectinosoma* spp. were noted as found between salinities of 12.4 and 33.9 by Kramer and Kiko (2011). This range covers *most* of the categories 0–25 and 25–40 and therefore each was coded as “2.” In the cases where a species was recorded as surviving a specific salinity or temperature but without movement, this was coded as “1.” Ranges (despite their difficulty in fuzzy coding) were

used in this study instead of maximum tolerances because of the scarcity of temperature and salinity tolerance data. Many species would have missing data or misleadingly low tolerances if only one data point was used.

Results

Taxonomic resolution and data availability

There were 308 trait-by-species instances in total from this study (28 species × 11 traits). In all cases, the proportion of information for each trait represents the highest taxonomic resolution found, and information was often used from multiple taxonomic levels for a single trait (Fig. 1). All data generated and analyzed in this study are included in this published article and its supplementary information files (see Online Resource #2).

Around 50% of the data were found at the species level and 20% at the genus level (Fig. 1). Almost a quarter of all data were found at the much coarser resolution levels of

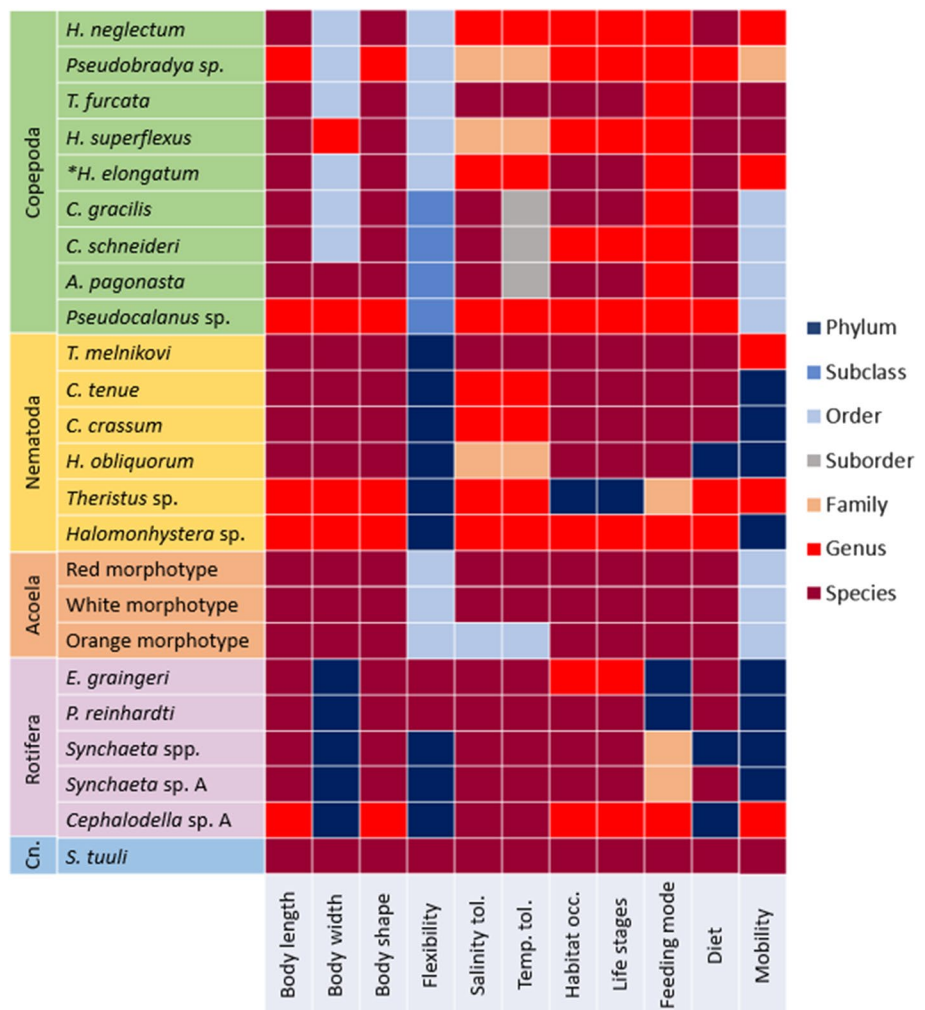
phylum (15%) and order (7%) (Fig. 1). However, in nearly every case this low-resolution data was only used for basic mobility and flexibility information; traits which do not vary beyond coarse taxonomic classifications in the studied taxa. The fraction of species-level specific information was highest for Cnidaria and Acoela at 100% and 76%, respectively. Rotifera, Copepoda, and Nematoda possessed 53%, 44%, and 44% species-level coverage, respectively (Fig. 1).

Trait modality composition in sea ice meiofauna

Body length

Sympagic meiofauna length varied widely by taxa (Fig. 2a). Interestingly, 18 species that represented Cnidaria, every entity of Copepoda and Nematoda and a majority of Acoela were listed in literature as capable of growing beyond the ~ 500-µm threshold commonly used to define meiofauna (Bluhm et al. 2017). On average, Rotifera possessed the smallest body size. All taxa except Nematoda typically grow to a maximum of less than 1 mm long, although some

Fig. 1 The taxonomic level of information found for 28 sea ice meiofauna covering 11 traits *Information pertaining directly to Acoela morphotypes is included as species-level data. ^atol. is an abbreviation for tolerance. ^bocc. is an abbreviation for occurrence



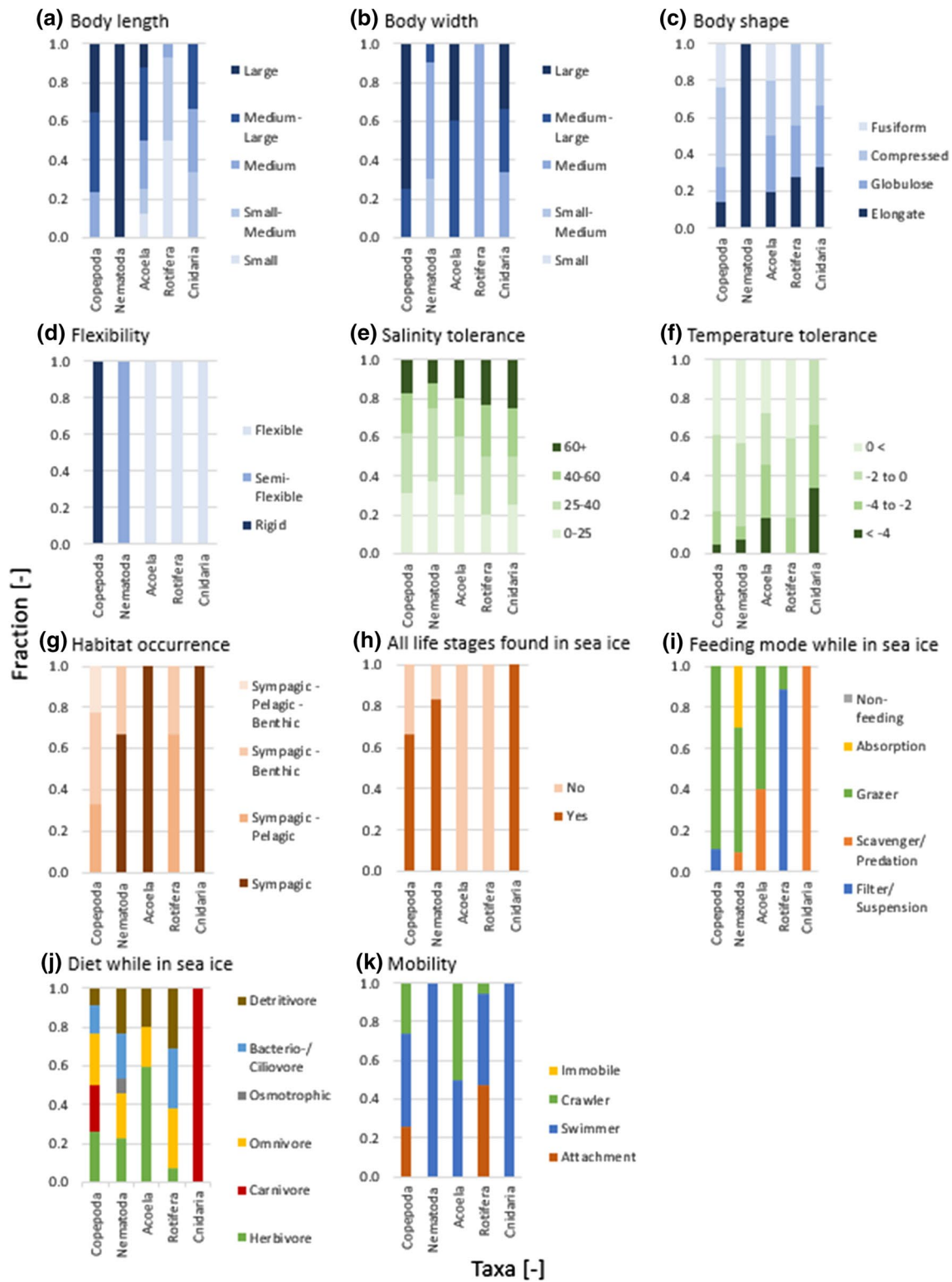


Fig. 2 Relative composition of trait categories within 11 traits coded for 28 sea ice meiofauna taxa. Traits are labeled from A-K accordingly

Copepoda taxa such as *Pseudocalanus* sp. can exceed this (Krøyer 1845).

Body width

The majority (57%) of species had body widths < 200 µm, consisting predominantly of Nematoda, Rotifera, and Cnidaria. However, all Copepoda species and a majority of Acoela species can grow wider than 200 µm (Fig. 2b) (Tchesunov and Riemann 1995; Friedrich 1997; Janssen and Gradinger 1999; Krembs et al. 2000; Bluhm et al. 2007; Kramer et al. 2011).

Body shape

Elongate and compressed body shapes represent the two most common categories found in ice meiofauna and are applicable to nearly all the taxa (Fig. 2c). In addition, many species in Copepoda and Acoela are characterized as “fusi-form” or tapered in shape (Sars 1911; Smirnov 1932; Janssen and Gradinger 1999).

Flexibility

All three flexibility trait categories are considerably represented in the fauna (Fig. 2d). Copepoda taxa were coded as rigid because they all possess a firm exoskeleton (Reid and Williamson 2001). Species of Nematoda are flexible in lateral movement but less yielding by cross-section due to the presence of a cuticle (Page et al. 2014) and were therefore coded as semi-flexible. Acoela, Rotifera, and Cnidaria are well documented as exhibiting high plasticity of their soft bodies (Krembs et al. 2000; Schünemann and Werner 2005; Piraino et al. 2008) and were hence coded as flexible.

Salinity tolerance

Most groups can tolerate salinities at either extreme; at least 20% of three taxa groups could tolerate brine salinities of 60+ and at least 25% of four taxa groups could tolerate 0–25 (Fig. 2e). Brine tolerance was best documented in Cnidaria (yet $n = 1$ only) and Rotifera and brackish tolerance was best documented in Nematoda and Copepoda. Otherwise, salinity tolerance was relatively uniform across all taxa. Almost all studied species could tolerate 0–25 to some degree (Heip et al. 1985; Grainger and Mohammed 1990; Friedrich and De Smet 2000; Moens and Vincx 2000). As earlier stated, it is assumed that Arctic marine organisms tolerate a salinity of 25–40 as a baseline.

Temperature tolerance

Less than 10% of sea ice Nematoda, Copepoda, and Rotifera are documented as capable of tolerating temperatures below -4 °C (Fig. 2f). At least 17% of all taxa except Nematoda are documented as tolerating -2 to -4 °C. Survival at low temperatures is best documented in sea ice Cnidaria and Acoela. All species except *S. tuuli* are believed to tolerate above-zero temperatures (Johnson and Olson 1948; Berzins and Peljer 1989; Moens and Vincx 2000; Siebert et al. 2009). As earlier stated, it is assumed that Arctic organisms tolerate the thermal range 0 to -2 °C as a baseline.

Habitat occurrence

Harpacticoida are mainly found in both sympagic and benthic habitats, while most Cyclopoida are found in sympagic–pelagic habitats (Fig. 2g) (Grainger et al. 1985; Horner and Murphy 1985; Mohammed and Neuhoof 1985; Grainger 1991; Carey 1992; Schünemann and Werner 2005). Most Nematoda are either only sympagic or sympagic–benthic (Fig. 2g) (Tchesunov and Riemann 1995; Tchesunov and Portnova 2005; Portnova et al. 2019; Pitusi 2021). All Acoela are only known from the ice (Fig. 2g). Rotifera of the genus *Synchaeta* are known as sympagic–pelagic, while *Encentrum*, *Proales*, and *Cephalodella* are sympagic–benthic (Fig. 2g) (Friedrich and De Smet 2000). The Cnidaria *S. tuuli* is only known from sea ice (Siebert et al. 2009).

All life stages found in sea ice

The bulk of Copepoda and Nematoda are found in all life stages in the ice, and no species of Acoela or Rotifera has been found in all life stages (Fig. 2h) (Grainger et al. 1985; Tchesunov and Riemann 1995; Friedrich 1997; Janssen and Gradinger 1999; Friedrich and De Smet 2000; Schünemann and Werner 2005). *Sympagohydra tuuli* exists in the sea ice at all life stages (Fig. 2h) (Siebert et al. 2009).

Feeding mode while in sea ice

For feeding mode information (Fig. 2i), 64% of the taxa were coded as “grazer,” consisting mostly of Copepoda, Nematoda, and Acoela (Grainger and Hsiao 1990; Tchesunov and Riemann 1995; Janssen and Gradinger 1999; Kramer 2011; Moens et al. 2013). “Filter/suspension feeding” describes 32% of taxa, mostly pelagic species of Rotifera and Copepoda (Pourriot 1979; Grainger and Hsiao 1990; Fontaneto and De Smet 2015; Wilke et al. 2020). “Scavenger/predation” included 14% of species and consists of Acoela, the Nematoda species *Cryonema crassum*, and the predatory Cnidaria *S. tuuli* (Friedrich 1997; Bluhm et al. 2007; Siebert et al. 2009; Kramer 2011). Many species are described by

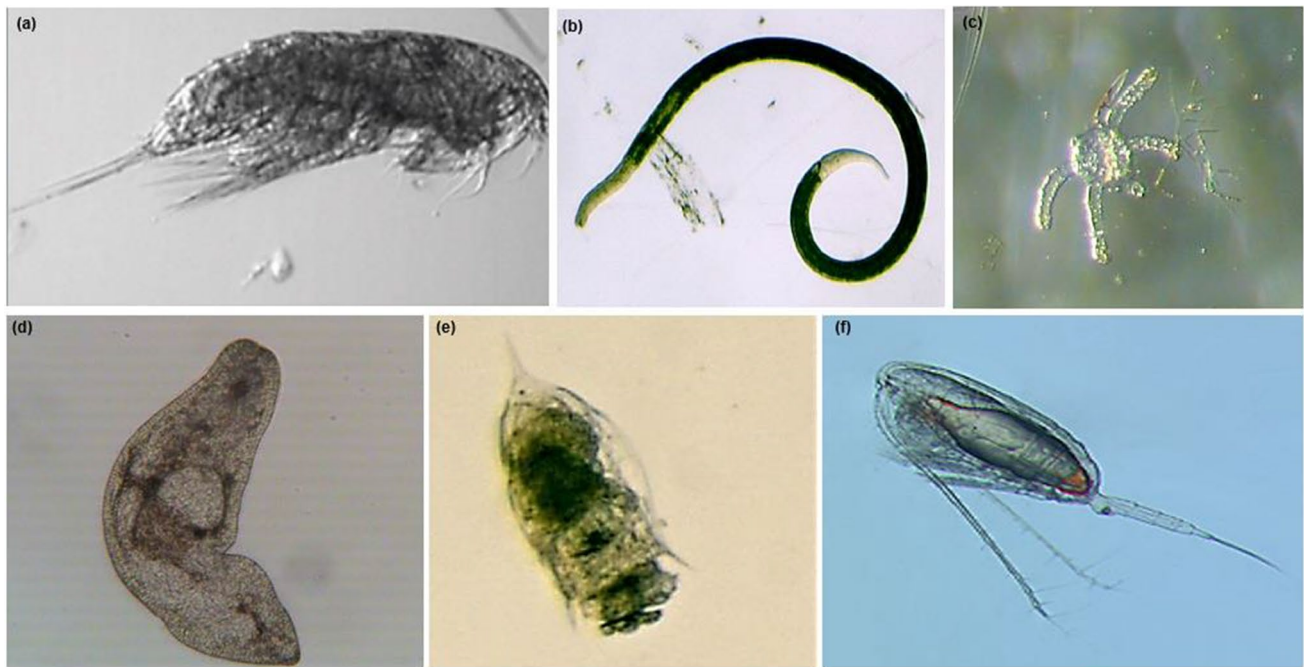


Fig. 3 **a** Harpacticoida, **b** Nematoda, **c** Cnidaria, **d** Acoela, **e** Rotifera, and **f** Calanoida. Photographs: **a** Julia Ehrlich, University of Hamburg, **b, c, e** Miriam Marquardt, UiT The Arctic University of

Norway/UNIS, **d** Kyle Dilliplaine, University of Alaska Fairbanks, **f** Russell Hopcroft, University of Alaska Fairbanks

multiple feeding types. Though inconclusive, the sympagic Nematoda *Theristus melnikovi* and *C. crassum* are suggested to absorb dissolved organic matter (DOM) for sustenance by Tchesunov and Riemann (1995) and Tchesunov and Portnova (2005) after many individuals were found with empty stomach contents. DOM has been experimentally shown to be a food source for some marine Nematoda (Pape et al. 2013).

Diet while in sea ice

Diet while in sea ice information is very diverse (Fig. 2j). While 71% of species were coded in some way as herbivores, most species show additional variety in their diets. For instance, Kramer (2011) stated that only Harpacticoida taxa *Tisbe* spp. and *Halectinosoma* spp. could be classified as almost exclusively herbivorous, while she classified the rest of the studied sea ice meiofauna as carnivorous–omnivorous–bacterivorous in the spring pre-bloom. Cyclopoida were considered carnivorous–omnivorous–detritivorous, relying much more on metazoan-derived food sources and less on diatoms than previously known. Nematoda, while also feeding on a high proportion of diatoms, were said to possess a “rather ciliate-based diet,” be herbivorous–bacterivorous in summer and cilivorous–omnivorous–bacterivorous–detritivorous in spring. Red Acoela were considered herbivorous–cilivorous and white Acoela (that could be

platyhelminths) herbivorous–detritivorous. Rotifera also feed more on ciliates than diatoms and were classified as cilivorous–omnivorous–bacterivorous–detritivorous (Kramer 2011). The Cnidaria *S. tuuli* is exclusively a top predator in the brine channel network and is assumed to play a key role in the sympagic ecosystem (Piraino et al. 2008).

Mobility

Swimming and crawling are the two most common mobility trait categories of sea ice meiofauna (Fig. 2k) and were observed in some capacity in 100% of the studied taxa. In addition, Harpacticoida are often particle attached (Kjørboe 2000; Koski et al. 2005) and can adhere to suspended particles. Rotifera also possess a cement gland and can temporarily attach to surfaces (Allen 1968; Yang and Hochberg 2018).

Discussion

High taxonomic resolution but limited data availability exists in ice meiofauna studies

Example imagery of each taxa group studied is presented below for reference (Fig. 3). The high proportion of species- and genus-level data found in the literature review

(Fig. 1) strengthens the confidence that most trait categories assigned in this study apply either directly or closely to the 28 species. Furthermore, although data on Cnidaria and Acoela (albeit only morpho-species for Acoela) possess a taxonomic resolution far higher than that of Rotifera, Copepoda, and Nematoda (Fig. 1), the former possess few species known from the ice. Acoela has just three morpho-species and Cnidaria just one, leading to a high proportion of species-level studies in the literature. The lower resolution of the other taxa was in part related to some genera being in taxonomic limbo like *Pseudocalanus* sp. in Copepoda (Holmborn et al. 2011) or remaining unidentified to species level like *Synchaeta* sp. A in Rotifera.

General trends in the availability and resolution of trait information can be inferred by examining the percent coverage heat map of Fig. 1. This indicates research gaps and identifies directions where traits require more research. First, body length and body shape were the traits with the highest coverage. In contrast, flexibility and mobility possessed the lowest resolution, largely because basic order- or phylum-level information was sufficient to cover these traits. Salinity and temperature tolerance were the two traits most difficult to find information for, likely as specific experimental approaches are necessary with sufficient animals to establish tolerance ranges. Species-level salinity tolerance information for ice meiofauna was only found for Copepoda in Grainger and Mohammed (1990), Cnidaria in Siebert et al. (2009), and a variety of sympagic meiofauna in Friedrich (1997). In general, more salinity tolerance than temperature tolerance studies existed, and cold tolerance was often neglected in favor of heat tolerance. Surprisingly, besides Friedrich (1997) and Siebert et al. (2009), no below-zero experimental temperature tolerance studies were found for ice meiofauna. Body width also possessed a low resolution, for species lengths were much more commonly listed than widths and very old taxonomic papers were often required to find this information (Krøyer 1845; Bastian 1895; Willey 1920). Feeding mode and diet possessed good resolution for all taxa except Rotifera.

Ice meiofauna morphological characteristics are well adapted to brine channel structure

Size is an important variable limiting access of biota to the sea ice brine channel network, where brine channels typically fill 5 to 25% of the sea ice volume (Golden et al. 1998). Individual channels vary in diameter from less than 1 μm to over 1 mm, while length can range from pockets just handfuls of μm long to several dm long drainage channels, depending on location in ice floe and season (Cole and Shapiro 1998). Therefore size matters and provides a strong constraint on what species may inhabit the ice. Because most of the ice meiofauna species studied grow to less than

1 mm (Fig. 2a), they can fit their entire bodies within many of these channels, presumably providing refuge from larger predators (Bluhm et al. 2017). Taxa with large body sizes are usually assumed to possess disadvantages in the sea ice brine channel network and may be unable to access certain brine capillaries. Yet, factors like small body widths or high flexibility can confound this trait and still allow for channel penetration (Krembs et al. 2000). For example, sympagic Nematoda couple extensive length with high flexibility and narrow body widths (Tchesunov and Riemann 1995). However, limited information is available of the confining role of body length and width for ice meiofauna, where in contrast to sediment habitats, individual ice crystals cannot be moved and the habitat is dimensionally fixed.

A diameter of < 200 μm is a threshold which represents the approximate width of roughly half the capillaries that comprise the brine channel network (Krembs et al. 2000). This study reveals that the majority of sympagic meiofauna species likewise possess widths < 200 μm (Fig. 2b) and hence are adapted to utilize these small channels for protection and feeding on microorganisms (Krembs et al. 2000). However, this also demonstrates that nearly 50% of the brine channels might not be inhabitable for meiofauna taxa, reducing grazing pressure on channel-inhabiting algae, protozoa, and bacteria.

Most ice meiofauna possess elongate, compressed, or fusiform body shapes (Fig. 2c). Species with especially elongated body shapes are better able to squeeze and snake their way through the narrow brine channel network (Krembs et al. 2000; Bluhm et al. 2017), comparable to benthic meiobenthos which share a similarly interstitial habitat (Urban-Malinga 2013). A tapered, fusiform shape may exemplify another adaptation to the narrow brine channel network, as this configuration may reduce the likelihood of becoming stuck.

As noted in Fig. 2d, all taxa except Copepoda are coded as either flexible or semi-flexible. Flexible and semi-flexible organisms possess an advantage in the narrow and twisting brine channel network. These traits are also common in organisms living in interstitial sediment habitats (Curini-Galletti et al. 2020) and may be a reason why benthic organisms like Nematoda and Acoela thrive in the ice (Krembs et al. 2000).

Salinity and temperature tolerance are key adaptations possessed by all ice meiofauna taxa

The relative uniformity of salinity tolerance depicted in Fig. 2e confirm our hypothesis that most ice meiofauna species are well adapted to the extreme salinity dynamics of the brine channel network (Grainger and Mohammed 1990; Gradinger et al. 1991; Friedrich 1997; Riemann and Sime- Ngando 1997; Arndt and Swadling 2006).

However, few studies describing full tolerance ranges existed, and most species-level information was instead inferred from the temperature and salinity at which an organism was sampled (e.g., from Friedrich and De Smet 2000; Marquardt et al. 2011). Most data were recorded at genus or family level and this lower taxonomic resolution, coupled with the fact that many sympagic species share genera and family (Friedrich and De Smet 2000; Bluhm et al. 2017; Pitusi 2021), naturally caused the data to tend toward uniformity among taxa. Additionally, brackish water tolerance was better documented than brine tolerance, and the fact that almost all studied species could tolerate 0–25 to some degree introduces a bias toward lower salinities in the data. Tolerance in the 40–60 and 60+ categories may exist at a higher frequency than documented, especially given the hardness that taxa like Harpacticoida and Nematoda exhibit in interstitial sediment habitats, hypersaline ponds, and other extreme environments (Ranade 1957; Heip et al. 1985; Damgaard and Davenport 1994; Zeppilli et al. 2018; Hotos 2021). Personal observations from experiments on unidentified fast ice Nematoda and the orange Acoela morphotype indeed confirm salinity tolerance upward of 60 (Kaufman, Bluhm and Gradinger, personal communication).

Tolerance of above-zero temperatures was far better documented than below-zero (Fig. 2f), which provides evidence that every species of all groups except Cnidaria can tolerate above-zero temperatures (Johnson and Olson 1948; Berzins and Peljer 1989; Moens and Vincx 2000; Siebert et al. 2009). Data in Fig. 2f exhibit the same uniformity as data in Fig. 2e and likewise suggest adaptations to the thermal fluctuations of the brine channel network (Friedrich 1997). Just as for salinity, limited data coupled with high rates of genus- and family-level information created taxa-wide uniformities that confound the results.

Habitat occurrence and portion of life cycle spent within sea ice varies by taxa and species

Sea ice meiofauna do not only occur within the ice, but a variety of habitats. The habitats Copepoda are found in break down predictably based on their order (Fig. 2g). Harpacticoida, common inhabitants of the benthos, are found in both sympagic and benthic habitats. Cyclopoida and Calanoida, regular inhabitants of the pelagic zone, are mostly found in sympagic–pelagic habitats. Most Nematoda, not typical inhabitants of the pelagic realm, are predictably either sympagic or sympagic–benthic (Moens et al. 2013). The fact that all Acoela are only known from the ice may be influenced by their unknown taxonomic status (Janssen and Gradinger 1999; Friedrich and Hendelberg 2001) and the fact that Acoela in general – along with other soft-bodied meiofauna – often do not preserve well with common preservatives and frequently remain unidentified

(Curini-Galletti et al. 2020). Generally, however, Acoela and Platyhelminthes (again we note one of the ice Acoela may be a platyhelminth) are most prominent at the seafloor (Achatz et al. 2013). Additionally, there is debate on whether the Cnidaria *S. tuuli* is endemic to the sea ice or not. Bluhm et al. (2007) and Marquardt et al. (2011) assume it has a sympagic–benthic lifestyle, supported by the fact it was found in seasonal sea ice within an isolated fjord and in very shallow coastal waters. Siebert et al. (2009), who found it above 3000-m deep water in the central Arctic Ocean and cite its extreme salinity and temperature tolerance, believe it is fully sympagic.

Some ice meiofauna species live in the sea ice for all stages of life, while others do not. Most Copepoda and Nematoda have been found at all life stages (Fig. 2h), thanks to numerous studies that identified these life stages to the species level (Cross 1982; Grainger et al. 1985; Friedrich 1997; Portnova et al. 2019). The reason no species of Acoela or Rotifera has been found in all life stages may potentially be a result of the limited research effort on sea ice meiofauna. Difficulty at distinguishing juvenile Acoela from adults was also noted in Friedrich (1997). Siebert et al. (2009) found reproducing individuals of *S. tuuli* within the ice.

These conclusions reinforce the fact that most stages of sympagic meiofauna utilize the sea ice as a nursery and feeding environment (Grainger 1991; Bluhm et al. 2017, 2018), irrespective of the additional habitats they are found in. Sympagic meiofauna species are often found in higher concentrations within the ice than in the pelagic or benthic zones (Carey and Montagna 1982; Grainger 1991; Bluhm et al. 2017), meaning that losing ice cover could have a disproportionate impact even if the same taxa are found in other habitats. Losses and reductions of sea ice meiofauna have already been reported due to changes in ice dynamics (Melnikov et al. 2001; Kiko et al. 2017; Leasi et al. 2021). A rich sea ice community contributes to strong sympagic–pelagic and sympagic–benthic coupling in the Arctic Ocean through processes, such as the vertical pump (Søreide 2013; Wiedmann et al. 2020), where the sinking of small invertebrates and algae out of the ice bring energy and nutrients from the surface toward the sea floor. Therefore, losses in diversity and abundance of ice meiofauna and the larger sea ice community due to habitat loss will not only impact sympagic food webs, but also pelagic and benthic ones if fewer meiofauna melt out of sea ice in the spring (Leasi et al. 2021).

Feeding mode and diet of ice meiofauna are reflective of seasonal changes in sea ice community

Most sea ice meiofauna species were at least coded as grazers (Fig. 2i). Of these, sympagic Copepoda possess mouth appendages specialized for grasping and holding (Grainger and Hsiao 1990). Certain Nematoda also feature buccal

teeth for scraping (Moens et al. 2013) and Acoela have been observed eating diatoms (Friedrich 1997; Janssen and Gradinger 1999). Suspension feeding Rotifera use cilia to filter small particles from the water column (Pourriot 1979). *Sympagohydra tuuli* has been observed preying on Nauplii and Rotifera, meaning the Cnidaria is a rare predator within the ice brine channel network (Siebert et al. 2009).

Although most sympagic meiofauna are thought to feed on microalgae (Grainger and Hsiao 1990; Nozais et al. 2001), this comprehensive literature study showed that diatoms make up a relatively small proportion of diet data (Kramer 2011) (Fig. 2j). This is probably largely thanks to seasonal flexibility, where species switch from a diatom-based diet in the productive period to an omnivore-based diet during other seasons (Kramer 2011; Gradinger and Bluhm 2020). Kramer (2011) used stable isotopes, fatty acids, and feeding experiments and discovered sympagic meiofauna possess a highly diverse diet year-round that does not match the earlier, mostly algae-based prey assessment that was only conducted in the productive period (Grainger and Hsiao 1990). Flexible feeding strategies can be an adaptation to the dynamic sea ice habitat which is both seasonal and extreme (Kramer 2011) and may prove to be an advantage given uncertainties of future diatom bloom timing and length (Bluhm et al. 2018). In summary, this compilation supports the emerging notion that the food web inside the sea ice is more complex than previously appreciated (Gradinger and Bluhm 2020).

Mobility modes are uniform across taxa, but variable in degree

Swimming and crawling were the two most common mobility categories of the species studied, but some taxa are better swimmers and crawlers than others (Fig. 2k). Crawling can be of benefit in interstitial habitats, like the ice brine channel network (Krembs et al. 2000). Of less certainty is how poorly swimming organisms, including Copepoda and Nematoda, can traverse the pelagic zone and make it into the ice (Kramer 2011; Kiko et al. 2017). Suggestions have ranged from being swept up from shallow sediments during storms at ice formation, captured with frazil ice crystals, or even via crustacean parasitism (Janssen and Gradinger 1999; Gradinger et al. 2009; Kiko et al. 2017). Taxa with better swimming ability like Rotifera, Acoela, and Cnidaria can enable quick access to food sources and may explain their more ciliorous and predatory natures (Kramer 2011). Ice-endemic organisms with low dispersal ability may have difficulties recolonizing new ice as seasonal differences in ice extent increase (Kiko et al. 2017).

Conclusion & Recommendations

In the present study, a range of morphological, physiological, life history, and behavioral trait categories were assigned to 28 species of Arctic sea ice meiofauna. This work is intended to be of use in establishing trait–function relationships in Arctic ecosystems and the trait information listed here can be paired with species abundance data to form spatial maps of characteristic traits, functional diversity, and vulnerability from a pan-Arctic perspective.

The 11 traits provided in this study are by no means exhaustive in characterizing the life history strategies and adaptations of sympagic meiofauna. Time/frequency of breeding, reproductive strategy, larval development, and life cycle duration could all be useful traits to code for, especially given the rapidly reducing duration of ice cover (Meredith et al. 2019) and the importance of sea ice to the protection and grazing of juvenile meiofauna (Bluhm et al. 2017, 2018). However, such trait data are difficult to generate as it requires lengthy experiments and establishing cultures.

To fill major gaps in literature scientists should record as much high-resolution species-level data as possible for sympagic fauna. Works which comprehensively study multiple traits at once can also be extremely useful for trait-based researchers and enable them to rely much less on low-resolution taxonomic data. Easy access to trait information will make trait-based methods, so valuable for the study of rapidly changing ecosystems, more accessible to the scientific community.

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Declarations

Competing interests The authors declare no competing interests.

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

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