On the rocks: recruitment and distribution patterns on deep-sea hard substrata in the Labrador Sea and Baffin Bay (Canada)

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Abstract

The study of larval recruitment and colonization patterns in hard-bottom benthic communities is crucial to the understanding of species distributions, community assembly, and the potential effects of anthropogenic activity and climate change on the maintenance of biodiversity. Expanding our knowledge of early and established communities is an important first step. To explore this need, I first examined recruitment patterns on four substratum types (mesh, plastic, stone, wood) deployed for ~1 y at four sites in bathyal Labrador Sea (Canada). I determined that colonial hydrozoan recruits dominated all substratum types and sites; arthropods, octocorals, and other anthozoans were sparser. The features of each substratum type facilitated differential recruitment patterns: the complex, three-dimensional structure of mesh had higher morphospecies richness and diversity, while the sheltered, larger surface area of plastic had higher abundance and density by recruits. Wood, as a single elongated panel, had the most surface and canopy coverage. Secondly, I examined regional diversity and zonation patterns of morphospecies colonizing terrigenous ice-rafted dropstones at bathyal depths in the Labrador Sea (LAB) and Baffin Bay (BAF). Based on in-situ images, dropstones exhibited more epibenthic megafaunal richness than surrounding finer-grained substrata and, following analysis of collected dropstones, a total of 101 taxa spanning 10 phyla were recorded with bryozoans dominating numerically at all depths. The richness of dropstone communities was higher in LAB than BAF overall, though 19 morphospecies spanned both locations. Zonation patterns were consistent, with a majority of morphospecies positioned above the stone-sediment boundary or at the boundary, and one morphospecies of polychaete below. Ecological interactions appeared to influence both positioning and regional distributions. By combining early and established

community studies, my thesis provides data on how deep-sea hard-bottom epibenthic assemblages form and develop.

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Co-Authorship Statement

The research outlined in this thesis, including experimental design and data collection and analysis, was conducted by Sophie Wolvin (noting that the deployment and retrieval of some larval recruitment frames occurred prior to this thesis) under the supervision and guidance of Annie Mercier, with additional input from Jean-François Hamel throughout the project. All manuscripts were written by Sophie Wolvin with intellectual and editorial input offered by co-authors as follows:

Authorship for Chapter 2: Wolvin, S; Hamel, J.-F.; Mercier, A. In preparation.

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Chapter 1: General Introduction

1.1 Hard-bottom habitats and associated communities in the deep sea

Hard substrata are less common in the deep sea than soft sediments but provide an essential habitat for the epifaunal communities that form on and around them (reviewed in Davis 2009). Benthic communities on hard substrata are primarily composed of sessile organisms and their epibionts, sometimes termed "fouling" species when they colonize hard substrata that are anthropogenic in nature, such as oil rigs (Page et al. 2008), wind farms (De Mesel et al. 2015), or ship hulls (Chan et al. 2016). Hard-bottom communities are phylogenetically diverse, though they are usually believed to converge into similar functional groups (Wahl 2009a). Sessile, suspension-feeding organisms are common, with many species forming relatively large biogenic structures, encrusting the surface, or building colonies (Wahl 2009a; Young 2009).

The function of a hard substratum in community formation is multifaceted. Firstly, it can act as an anchor for sessile, suspension-feeding organisms; it can also elevate them above the surrounding seafloor for better access to food and vantage during broadcast spawning (Jenkins et al. 2009). Secondly, hard substrata contain features or "microhabitats" that different organisms can exploit, providing heterogeneity in an otherwise potentially homogeneous finer-grained soft sediment environment (Hasemann et al. 2013). Thirdly, when providing anchors for large, autogenic engineers like corals or sponges, hard substrata also provide habitats for brittle stars, juvenile fish, and other epibionts (Metaxas and Davis 2005; Roberts et al. 2009; Buhl-Mortensen and Buhl-Mortensen 2018; Dunham et al. 2018). In polar and subpolar regions, assemblages of structure-forming corals and sponges support critical populations by creating complex heterogenous microhabitats in which prey can hide and predators can feed, including

commercially important species such as rockfishes and squid, as well as allowing epibiotic species better access to food (Dale et al. 1989, Beaulieu 2001; Miller et al. 2012; Pierrejean et al. 2020).

Community composition on hard substrata typically changes over time as it matures, from the first opportunistic recruits to a more species-rich and diverse community (Noël et al. 2009). Though species vary, prevalent megabenthic epifauna on hard substrata in the deep sea include cnidarians, arthropods, bryozoans, echinoderms, annelids, and nematodes (Wahl 2009a; Young 2009; Roy et al. 2015). Moreover, many species of bacteria also play an important role in stimulating metamorphosis and settlement of other species to hard substrata (Hadfield 2011). The patterns of early colonization and ecological succession within a community depend on a complex interaction of factors, including but not limited to larval supply, intra- and interspecific tolerance or facilitation, and the nature of the substrata, among others (Jenkins et al. 2009; Wootton et al. 2009). Aspects of these patterns, such as the role of biofilms in settlement and species distributions within macrofouling communities have been studied in shallow, warm-water environments for the better part of a century (McDougall 1943; Richmond and Seed 1991; Wahl 2009b). However, only in the last few decades have similar studies in the deep sea of mid latitudes begun (reviewed by Young 2009), and even fewer have addressed high latitudes (Kukliński 2009; Meyer-Kaiser et al. 2019, 2022).

1.2 Study of recruitment, colonization, and succession in the deep sea

Hard-bottom communities in the deep sea have historically been difficult to study, especially in regions such as the polar and subpolar seas where factors such as remoteness, weather limitations or high cost to access can limit the frequency and duration of field expeditions. More recently, the use of remotely operated vehicles (ROVs) has opened deep-sea

regions around the world to artificial substrate deployments, video surveys, and high-resolution imaging, as well as targeted collection of natural substrata with their associated epi- or endofaunal communities (Schulz et al. 2010, Schoening et al. 2012; Girard et al. 2016; Meyer-Kaiser et al. 2019; Górska et al. 2020). However, months when ice conditions enable research vessel access limit data collection to this window and only occur under calm weather conditions, except where researchers overwinter on site or leave equipment in situ until collected by the next expedition opportunity.

Larval settlement and recruitment patterns have long been studied using artificial and natural substratum deployments wherein standardized panels or blocks are placed in target locations and recovered after a period of time. Such studies can examine colonization and growth rates (Beaulieu 2001; Barnes 2017); preferences between differing surface structures and substratum types (Cuvelier et al. 2014; Girard et al. 2016), and the role of grazing, predation, and other species interactions (Konar 2007; Kukliński and Bader 2007; Vieira et al. 2016). However, these types of studies are less useful in examining more mature communities given that their development in the deep sea has been estimated to take decades, especially at higher latitudes where they appear to form more slowly (Meyer-Kaiser et al. 2019). Natural hard substrata such as rocks and biogenic material such as sunken wood or a dead coral skeleton on the sea floor are useful for examining epifaunal communities formed over these lengthier time scales because they are limited in size, often isolated from other hard substrata by surrounding finer-grained sediments, and therefore hard-bottom fauna (Osman 1977; Meyer et al. 2016). In polar and subpolar regions, hard substrata are largely introduced in the form of ice-rafted terrigenous "dropstones" carried out and deposited into the deep sea by glacial melt-out and icebergs (Heinrich 1988, Bennett et al. 1996; Edinger et al. 2011). Studying colonization patterns in both

early and mature epifaunal communities is integral to understanding how well they withstand and recover from disturbances (Ramirez-Llodra et al. 2011), especially as the polar regions become more and more accessible to and impacted by human activity.

1.3 Polar and subpolar deep-sea community recovery and resilience

Globally, deep-sea benthic species face growing risk from anthropogenically-driven disturbances that include harvesting of natural resources, pollution, and accelerated climate change (Ramirez-Llodra et al. 2011); polar and subpolar deep seas are not exempt. In some cases, temperate epifaunal hard-bottom communities in shallow waters can recover to pre-disturbed community composition over time periods as short as several months if the disturbance occurs at highly productive periods of the annual cycle (LaCroce et al. 2020). In deeper waters of 100 to 800 m, recovery of some benthic species from bottom fishing disturbances has been projected to take up to a decade (Lambert et al. 2014). Beyond those depths, in bathyal seamounts impacted by deepwater trawling for commercially valuable species such as the orange roughy, reversal of the impacts on epifaunal communities cannot be achieved within several decades (reviewed by Clarke et al. 2016, Goode et al. 2020). Sponges and corals up to ~ 3000 m deep showed more colony damage in trawled areas of the Aleutian Islands of Alaska than in untrawled areas (Heifetz et al. 2009), and heavy trawling in sponge gardens at the Schulz Bank seamount in the Arctic Mid-Ocean Ridge (~ 600 to 1500 m depths) resulted in little to no recovery of many larger epibenthic species, even after four years (Morrison et al. 2020). The long recovery times of these communities have been attributed to many factors, including slow larval recruitment rates (Meyer-Kaiser et al. 2019), fragmented populations (Hilário et al. 2015), and life-history traits of habitat-forming corals (Sherwood and Edinger 2009). For instance, colonies of *Primnoa resedaeformis* can be as old as 700 years (Sherwood et al. 2006) and exhibit

growth rates of just a few centimetres or even millimetres per year (Risk et al. 2002; Sherwood and Edinger 2009).

Indirect anthropogenic disturbances such as species invasions can also impact benthic communities. One such pathway is through colonization of plastic debris, which in the deep Arctic Ocean has increased along with human activity in the region (Tekman et al. 2017). Benthic organisms quickly colonize this debris, along with anthropogenic structures such as wind farms, oil rigs, and ship hulls, facilitating species invasions by bridging gaps in natural hard substrata that would otherwise limit range extensions (De Mesel et al. 2015; Chan et al. 2016; Tekman et al. 2017; Meyer et al. 2018). Changing environmental conditions associated with accelerated climate change can also facilitate the northward geographic expansion of taxa, potentially driving species invasions (Renaud et al. 2015). The seas between eastern Canada and West Greenland are predicted to undergo a shift in thermal regime; an increase in warming that would enable boreal species expansion into Arctic waters (Christiansen et al. 2014, CAFF 2017, Renaud et al. 2015). These environmental changes are also anticipated to negatively impact the recruitment and distribution rates of native species in the deep sea, as already documented in shallow-water polar environments (Kortsch et al. 2012; Al-Habahbeh et al. 2020). Collectively, these factors could have cascading impacts on an area of ecological, oceanographic, and economic importance.

1.4 Focal regions

The deep sea of eastern Canada is an important location in the global thermohaline circulation system, given that the Labrador Sea is one of few major sites where deep convective sinking occurs (Thornalley et al. 2011, McCartney 1992) (Figure 1.1). In this region, the Labrador Sea Water (LSW) mass enters the Deep Western Boundary Current (DWBC)

convectively to supply cold, fresh seawater into the North Atlantic Deep Water (NADW) mass that moves equatorially, acting as a global heat sink and contributing to meridional overturning circulation (Pickart et al. 2003; Saenko et al. 2014; Handmann et al. 2018). The West Greenland Current (WGC) supplies much of the freshwater in this convection as it enters the Labrador Sea, but Baffin Bay to the north contributes some, where the WGC enters along the east side of Davis Strait (Myers 2005). Recirculation in Baffin Bay occurs with additional water supplied from the Canadian Arctic Archipelago through Lancaster Sound, Jones Sound, and Nares Strait, before exiting in the Baffin Island Current on the west side of Davis Strait, entering the Labrador Sea along with outflow from Hudson Strait to form the Labrador Current (Curry et al. 2014). The Labrador Current supplies cold surface waters down the east coast of North America, but also influences deep convection when fluctuations occur in surface temperature and salinity (Lochte et al. 2020) (Figure 1.1).

These regions also harbour economically important fisheries for commercially valuable species such as Atlantic cod, herring, redfish, and snow crab (DFO 2021). Many of these species utilize hard-bottom communities of the deep sea as nursery grounds (Metaxas and Davis 2005; Baillon et al. 2012; Thurber et al. 2014; Pierrejean et al. 2020; DFO 2021). The continental slope of the Northwest North Atlantic is home to many coral habitats (Figure 1.2) that provide hotspots of biodiversity (Buhl-Mortensen and Mortensen 2005; Metaxas and Davis 2005; Baillon et al. 2014; Guy and Metaxas 2022), now at risk from trawling and pollution, with potential cascading effects to the fisheries (Clark et al. 2016; FAO 2019). Baffin Bay harbours unique methane seep habitats, delicate and easily disturbed ecosystems (Figure 1.2; Cramm et al. 2021) and is projected to be at risk of accelerated changes in salinity and temperature because of their unique water recirculation that traps freshwater melt-out from West Greenland glaciers (Castro de la

Guardia et al. 2015). Though both the Labrador Sea and Baffin Bay are critical to North Atlantic and global recirculation, their hard-bottom communities are poorly known.

1.5 Research gaps

Extant epibenthic macro- and megafaunal communities associated with isolated hard substrata in the deep sea have rarely been studied, despite examples of polar dropstones and tropical polymetallic nodules as "biodiversity islands" that concentrate hard-bottom epifauna at a higher richness than on surrounding finer-grained soft substrata (Mullineaux 1987; Hasemann et al. 2013; Amon et al. 2016; Meyer et al. 2016; Ziegler et al. 2017) (Figure 1.2). Studies have addressed larger-scale hard-bottom communities at both early (i.e., larval recruitment to artificial substratum deployments) and mature stages (i.e., natural substrata collections or video survey) at deep-sea hydrothermal vents (Gaudron et al. 2010; Metaxas and Kelly 2010; Cuvelier et al. 2014; Gollner et al. 2017; Sotomayor-García et al. 2023), seamounts (Genin et al. 1986; Mullineaux 1987; Mullineaux and Butman 1990; Clark et al. 2016; Goode et al. 2020; Morrison et al. 2020; Uhlenkott et al. 2023), rocky reefs (Meyer et al. 2014; Dunham et al. 2018), and canyons (Blankenship and Levin 2007; Miller et al. 2012; Girard et al. 2016; Guy and Metaxas 2022). However, individual, isolated stones that create a limited system for study of colonization patterns and distribution enable a more holistic understanding of mature hard-bottom communities (Osman 1977). Studies at this scale in the polar regions have been limited to a few video surveys using ROVs (Schulz et al. 2010, Hasemann et al. 2013; Meyer et al. 2016; Ziegler et al. 2017) or random sampling as part of surveys of both soft- and hard-bottom species (Atkinson 1989; Bluhm et al. 2005; Roy et al. 2015). The increasing risk to these habitats from anthropogenic impacts adds urgency to studies of the communities associated with hard substrata in the deep sea at a much closer scale to develop a more comprehensive baseline understanding.

Similarly, few studies of early successional communities in the deep sea through larval recruitment have examined the role of substratum type in recruitment patterns (Figure 1.3). Most studies have examined factors such as local environmental conditions, depth, altitude (i.e., height above the sea floor), proximity of larval supply, predation, and others (Jenkins et al. 2009; Vieira et al. 2016; Meyer et al. 2018). Typically, studies use just one substratum type, such as a roughened or otherwise prepared plastic panel (Mullineaux and Butman 1990; Bowden et al. 2006; Kukliński et al. 2013; Barnes 2017), or biogenic substrata such as glass sponge stalks, wood, or shells (Yund et al. 1987; Beaulieu 2001a, 2001b; Romano et al. 2014). Studies of substratum preference most often use paired substratum types with differing features such as stone and plastic or wood (Lacharité and Metaxas 2013, Cuvelier et al. 2014; Girard et al. 2016; Meyer-Kaiser et al. 2019) or more rarely three (Gaudron et al. 2010; Burkett et al. 2016). Even though these experiments provide useful information, more studies are needed to establish a better understanding of how all the differing features of substratum types can affect larval recruitment. Moreover, limiting the number of substrata available in a study could exclude certain species whose larval preferences are not met by the selection offered.

Finally, few studies have addressed recruitment and species distribution in the deep sea of the Canadian North Atlantic and Arctic, with the Greenland Sea and the coastal waters of Svalbard as the closest past study locations (Ronowicz 2007; Ørberg et al. 2018; Meyer-Kaiser et al. 2019), or more temperate waters to the south, between Nova Scotia and Bermuda (Calder 1996; Osman, Whitlatch, and Malatesta 1992; Lacharite and Metaxas 2013; Girard et al. 2016; Guy and Metaxas 2022). Therefore, how closely hard-bottom benthic communities in the northeastern Canadian regions might resemble these more southeastern Canadian regions remains unclear, because numerous biotic and abiotic factors could potentially affect species

distribution patterns among different regions. Benthic recruitment rates to hard surfaces drop rapidly with increasing distance from another hard substratum, given that nearby hard-bottom communities generally supply recruits (Meyer et al. 2016), and recruitment generally increases in the presence of "stepping stones" of hard substrata that enhance horizontal colonization (Meyer et al. 2018). In shallow-water environments, remoteness of a community affects species richness and recruitment (Barnes 2017) and in the deep sea of Antarctica, "remote" dropstones exhibit similar patterns (Ziegler et al. 2017). This dependence on proximity means that longitudinal variation could occur between these regions if intermediary hard substrata are not present to enable migration, and environmental conditions differ markedly. Latitudinal variation in the occurrence of species, especially crossing into polar regions, is well documented, indicating that findings in lower latitudes do not necessarily transpose onto those at higher latitudes (reviewed by Canning-Clode 2009). The vertical range boundaries discussed earlier (Calder 1996; Vedenin et al. 2021) as well as differing water masses that can restrict larval distribution (Meyer-Kaiser et al. 2022) present another potential barrier for species migration across the abyssal zones of the North Atlantic and Arctic. The present study was developed in an effort to increase our understanding of species distribution and recruitment patterns as a whole in arctic and subarctic seas.

1.6 Thesis objectives

This thesis aimed to further knowledge of how recruitment patterns and ecological dynamics in deep-sea benthic communities modulate colonization patterns and species distribution on hard substrata in the Northwest Atlantic and Arctic. Noting the many knowledge gaps for these biological systems, particularly at high latitudes, a major objective of this study was to examine and compare benthic community structures across the Low and High Arctic focal

regions and in both early and mature communities. Establishing a baseline understanding of the deep-sea benthic ecology of the Canadian Northwest Atlantic and Arctic regions critically depends on such information. This thesis is composed of two data chapters.

Chapter 2 examines morphospecies richness, recruitment, and growth patterns in early successional epibenthic communities colonizing different substrata in the deep sea of a Northwest Atlantic region located at the gateway of the Arctic (i.e., Low Arctic). At three sites in the Labrador Sea (Canada), four different year-long experiments conducted between 2017 and 2020 investigated short-term recruitment patterns of benthic taxa. A standardized settlement frame was used, which contained four types of substrata; three of these offered in checkerboard randomized triplicates (plastic, stone, and mesh); and one as a single plate (wood). Comparisons focused on morphospecies richness, abundance, and size across all substratum types. The objectives were framed around analyzing morphospecies richness and abundance, and recruit size, with the goal of determining whether substratum differences drive community composition, including surficial location and microhabitat complexity, and whether recruitment patterns vary across geographic sites (as well as depths and years). The study also aimed to compare recruitment metrics across taxa, especially between unitary and colonial forms.

Chapter 3 examines established hard-bottom community composition on natural substrata in the deep sea of the Canadian Northwest Atlantic and Arctic. At five sites in the Labrador Sea (Newfoundland and Labrador; Low Arctic) and three sites in Baffin Bay (Nunavut; High Arctic), collections focused on natural hard substrata in the form of cobble-sized “dropstones” and their associated epifaunal communities resting on the soft sediment. The dropstones were examined to assess morphospecies diversity, spatial distribution, and evidence of competition, and these metrics were compared across all sites and depths to test the hypotheses that (1) colonizers

exhibit consistent patterns of zonation (i.e., distance from the sediment line) as a result of preferential positioning relative to height above the sea floor; and (2) the community assemblages on dropstones collected from sites within a geographic region more closely resemble those on nearby dropstones than those collected across distant geographic regions. The study also sought to explore the potential influence of ecological interactions (e.g., epibiosis) on positioning both at fine scales and at regional assemblages.

Chapter 4 summarizes the general conclusions from both investigations and identifies potential areas for future studies.

1.7 References

Al-Habahbeh AK, Kortsch S, Bluhm BA, Beuchel F, Gulliksen B, Ballantine C, Cristini D, Primicerio R. 2020. Arctic coastal benthos long-term responses to perturbations under climate warming. Philos Trans R Soc Lond Ser Math Phys Eng Sci. 378(2181):20190355. doi:10.1098/rsta.2019.0355.

Amon DJ, Ziegler AF, Dahlgren TG, Glover AG, Goineau A, Gooday AJ, Wiklund H, Smith CR. 2016. Insights into the abundance and diversity of abyssal megafauna in a polymetallic-nodule region in the eastern Clarion-Clipperton Zone. Sci Rep. 6:30492. doi:10.1038/srep30492.

Atkinson EG. 1989. Benthic invertebrates collected from the western Canadian Arctic, 1951 to 1985. Ste.-Anne-de-Bellevue, Que: Arctic Biological Station of the Institut Maurice-Lamontagne, Dept. of Fisheries and Oceans. Can. Manuscr. Rep. Fish. Aquat. Sci.

Baillon S, Hamel J-F, Mercier A. 2014. Diversity, distribution and nature of faunal associations with deep-sea pennatulacean corals in the Northwest Atlantic. PLOS One . 9(11):e111519. doi:10.1371/journal.pone.0111519.

Baillon S, Hamel J-F, Wareham VE, Mercier A. 2012. Deep cold-water corals as nurseries for fish larvae. Front Ecol Environ. 10(7):351–356.

Barnes DK. 2017. Marine colonization and biodiversity at Ascension Island and remote islands. J Mar Biol Assoc UK. 97(4):771–782. doi:10.1017/S0025315415001526.

Beaulieu SE. 2001. Life on glass houses: Sponge stalk communities in the deep sea. Mar Biol. 138(4):803–817.

Beaulieu SE. 2001. Colonization of habitat islands in the deep sea: recruitment to glass sponge stalks. Deep Sea Res Part I: Oceanogr Res Pap. 48(4):1121–1137. doi:10.1016/S0967-0637(00)00055-8.

Bennett MR, Doyle P, Mather AE. 1996. Dropstones: their origin and significance. Palaeogeogr Palaeoclimatol Palaeoecol. 121(3):331–339. doi:10.1016/0031-0182(95)00071-2.

Blankenship LE, Levin LA. 2007. Extreme food webs: foraging strategies and diets of scavenging amphipods from the ocean's deepest 5 kilometers. Limnol Oceanogr. 52(4):1685–1697. doi:10.4319/lo.2007.52.4.1685.

Bluhm BA, Macdonald IR, Debenham C, Iken K. 2005. Macro- and megabenthic communities in the high Arctic Canada Basin: initial findings. Polar Biol. 28(3):218–231. doi:10.1007/s00300-004-0675-4.

Bowden DA, Clarke A, Peck LS, Barnes DKA. 2006. Antarctic sessile marine benthos: colonisation and growth on artificial substrata over three years. Mar Ecol Prog Ser. 316:1–16. doi:10.3354/meps316001.

Buhl-Mortensen L, Buhl-Mortensen P. 2018. Cold temperate coral habitats. In: Corals in a Changing World. IntechOpen. https://www.intechopen.com/chapters/58875.

Buhl-Mortensen L, Mortensen PB. 2005. Distribution and diversity of species associated with deep-sea gorgonian corals off Atlantic Canada. In: Freiwald A, Roberts JM, editors. Cold-Water Corals and Ecosystems. Berlin, Heidelberg: Springer. p. 849–879. https://doi.org/10.1007/3-540-27673-4_44.

Burkett AM, Rathburn AE, Elena Pérez M, Levin LA, Martin JB. 2016. Colonization of over a thousand *Cibicidoides wuellerstorfi* (Foraminifera: Schwager, 1866) on artificial

substrates in seep and adjacent off-seep locations in dysoxic, deep-sea environments. Deep Sea Res Part I: Oceanogr Res Pap. 117:39–50. doi:10.1016/j.dsr.2016.08.011.

Calder DR. 1996. Hydroids (Cnidaria: Hydrozoa) recorded from depths exceeding 3000 m in the abyssal western North Atlantic. Can J Zool. 74(9):1721–1726. doi:10.1139/z96-190.

Canning-Clode J. 2009. Latitudinal patterns of species richness in hard-bottom communities. In: Wahl M, editor. Marine Hard Bottom Communities: Patterns, Dynamics, Diversity, and Change. Berlin, Heidelberg: Springer. (Ecological Studies). p. 81–87. https://doi.org/10.1007/b76710_5.

Castro de la Guardia L, Hu X, Myers PG. 2015. Potential positive feedback between Greenland Ice Sheet melt and Baffin Bay heat content on the west Greenland shelf. Geophys Res Lett. 42(12):4922–4930. doi:10.1002/2015GL064626.

Chan FT, MacIsaac HJ, Bailey SA. 2016. Survival of ship biofouling assemblages during and after voyages to the Canadian Arctic. Mar Biol. 163(12):1–14. doi:10.1007/s00227-016-3029-1.

Christiansen JS, Mecklenburg CW, and Karamushko OV. (2014), Arctic marine fishes and their fisheries in light of global change. Glob Change Biol, 20: 352-359. https://doi.org/10.1111/gcb.12395.

Clark MR, Althaus F, Schlacher TA, Williams A, Bowden DA, Rowden AA. 2016. The impacts of deep-sea fisheries on benthic communities: a review. ICES J Mar Sci. 73(suppl_1):i51–i69. doi:10.1093/icesjms/fsv123.

Conservation of Arctic Flora and Fauna (CAFF). 2017. State of the Arctic Marine Biodiversity Report. http://hdl.handle.net/11374/1945

Cramm MA, Neves B de M, Manning CCM, Oldenburg TBP, Archambault P, Chakraborty A, Cyr-Parent A, Edinger EN, Jaggi A, Mort A, et al. 2021. Characterization of marine microbial communities around an Arctic seabed hydrocarbon seep at Scott Inlet, Baffin Bay. Sci Total Environ. 762:143961. doi:10.1016/j.scitotenv.2020.143961.

Curry B, Lee CM, Petrie B, Moritz RE, Kwok R. 2014. Multiyear volume, liquid freshwater, and sea ice transports through Davis Strait, 2004–10. J Phys Oceanogr. 44(4):1244–1266. doi:10.1175/JPO-D-13-0177.1.

Cuvelier D, Beesau J, Ivanenko VN, Zeppilli D, Sarradin P-M, Sarrazin J. 2014. First insights into macro- and meiofaunal colonisation patterns on paired wood/slate substrata at Atlantic deep-sea hydrothermal vents. Deep Sea Res Part I: Oceanogr Res Pap. 87:70–81. doi:10.1016/j.dsr.2014.02.008.

Dale JE, Aitken AE, Gilbert R, Risk MJ. 1989. Macrofauna of Canadian arctic fjords. Mar Geol 85(2):331–358. doi:10.1016/0025-3227(89)90159-X.

Davis AR. 2009. The role of mineral, living and artificial substrata in the development of subtidal assemblages. In: Wahl M, editor. Marine Hard Bottom Communities: Patterns, Dynamics, Diversity, and Change. Berlin, Heidelberg: Springer. (Ecological Studies). p. 19–37. https://doi.org/10.1007/b76710_2.

De Mesel I, Kerckhof F, Norro A, Rumes B, Degraer S. 2015. Succession and seasonal dynamics of the epifauna community on offshore wind farm foundations and their role as stepping stones for non-indigenous species. Hydrobiologia. 756(1):37–50. doi:10.1007/s10750-014-2157-1.

DFO. 2021. Science review of the Labrador shelf offshore area Strategic Environmental Assessment (SEA) Update. DFO Can Sci Advis Sec Sci Resp. 2021/031.

Dunham A, Archer SK, Davies SC, Burke LA, Mossman J, Pegg JR, Archer E. 2018. Assessing condition and ecological role of deep-water biogenic habitats: Glass sponge reefs in the Salish Sea. Mar Environ Res. 141:88–99. doi:10.1016/j.marenvres.2018.08.002.

Edinger EN, Sherwood OA, Piper DJW, Wareham VE, Baker KD, Gilkinson KD, Scott DB. 2011. Geological features supporting deep-sea coral habitat in Atlantic Canada. Cont Shelf Res. 31(2, Supplement):S69–S84. doi:10.1016/j.csr.2010.07.004.

FAO. 2019. Deep-ocean climate change impacts on habitat, fish, and fisheries - Memorial University of Newfoundland. FAO Fish Aquac Tech Pap. 638(192).

Gaudron SM, Pradillon F, Pailleret M, Duperron S, Le Bris N, Gaill F. 2010. Colonization of organic substrates deployed in deep-sea reducing habitats by symbiotic species and associated fauna. Mar Environ Res. 70(1):1–12. doi:10.1016/j.marenvres.2010.02.002.

Genin A, Dayton PK, Lonsdale PF, Spiess FN. 1986. Corals on seamount peaks provide evidence of current acceleration over deep-sea topography. Nature. 322(6074):59–61. doi:10.1038/322059a0.

Girard F, Lacharité M, Metaxas A. 2016. Colonization of benthic invertebrates in a submarine canyon in the NW Atlantic. Mar Ecol Prog Ser. 544:53–64. doi:10.3354/meps11555.

Gollner S, Kaiser S, Menzel L, Jones DOB, Brown A, Mestre NC, van Oevelen D, Menot L, Colaço A, Canals M, et al. 2017. Resilience of benthic deep-sea fauna to mining activities. Mar Environ Res. 129:76–101. doi:10.1016/j.marenvres.2017.04.010.

Goode SL, Rowden AA, Bowden DA, Clark MR. 2020. Resilience of seamount benthic communities to trawling disturbance. Mar Environ Res. 161:105086. doi:10.1016/j.marenvres.2020.105086.

Górska B, Soltwedel T, Schewe I, Włodarska-Kowalczuk M. 2020. Bathymetric trends in biomass size spectra, carbon demand, and production of Arctic benthos (76-5561 m, Fram Strait). Prog Oceanogr. 186:102370-. doi:10.1016/j.pocean.2020.102370.

Guy G, Metaxas A. 2022. Recruitment of deep-water corals and sponges in the Northwest Atlantic Ocean: implications for habitat distribution and population connectivity. Mar Biol. 169(8):107. doi:10.1007/s00227-022-04089-w.

Hadfield MG. 2011. Biofilms and marine invertebrate larvae: what bacteria produce that larvae use to choose settlement sites. Annu Rev Mar Sci. 3(1):453–470. doi:10.1146/annurev-marine-120709-142753.

Handmann P, Fischer J, Visbeck M, Karstensen J, Biastoch A, Böning C, Patara L. 2018. The Deep Western Boundary Current in the Labrador Sea from observations and a high-resolution model. J Geophys Res Oceans. 123(4):2829–2850. doi:10.1002/2017JC013702.

Hasemann C, Bergmann M, Kanzog C, Lochthofen N, Sauter E, Schewe I, Soltwedel T. 2013. Effects of dropstone-induced habitat heterogeneity on Arctic deep-sea benthos with special reference to nematode communities. Mar Biol Res. 9(3):229–245. doi:10.1080/17451000.2012.739694.

Heifetz J, Stone RP, Shotwell SK. 2009. Damage and disturbance to coral and sponge habitat of the Aleutian Archipelago. Mar Ecol Prog Ser. 397:295–303.

Heinrich H. 1988. Origin and consequences of cyclic ice rafting in the Northeast Atlantic Ocean during the past 130,000 years. Quat Res. 29(2):142–152. doi:10.1016/0033-5894(88)90057-9.

Hilário A, Metaxas A, Gaudron SM, Howell KL, Mercier A, Mestre NC, Ross RE, Thurnherr AM, Young C. 2015. Estimating dispersal distance in the deep sea: challenges and applications to marine reserves. Front Mar Sci. 2:1–14. doi:10.3389/fmars.2015.00006.

Jenkins SR, Marshall D, Fraschetti S. 2009. Settlement and recruitment. In: Wahl M, editor. Marine Hard Bottom Communities: Patterns, Dynamics, Diversity, and Change. Berlin, Heidelberg: Springer. (Ecological Studies). p. 177–190. https://doi.org/10.1007/b76710_12.

Konar B. 2007. Recolonization of a high latitude hard-bottom nearshore community. Polar Biol. 30(5):663–667. doi:10.1007/s00300-007-0261-7.

Kortsch S, Primicerio R, Beuchel F, Renaud PE, Rodrigues J, Lønne OJ, Gulliksen B. 2012. Climate-driven regime shifts in Arctic marine benthos. Proc Natl Acad Sci 109(35):14052–14057. doi:10.1073/pnas.1207509109.

Kukliński P. 2009. Ecology of stone-encrusting organisms in the Greenland Sea—a review. Polar Res. 28(2):222–237. doi:10.1111/j.1751-8369.2009.00105.x.

Kukliński P, Bader B. 2007. Diversity, structure, and interactions of encrusting lithophyllic macrofaunal assemblages from Belgica Bank, East Greenland. Polar Biol. 30(6):709–717. doi:10.1007/s00300-006-0228-0.

Kukliński P, Berge J, McFadden L, Dmoch K, Zajaczkowski M, Nygård H, Piwosz K, Tatarek A. 2013. Seasonality of occurrence and recruitment of Arctic marine benthic invertebrate larvae in relation to environmental variables. Polar Biol. 36(4):549–560. doi:10.1007/s00300-012-1283-3.

LaCroce ME, Long ZT, Freshwater DW. 2020. Seasonality and disturbance recovery of the epibenthic community on a warm-temperate hard bottom. J Exp Mar Biol Ecol. 524:151283. doi:10.1016/j.jembe.2019.151283.

Lambert GI, Jennings S, Kaiser MJ, Davies TW, Hiddink JG. 2014. Quantifying recovery rates and resilience of seabed habitats impacted by bottom fishing. J Appl Ecol. 51(5):1326–1336. doi:10.1111/1365-2664.12277.

Lochte AA, Schneider R, Kienast M, Repschläger J, Blanz T, Garbe-Schönberg D, Andersen N. 2020. Surface and subsurface Labrador Shelf water mass conditions during the last 6000 years. Clim Past. 16(4):1127–1143. doi:10.5194/cp-16-1127-2020.

McCartney MS. 1992. Recirculating components to the deep boundary current of the northern North Atlantic. Prog Oceanogr. 29(4):283–383. doi:10.1016/0079-6611(92)90006-L.

McDougall KD. 1943. Sessile marine invertebrates of Beaufort, North Carolina: a study of settlement, growth, and seasonal fluctuations among pile-dwelling organisms. Ecol Monogr. 13(3):321–374. doi:10.2307/1943225.

Metaxas A, Davis J. 2005. Megafauna associated with assemblages of deep-water gorgonian corals in Northeast Channel, off Nova Scotia, Canada. J Mar Biol Assoc UK. 85(6):1381–1390. doi:10.1017/S0025315405012567.

Metaxas A, Kelly NE. 2010. Do larval supply and recruitment vary among chemosynthetic environments of the deep sea? PLOS One. 5(7):e11646–e11646. doi:10.1371/journal.pone.0011646.

Meyer KS, Li Y, Young CM. 2018. Oceanographic and biological influences on recruitment of benthic invertebrates to hard substrata on the Oregon shelf. Estuar Coast Shelf Sci. 208:1–8. doi:10.1016/j.ecss.2018.04.037.

Meyer KS, Soltwedel T, Bergmann M. 2014. High biodiversity on a deep-water reef in the eastern Fram Strait. PLOS One . 9(8):e105424–e105424. doi:10.1371/journal.pone.0105424.

Meyer KS, Young CM, Sweetman AK, Taylor J, Soltwedel T, Bergmann M. 2016. Rocky islands in a sea of mud: biotic and abiotic factors structuring deep-sea dropstone communities. Mar Ecol Prog Ser. 556:45–57. doi:10.3354/meps11822.

Meyer-Kaiser K, Bergmann M, Soltwedel T, Klages M. 2019. Recruitment of Arctic deep-sea invertebrates: Results from a long-term hard-substrate colonization experiment at the Long-Term Ecological Research observatory HAUSGARTEN. Limnol Oceanogr. 64(5):1924–1938. doi:10.1002/lno.11160.

Meyer-Kaiser KS, Schrage KR, von Appen W-J, Hoppmann M, Lochthofen N, Sundfjord A, Soltwedel T. 2022. Larval dispersal and recruitment of benthic invertebrates in the Arctic Ocean. Prog Oceanogr. 203:102776. doi:10.1016/j.pocean.2022.102776.

Miller RJ, Hocevar J, Stone RP, Fedorov DV. 2012. Structure-forming corals and sponges and their use as fish habitat in Bering Sea submarine canyons. PLOS One . 7(3):e33885. doi:10.1371/journal.pone.0033885.

Morrison KM, Meyer HK, Roberts EM, Rapp HT, Colaço A, Pham CK. 2020. The first cut is the deepest: trawl effects on a deep-sea sponge ground are pronounced four years on. Front Mar Sci. doi:10.3389/fmars.2020.605281.

Mullineaux LS. 1987. Organisms living on manganese nodules and crusts: distribution and abundance at three North Pacific sites. Deep Sea Res Part I: Oceanogr Res Pap. 34(2):165–184. doi:10.1016/0198-0149(87)90080-X.

Mullineaux LS, Butman CA. 1990. Recruitment of encrusting benthic invertebrates in boundary-layer flows: A deep-water experiment on Cross Seamount. Limnol Oceanogr. 35(2):409–423.

Myers PG. 2005. Impact of freshwater from the Canadian Arctic Archipelago on Labrador Sea Water formation. Geophys Res Lett. 32(6). doi:10.1029/2004GL022082.

Noël LM-LJ, Griffin JN, Moschella PS, Jenkins SR, Thompson RC, Hawkins SJ. 2009. Changes in diversity and ecosystem functioning during succession. In: Wahl M, editor. Marine Hard Bottom Communities: Patterns, Dynamics, Diversity, and Change. Berlin, Heidelberg: Springer. (Ecological Studies). p. 213–223. https://doi.org/10.1007/b76710_15.

Ørberg SB, Krause-Jensen D, Meire L, Sejr MK. 2018. Subtidal benthic recruitment in a sub-Arctic glacial fjord system: temporal and spatial variability and potential drivers. Polar Biol. 41(12):2627–2634. doi:10.1007/s00300-018-2390-6.

Osman RW. 1977. The establishment and development of a marine epifaunal community. Ecol Monogr. 47(1):37–63. doi:10.2307/1942223.

Osman RW, Whitlatch RB, Malatesta RJ. 1992. Potential role of micro-predators in determining recruitment into a marine community. Mar Ecol Prog Ser. 83(1):35–43.

Page HM, Culver CS, Dugan JE, Mardian B. 2008. Oceanographic gradients and patterns in invertebrate assemblages on offshore oil platforms. ICES J Mar Sci. 65(6):851–861. doi:10.1093/icesjms/fsn060.

Pickart RS, Straneo F, Moore GWK. 2003. Is Labrador Sea Water formed in the Irminger basin? Deep Sea Res Part I: Oceanogr Res Pap. 50(1):23–52. doi:10.1016/S0967-0637(02)00134-6.

Pierrejean M, Grant C, de Moura Neves B, Chaillou G, Edinger E, Blanchet FG, Maps F, Nozais C, Archambault P. 2020. Influence of deep-water corals and sponge gardens on infaunal community composition and ecosystem functioning in the Eastern Canadian Arctic. Front Mar Sci. 7.

Ramirez-Llodra E, Tyler PA, Baker MC, Bergstad OA, Clark MR, Escobar E, Levin LA, Menot L, Rowden AA, Smith CR, et al. 2011. Man and the last great wilderness: human impact on the deep sea. PLOS One. 6(8):e22588-. doi:10.1371/journal.pone.0022588.

Renaud PE, Sejr MK, Bluhm BA, Sirenko B, Ellingsen IH. 2015. The future of Arctic benthos: expansion, invasion, and biodiversity. Prog Oceanogr. 139:244–257. doi:10.1016/j.pocean.2015.07.007.

Richmond MD, Seed R. 1991. A review of marine macrofouling communities with special reference to animal fouling. Biofouling. 3(2):151–168. doi:10.1080/08927019109378169.

Risk MJ, Heikoop JM, Snow MG, Beukens R. 2002. Lifespans and growth patterns of two deep-sea corals: *Primnoa resedaeformis* and *Desmophyllum cristagalli*. Hydrobiologia. 471(1–3):125–131. doi:10.1023/A:1016557405185.Roberts JM, Wheeler A, Freiwald A, Cairns S. 2009. Habitats and ecology. In: Cold-Water Corals: The Biology and Geology of Deep-Sea Coral Habitats. Cambridge University Press. p. 142–174.

Romano C, Voight JR, Pérez-Portela R, Martin D. 2014. Morphological and genetic diversity of the wood-boring Xylophaga (Mollusca, Bivalvia): New species and records from deep-sea Iberian canyons. PLOS One. 9(7):1–20. doi:10.1371/journal.pone.0102887.

Ronowicz. 2007. Benthic hydroids (Cnidaria: Hydrozoa) from Svalbard waters-biodiversity and distribution. J Mar Biol Assoc UK. 87(5):1089–1094.

Roy V, Iken K, Archambault P. 2015. Regional variability of megabenthic community structure across the Canadian Arctic. Arctic. 68(2):180–192. doi:10.14430/arctic4486.

Saenko OA, Dupont F, Yang D, Myers PG, Yashayaev I, Smith GC. 2014. Role of resolved and parameterized eddies in the Labrador Sea balance of heat and buoyancy. J Phys Oceanogr. 44(12):3008–3032. doi:10.1175/JPO-D-14-0041.1.

Schoening T, Bergmann M, Ontrup J, Taylor J, Dannheim J, Gutt J, Purser A, Nattkemper TW. 2012. Semi-automated image analysis for the assessment of megafaunal densities at the Arctic deep-sea observatory HAUSGARTEN. PLOS One. 7(6):1–14. doi:10.1371/journal.pone.0038179.

Schulz M, Bergmann M, von Juterzenka K, Soltwedel T. 2010. Colonisation of hard substrata along a channel system in the deep Greenland Sea. Polar Biol. 33(10):1359–1369. doi:10.1007/s00300-010-0825-9.

Sherwood OA, Edinger EN. 2009. Ages and growth rates of some deep-sea gorgonian and antipatharian corals of Newfoundland and Labrador. Can J Fish Aquat Sci. 66(1):142–152. doi:10.1139/F08-195.

Sherwood OA, Scott DB, Risk MJ. 2006. Late Holocene radiocarbon and aspartic acid racemization dating of deep-sea octocorals. Geochim Cosmochim Acta. 70(11):2806–2814. doi:10.1016/j.gca.2006.03.011.

Sotomayor-García A, Rueda JL, Sánchez-Guillamón O, Urra J, Martín-Arjona A, González-Porto M, Vazquez JT, Palomino D, López-González N, Fernández-Salas LM, et al. 2023. Impact of Tagoro volcano formation on benthic habitats and associated biota: a review. In: González PJ, editor. El Hierro Island. Cham: Springer International Publishing.

(Active Volcanoes of the World). p. 217–239. https://doi.org/10.1007/978-3-031-35135-8_11.

Tekman MB, Krumpen T, Bergmann M. 2017. Marine litter on deep Arctic seafloor continues to increase and spreads to the North at the HAUSGARTEN observatory. Deep Sea Res Part I: Oceanogr Res Pap. 120:88–99. doi:10.1016/j.dsr.2016.12.011.

Thornalley DJR, Barker S, Broecker WS, Elderfield H, McCave IN. 2011. The deglacial evolution of North Atlantic deep convection. Science. 331(6014):202–205.

Thurber AR, Sweetman AK, Narayanaswamy BE, Jones DOB, Ingels J, Hansman RL. 2014. Ecosystem function and services provided by the deep sea. Biogeosciences. 11(14):3941. doi:10.5194/bg-11-3941-2014.

Uhlenkott K, Meyn K, Vink A, Martínez Arbizu P. 2023. A review of megafauna diversity and abundance in an exploration area for polymetallic nodules in the eastern part of the Clarion Clipperton Fracture Zone (North East Pacific), and implications for potential future deep-sea mining in this area. Mar Biodivers. 53(2). doi:10.1007/s12526-022-01326-9.

Vedenin A, Galkin S, Mironov AN, Gebruk A. 2021. Vertical zonation of the Siberian Arctic benthos: bathymetric boundaries from coastal shoals to deep-sea Central Arctic. PeerJ 9:e11640–e11640. doi:10.7717/peerj.11640.

Vieira EA, Dias GM, Flores AAV. 2016. Effects of predation depend on successional stage and recruitment rate in shallow benthic assemblages of the Southwestern Atlantic. Mar Biol. 163(4):1–12. doi:10.1007/s00227-016-2872-4.

Wahl M. 2009a. Habitat characteristics and typical functional groups. In: Wahl M, editor. Marine Hard Bottom Communities: Patterns, Dynamics, Diversity, and Change. Berlin, Heidelberg: Springer. (Ecological Studies). p. 7–17. https://doi.org/10.1007/b76710_1.

Wahl M. 2009b. Marine Hard Bottom Communities: Patterns, Dynamics, Diversity, and Change. 1. Aufl. Berlin, Heidelberg: Springer-Verlag (Ecological Studies).

Wootton JT, Cusson M, Navarrete S, Petraitis PS. 2009. Disruption, succession and stochasticity. In: Wahl M, editor. Marine Hard Bottom Communities: Patterns, Dynamics, Diversity, and Change. Berlin, Heidelberg: Springer. (Ecological Studies). p. 201–212. https://doi.org/10.1007/b76710_14.

Young CM. 2009. Communities on deep-sea hard bottoms. In: Wahl M, editor. Marine Hard Bottom Communities: Patterns, Dynamics, Diversity, and Change. Berlin, Heidelberg: Springer. (Ecological Studies). p. 39–60. https://doi.org/10.1007/b76710_3.

Yund PO, Cunningham CW, Buss LW. 1987. Recruitment and postrecruitment interactions in a colonial hydroid. Ecology. 68(4):971–982. doi:10.2307/1938368.

Ziegler AF, Smith CR, Edwards KF, Vernet M. 2017. Glacial dropstones: islands enhancing seafloor species richness of benthic megafauna in West Antarctic Peninsula fjords. Mar Ecol Prog Ser. 583:1–14. doi:10.3354/meps12363.

1.8 Figures

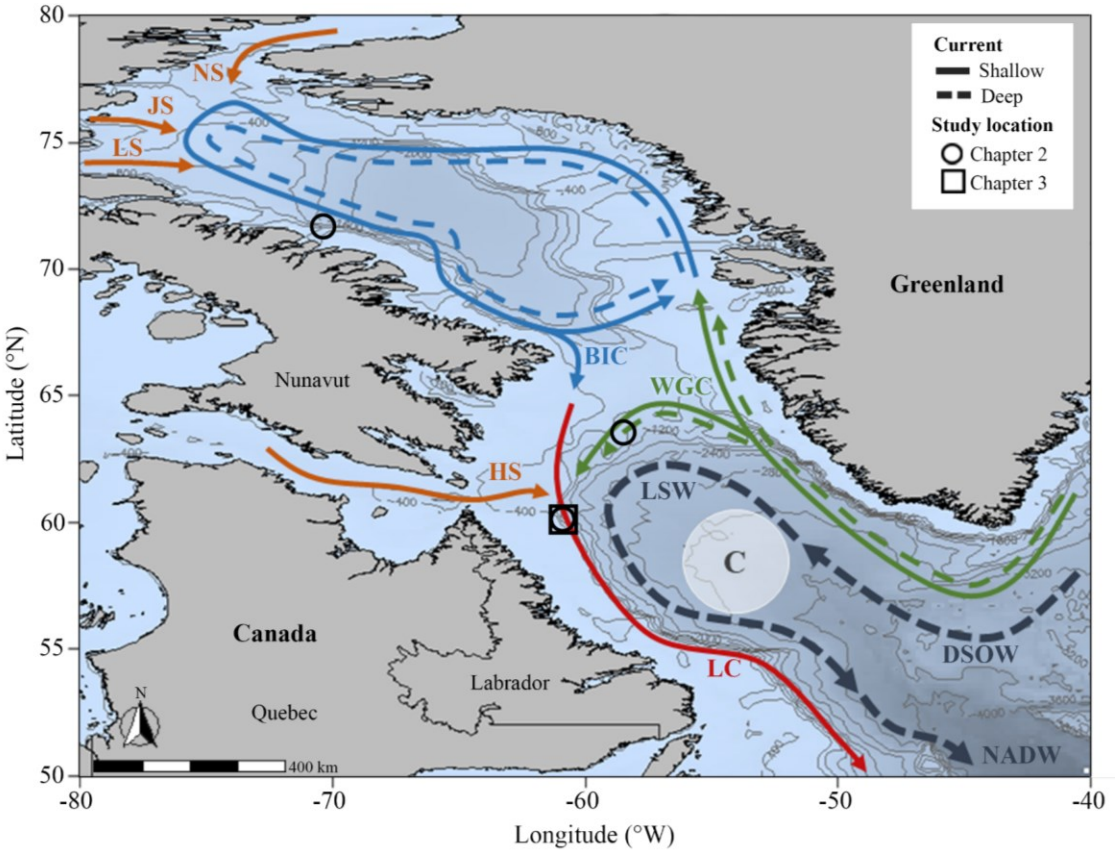

Figure 1.1 Map of oceanic currents in the eastern Canadian Arctic and North Atlantic. Arrows indicate direction of currents. West Greenland Current (WGC) in green splits and enters Baffin Bay on the eastern side of Davis Strait as well as joining the Labrador Current (LC) on the western side of the Labrador Sea, the shallow part of the current containing Arctic water and the deep Atlantic. Fresh, cold water also enters Baffin Bay from the Canadian Arctic Archipelago from Nares Strait (NS), Jones Sound (JS), and Lancaster Sound (LS) in orange. Recirculation occurs in Baffin Bay, and the shallow Baffin Island Current (BIC) in light blue exits on the western side of Davis Strait to join the LC along with water from the Hudson Strait (HS; orange). Deep convection occurs in the Labrador Sea, identified in the white circle with a "C". The deep-water masses joining the Deep-Water Boundary Current in dark blue are the Denmark Strait Overflow Water (DSOW), Labrador Sea Water (LSW), carried out meridionally as North Atlantic Deep Water (NADW). Adapted from Castro de la Guardia et al. (2015) and Handmann et al. (2018).

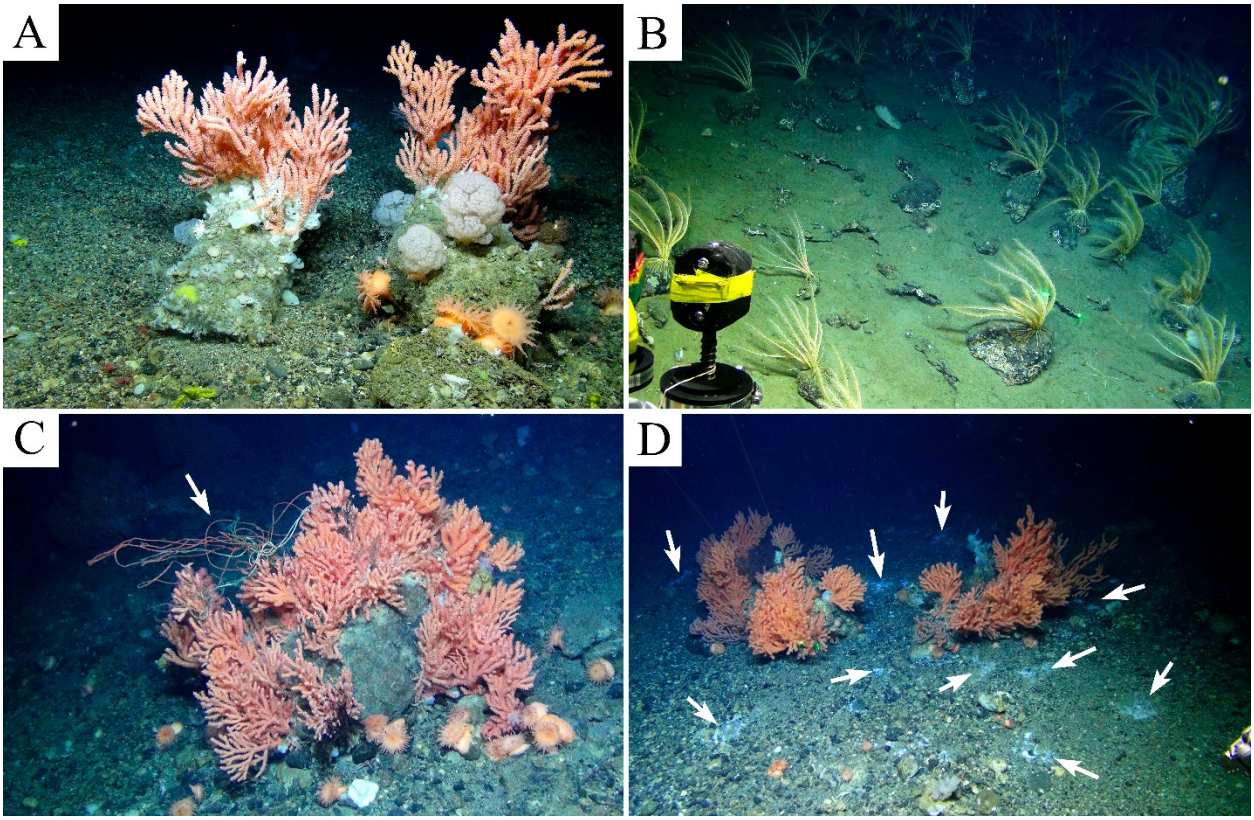

Figure 1.2 Hard-bottom communities on terrigenous stones on the continental slope of eastern Canada photographed using the remotely operated vehicle (ROV) *ASTRID* in July and August 2021, courtesy of Amundsen Science, examined in Chapter 3. (A) Primnoid and soft corals, sponges, and anemones growing on three clustered stones in the Labrador Sea at 630 m. (B) Crinoids and serpulid worm tubes encrusting dispersed stones on a slope in Baffin Bay at 239 m. (C) Primnoid coral colonies on a large stone, tangled in anthropogenic pollution (fishing gear) indicated with a white arrow, in the Labrador Sea at 772 m. (D) Primnoid coral colonies on large stones in the Labrador Sea at 794 m surrounded by gravel, with white arrows indicating bacterial mats growing at methane seep locations.

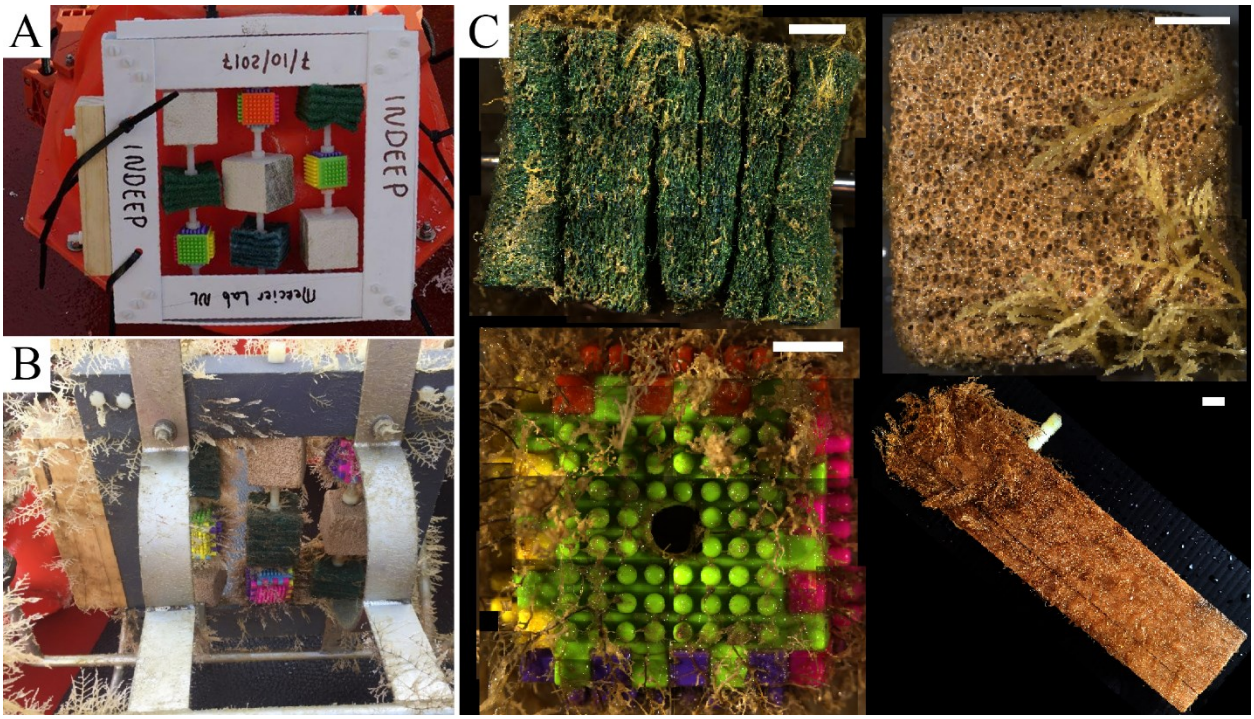

Figure 1.3 Settlement frames used in Chapter 2 to examine substratum recruitment patterns in larval recruitment of early colonizers to four different substratum types (mesh, plastic, stone, wood) deployed for ~1 year each in Labrador Sea (Newfoundland and Labrador, Canada). (A) Pre-deployment settlement frame exhibiting standardized four substratum types including three each of mesh, stone, and plastic blocks, and one wood panel bolted to the side; it is connected to a buoy on a scientific mooring deployed by ArcticNet in 2017. (B) Post-deployment settlement frame exhibiting colonization by hydrozoan colonies across all substratum types. (C) The four substratum types seen enlarged, clockwise from top left: mesh, a kitchen sponge folded into a block shape showing sparse hydrozoan colony growth; stone, a basalt block showing a second type of hydrozoan; wood, a long block of pine with hydrozoan colonies heavily colonizing one end; and plastic, an interlocking DIMPLE™ Bristle Stacking Block with a third hydrozoan present. Each were bolted through the centre of two opposing faces to the frame. White scale bars indicate 1 cm.

Chapter 2: Between a rock and a hard place: experimental assessment of recruitment patterns in a bathyal environment of the Low Arctic

2.1 Abstract

The study of larval transport and recruitment in the deep sea is crucial to the understanding of species distributions, community assembly, and the potential effects of anthropogenic activity and climate change on the maintenance of biodiversity. We sought to understand better the role of substratum types and their features in deep-sea larval recruitment at high latitudes. Four settlement frames composed of blocks of different substrata (mesh, plastic, stone, and wood) were deployed for 9 to 13 months at bathyal depths in the Labrador Sea (northeastern Canada). Colonial hydrozoans dominated as recruits, with one taxon (family Campanulariidae) colonizing all substratum types through all geographic sites. Other taxa, including arthropods, octocorals, and other anthozoans differed in distribution patterns, recruiting only onto specific substrata and consistent microhabitats within them. Overall, higher morphospecies and phylum richness characterized the three-dimensional mesh substratum relative to other substratum types, whereas the complex surface area offered by projections in the plastic substratum had higher densities of individuals or colonies for all morphospecies combined. Wood, offered as a single elongated panel, was the most heavily colonized, whereas both mesh and stone hosted morphospecies not found on any other substratum type. Geographic site also influenced all metrics: Site 1 (499 m) dominated in abundance and density, Site 4 (505 m) in coverage and richness, and Site 3 (409 m) in biodiversity. Characteristics of the deployment apparatus, such as altitude (i.e., height above the sea floor), partial obstruction of the frame, and depth, also appear to play a role in

recruitment. These results address key knowledge gaps by characterizing larval recruitment patterns and early colonization by opportunistic hard-bottom benthic taxa in a poorly-studied region of the Eastern Canadian deep sea.

2.2 Introduction

Rising anthropogenic influences such as plastic pollution, deep-sea mining, and construction of human structures that facilitate invasive species transmission all increasingly threaten deep-sea communities (Ramirez-Llodra et al. 2011; Meyer et al. 2018). Past studies document recovery rates and resilience of deep benthic communities following anthropogenic interference, and the succession of species involved in the process, in mined seamounts (Goode et al. 2020) and other temperate deep-sea environments (reviewed by Canning-Clode 2009; Metaxas and Kelly 2010; Gollner et al. 2017). Documenting early successional stages of deep-sea communities on hard substrata in polar regions is comparatively new, in part because of their remoteness and the research challenges associated with severe fall and winter meteorological conditions and seasonal ice cover.

Multiple studies have examined early recruitment and succession in shallow-water polar benthic environments, where ice-scour regularly impacts communities (Dayton 1989; Stanwell-Smith and Barnes 1997; Brown et al. 2004; Barnes and Kukliński 2005; Bowden 2005; Bowden et al. 2006; Konar 2007, 2013; Kukliński et al. 2013; Al-Habahbeh et al. 2020). Studies have shown a marked recruitment seasonality in both the Arctic and Antarctic (Bowden 2005; Kukliński et al. 2013; Meyer et al. 2017), with slow colonization rates of new substrates extending years to decades (Stanwell-Smith and Barnes 1997; Brown et al. 2004; Konar 2007; Konar 2013; Al-Habahbeh et al. 2020). Whereas species richness in the shallows of polar regions sometimes resembles that of temperate regions (Barnes and Kukliński 2005), local habitat, depth

(experimental ranges from 8 – 200 m), and remoteness of the site from other similar habitats heavily influences recruitment at high latitudes (Bowden et al. 2006; Barnes 2017; Meyer et al. 2017).

Sessile and sedentary species dominate hard-bottom marine communities worldwide, mostly settling on the substratum as planktonic larvae (reviewed in Jenkins et al. 2009) after a more or less extended period of epibenthic exploration at the end of their pelagic life. Recruitment patterns on a specific substratum typically relate to the nature, texture or roughness of a surface (Walters and Wethey 1996; Gilg et al. 2010; Sun et al. 2010, 2011; Meyer et al. 2018), chemical cues emanating from the biofilm (Morse et al. 1996; Sun et al. 2010; Hadfield 2011), and the presence of conspecifics for certain gregarious species (Pawlik 1986; Johnson and Woollacott 2010). Other confounding factors influence recruitment rates and patterns, including regional variation in larval supply and dispersal rates, direction or strength of water flow, and rates of post-settlement mortality resulting from predation, competition, physiological stress, and physical or biological disturbances (Gaines and Bertness 1992; Hunt and Scheibling 1997; Palardy and Witman 2013; Hilário et al. 2015; Guy and Metaxas 2022). In the deep sea, spatial fragmentation of communities complicates population connectivity and larval dispersal (Hilário et al. 2015).

Recruitment studies often use deployments of replicable settlement frames, arrays, or "collectors" to mimic a range of hard substrata available on the ocean floor to examine the appearance of pioneer species (reviewed in Davis 2009). Several studies have used such arrays, especially in shallow temperate and tropical coral reefs (Chalmer 1982; Jenkins et al. 2009) and coastal waters (Walters and Wethey 1996; Migotto et al. 2001; Denitto et al. 2007; Gilg et al. 2010). Studies may offer mixed blocks or panels of natural substrata, e.g. basalt, wood, glass-

sponge fragments (Beaulieu 2001; Cuvelier et al. 2014), as well as plastic and other synthetic surfaces (Girard et al. 2016; Meyer-Kaiser et al. 2019) representing increasingly common anthropogenic contaminants. The inclusion of variable surficial or internal complexities is important, in that species can exhibit selective preference towards certain substratum features or "microhabitats" (Dumont et al. 2011). Microhabitat heterogeneity also enhances recruitment (Barnes and Kukliński 2005). Despite their popularity in benthic studies globally and in shallow polar environments (Teichert et al. 2012; Wisshak et al. 2022), few studies have used settlement frames or similar apparatuses with checkerboard substratum designs to evaluate larval recruitment to deep-sea habitats.

In the Gulf of Maine (western North Atlantic), Lacharité and Metaxas (2013) deployed larval collector arrays composed of mosaic basalt rock plates and mesh pads distributed randomly on a steel frame in three locations of the Middle Canyon of the Northeast Channel Coral Conservation Area (NECCCA; Nova Scotia, Canada) for four years. They identified environmental and substratum patterns in the recruitment of the cold-water corals *Primnoa resedaeformis* and *Paragorgia arborea*. The former colonized both substratum types, with greater abundance on more structurally complex portions of the frame than on the flat surfaces of the collectors. Moreover, Girard et al. (2016) used these larval collectors to compare colonization of simple (basalt stone) and complex (mesh pads) substratum types, and reported both higher diversity in species assemblages on the complex substratum and distinct clustering of species assemblages by substratum type. Anthozoans dominated simple substrata, with more evenly distributed abundances on complex substrata across taxa (Girard et al. 2016). In recruitment experiments deployed at 595–777 m involving three different substratum types (mesh, polypropylene rope, and wood) in the Pacific, the opportunistic epibenthic foraminifer

Cibicidoides wuellersdorfi preferentially colonized mesh over polypropylene with no colonization on wood (Burkett et al. 2016). More recently, a video transect at each of three sites adjacent to the NECCCA and the nearby Corsair and Georges Canyon Coral Conservation Area reported peak recruitment of both *P. resedaeformis* and *P. arborea* at depths below 500 m, and dense aggregations of the glass sponge *Vazella pourtalesi* at 220–320 m (Guy and Metaxas 2022), suggesting that small-scale environmental conditions, post-settlement processes, and supply of larvae play important roles.

Meyer-Kaiser et al. (2019) deployed a steel-frame scientific lander with settlement plates composed of brick and plastic panels at 2467 m in the Fram Strait (between Greenland and Svalbard, Norway). Using a remotely operated vehicle (ROV), their monitoring indicated low biodiversity and recruitment rates for over a decade. However, once they recovered the apparatus after 19 y, they noted higher recruitment on brick than plastic substrata and species-specific preferences for panel altitude above the sea floor (Meyer-Kaiser et al. 2019). In the same region, Meyer-Kaiser et al. (2021) showed opportunistic recruitment of the otherwise rare solitary hydrozoan *Boullonia cornucopia* on polycarbonate plastic panels. More recently, Meyer-Kaiser et al. (2022) compared early recruitment in shallow and deep-sea habitats of Atlantic and Arctic waters of the Fram Strait across 15 locations at depths ranging 60 – 2700 m. The one- to two-year deployments of polycarbonate plastic panels and larval traps revealed that species composition differed mainly between the locations, with higher species richness in panels from the Atlantic. Moreover, the hydrozoans *B. cornucopia* and *Halisophonia arctica* tended to dominate at all depths (Meyer-Kaiser et al. 2022).

Previous experimental assessments of recruitment patterns in the deep sea at northern latitudes have tested only one or two substratum types. Ours is the first study to rely on a

checkerboard multiple-choice design to explore substratum colonization patterns in deep water at high latitudes. We used standardized recruitment frames containing replicated substratum blocks of varying surficial and internal complexity (mesh, plastic, stone, and wood) deployed for about a year (9 to 13 months) at each of three sites in the bathyal zone of the northern Labrador Sea (northeastern Canada) between 2017 and 2020. We analyzed species richness and abundance, and recruit size with the goal of verifying whether substratum differences, including surficial location and microhabitat complexity drive community composition, and whether recruitment patterns vary across geographic sites (as well as depths and years). Our study also aimed to compare recruitment metrics across taxa, especially among unitary and colonial forms.

2.3 Methods

2.3.1 Settlement frames

The settlement frames were built following the specifications used in the INDEEP project (www.indeep-project.org) designed in conjunction with project SERPENT (Scientific and Environmental ROV Partnership using Existing Industrial Technology) and Transocean to maximize recruitment (Gates et al. 2017; Metaxas et al. 2022). They were composed of three replicates of three different substratum types in a standardized block shape: folded pads of mineral and synthetic fibres (Scotch-Brite™), hereafter called “mesh”; interlocking plastic blocks (DIMPLE™ Bristle Stacking Blocks), hereafter called “plastic”; and blocks of limestone (calcium carbonate), hereafter called “stone”. Each block measured approximately 5 x 5 x 5 cm and was bolted horizontally through the center to a fiberglass frame in a randomized 3 x 3 checkerboard grid, where four faces were fully exposed and two opposing faces contained the bolt hole by which it was attached to the frame (Figure 2.1). A fourth substratum type, a single piece of pine wood measuring 5 x 5 x 20 cm and hereafter called “wood”, was bolted externally

to one side of the frame. Each substratum block (except wood) was made up of six faces of equal size (10 cm^2 each), which for this study were additionally subdivided into recruitment locations: edge or centre (Figure 2.1A, Supplementary table 2.1) and sheltered or unsheltered surface features or "microhabitats" (Figure 2.1B, Supplementary table 2.2). The wood panel had five unequal exposed surfaces (three faces of 100 cm^2 and two faces of 10 cm^2) (Figure 2.1).

2.3.2 Deployment method and sites

Six settlement frames were deployed initially on either moorings or landers (Figure 2.2); four were recovered successfully (at Sites 1, 2, 3, and 4) while fatal corrosion of mooring anchors resulted is loss of two before they could be retrieved (Sites 5 and 6). All frames were deployed from the icebreaker CCGS *Amundsen* in the Labrador Sea, approximately 170 km offshore of the northernmost tip of Labrador, Canada, at depths between 400–1000 m (Figure 2.2; Supplementary table 2.3). Deployments occurred from 2017 to 2021, and the frames remained in the water for a period of 9 to 13 months (Supplementary table 2.3). The Site 1 frame was deployed on a mooring to 499 m depth at 11 m altitude (i.e., height above sea floor). The Site 2 frame was deployed on a mooring to 960 m depth and 60 m altitude, approximately 6 km from Site 1. The Site 3 frame was deployed on a lander to 409 m depth and 1 m altitude, approximately 2 km from Site 1 and 7 km from Site 2. The Site 4 frame was deployed on a mooring at 505 m depth and 11 m altitude, approximately 2 km from both Sites 1 and 3, and 6 km from Site 2 (Figure 2.1). As a result of logistical constraints, frames at Sites 1 and 2 were laid flat on the mooring or lander apparatus (i.e., obstructed and no flow through the frame), whereas frames at Sites 3 and 4 were attached from the side (i.e., unobstructed and allowing flow through the frame) (Figure 2.2).

At recovery, we removed and disassembled settlement frames from the supporting apparatus and immediately preserved substrata either in 100% ethanol (all mesh, plastic, and stone blocks unless otherwise noted) or froze them (all wood panels, and the entire frame from Site 3). The wood block from Site 3 was lost during recovery. Samples initially preserved by freezing were transferred to 100% ethanol prior to analysis. All preserved samples were transported to and analyzed at the Ocean Sciences Centre of Memorial University (Newfoundland and Labrador).

2.3.3 Data collection and analysis

We used a Leica M205 stereo microscope and the Leica Application Suite X (LAS X) Life Science Microscope Software Platform to generate mosaic images of each face of each substratum block, and then stitched them together in Adobe Photoshop to complement direct analysis of each substratum surface under the stereo microscope. In the case of the wood block, we used a diagram in place of a mosaic image. To provide a spatial reference, we overlaid a grid composed of 1 x 1 cm squares digitally on the mosaic image (Supplementary figure 2.1). We used the mosaic images to map the locations and percent cover of each individual/colony of each species, and the grid overlay for digital analysis of species abundance (described below).

Identification. Because most colonizers observed on the various substrata were juveniles (often not showing the taxonomic characters required for identification to species), we assigned them to the lowest taxonomic level possible and to a morphospecies (e.g., "*Eudendrium* sp. 1"). Each morphospecies (msp / mspp) was also categorized as either unitary or colonial, defining a colony as any biogenic structure that connected down to a single base (excluding horizontal stolonization). We scored and referred to both singletons and colonies as "individuals". Morphospecies were also characterised as motile (capable of movement away from initial

location of larval recruitment, including sedentary taxa) or sessile (incapable of movement away from initial recruitment location). After photographing all individuals in the original place on the substratum blocks, we detached and preserved them in 100% ethanol.

Reproductive status. For each individual we estimated ontogenetic stage, categorized as established (e.g., adult unitary, or colony containing more than one module), juvenile (e.g., identifiably juvenile or colony of just one module), or eggs. We defined reproductive individuals as those with visible gametes/embryos (arthropods) or gonozooids (hydrozoans).

Richness, biodiversity, and frequency of occurrence. We defined richness as the number of morphospecies present per substratum block and phylum richness as the number of phyla per substratum block. We also examined morphospecies richness within a phylum. Richness was examined both as a total for all blocks combined (sum of all morphospecies or phyla) as well as an average per substratum block (across the three substratum blocks of each type in each frame ± SD; except wood). We calculated diversity as the Shannon Index (Shannon 1948) using abundance of morphospecies:

$$\mathrm{H}' = \sum_{i=1}^{s} (\rho_i) \ln \rho_i$$

where ρi is the proportion of individuals of one morphospecies divided by the total number of individuals, ln is the natural log, and s is the number of morphospecies.

We defined frequency of occurrence as the percentage of substratum types or geographic sites a morphospecies recruited to out of the total number of substratum types or sites examined.

Morphospecies abundance. Abundance was calculated as the total number of individuals as well as individuals per substratum block (ind block^{-1}). We estimated abundances of colonial or high-density unitary morphospecies (e.g., colonial hydrozoans) as the total number of individuals counted within three randomly selected 1 cm^2 squares of a grid overlay on the mosaic image of each face (see above; Supplementary Figure 2.1), which we averaged and then extrapolated to the whole face (± SD). The eroded corners of all substratum blocks (as defined in Figure 2.1 and Supplementary table 2.1) were excluded from the analysis of high-density or colonial morphospecies. At the level of the block, we calculated morphospecies abundance both as a sum of individuals (total abundance) and as the average number of individuals on each face of the block (abundance per block face) to include the variability of recruitment on different faces. In the case of abundance per block face, we omitted the least colonized face from all blocks to account for obstructed faces in Site 1 and 2.

Surface cover. We estimated the proportion of the block surface occupied by a given morphospecies (or group of morphospecies) using estimated increments of 5% visually at two levels: 1) at the surface of the substratum (up to 1 mm height) and 2) at the canopy (over 1 mm; particularly for arborescent forms like colonial hydrozoans). Global and morphospecies-specific cover represented an average across the three blocks of each substratum type at each site (± SD; except wood).

Spatial recruitment and colonization patterns. We categorized how each morphospecies spatially recruited to and colonized the surface of the block in two ways: location and microhabitat. Recruitment location was established per morphospecies on each face of a given block by scoring its presence/absence at the edges or in the centre (Figure 2.1; see details of the locations in Supplementary table 2.1). The following equation calculated the percentage of

occurrences in each recruitment location of the total number of occurrences of each morphospecies:

$$\%\ (y)\text{occurences} = \frac{\text{Total faces on (x) the morphospecies occurred in (y)}}{\text{Total faces on (x) the morphospecies occurred}}$$

where x is substratum type and y is location.

Pores, projecting pegs, and folds characterized the stone, plastic and mesh substrata respectively, whereas colonizers could bore into wood. To consider this three-dimensional aspect, we treated these features to be "sheltered" microhabitats, in contrast to the "unsheltered" remainder of the surface (i.e., outermost surface area around pores on stone or folds in mesh, and the flat tops of pegs on plastic) (Figure 2.1; see details of the various microhabitats in Supplementary table 2.2). To examine the occurrences of colonizers in each microhabitat of the total number of occurrences of each morphospecies, we used the same equation as described above for recruitment location, with x as substratum type and y as microhabitat category. Morphospecies that occurred as epibionts (i.e., not touching any part of the substratum block) were categorized separately and excluded from the location and microhabitat calculations (Figure 2.1B).

Effect of substratum and geographic site. The effect of substratum type (sites pooled) and geographic site (substrata pooled) were both assessed for each metric defined above.

Epibiosis. Any epibiotic pairings (i.e., one basibiont and one epibiont) present were documented opportunistically for observations on succession in early communities. Richness and abundance measurements included epibiota, defined as individuals that occurred on other individuals, but were included only in the canopy for percent cover measurements.

2.3.4 Statistical analyses

Multivariate analyses used PRIMER v7 software. Differences in morphospecies abundance, density, base and canopy coverage, richness, and diversity (H') between substratum types and geographic sites were explored using PERMANOVA (unrestricted permutation of raw data; type III partial) on Bray-Curtis resemblance matrices and visualized with non-metric multidimensional scaling (nMDS). A two-way crossed analysis of similarity (ANOSIM) test with Spearman rank correlation compared between sites and substratum types. Density, coverage, richness, and diversity were square root transformed to balance between both the most common and rarer morphospecies; abundance values were fourth-root transformed as the wide range of values needed further balancing (Clarke et al. 2014).

2.4 Results

2.4.1 Overall trends in abundance, richness, diversity, and coverage

Combining all substratum types and geographic sites yielded a total of 127 724 individuals representing 28 mspp across seven phyla, as well as three unidentifiable taxa (107 ind) that we excluded from further analyses unless otherwise stated. We documented an overall density of 1.8 ± 1.3 mspp per block with 25.0 ± 18.4% surface coverage and 22.1 ± 20.4% canopy coverage. This fauna included a mix of 11 colonial (127 191 ind) and 17 unitary mspp (426 ind), as well as 17 sessile mspp (127 451 ind) and 11 motile mspp (165 ind).

Across geographic sites and settlement frames, the diversity of morphospecies was composed of nine cnidarian mspp including one octocoral, one actiniarian, and seven colonial hydrozoans (Figure 2.3A); one of the latter occurred in two forms, i.e. an erect branching colony (Campanulariidae sp. 2A) and another of stolonate polyps (Campanulariidae sp. 2B; i.e.,

horizontal growth). There were also seven arthropods including one halacarid, one ostracod, one motile and one tube-dwelling gammarid amphipod, one caprellid amphipod, one isopod, and one copepod (Figure 2.3E); four foraminifers (Figure 2.3B); four poriferans (sponges; Figure 2.3G); two annelids which included one free-living and one tube-dwelling polychaete (Figure 2.3F); two molluscs which included one gastropod, and one gastropod egg mass (Figure 2.3D); and one radiolarian (Figure 2.3C). The three unknown mspp included individual eggs seen on multiple occasions, one egg mass, and one unidentifiable aggregate of biological origin (Figure 2.3H). Table 2.1 details all morphospecies present and their occurrences. No morphospecies occurred everywhere (e.g., on all substratum types at all sites); however, the colonial hydrozoan Campanulariidae sp. 3 and Foraminifera sp. 1 colonized all substratum types when pooling sites, and at all sites when pooling substratum types. Of all morphospecies, Campanulariidae sp. 3 dominated with 114 821 recorded individuals (Table 2.2; Supplementary table 2.4), a density of 4.2 ± 1.4 ind cm^{-1} (Supplementary table 2.5) and the most surface and canopy coverage ($18 \pm 11\%$ and $12 \pm 9\%$ respectively). Four mspp (Halacaridae sp. 1, Ostracoda sp. 1, Gastropoda sp. 1, and Porifera sp. 3) occurred as only one individual or colony across all substratum types and geographic sites.

By phylum, cnidarians exhibited the highest richness (Figure 2.4) as well as highest abundance (130 859 ind; Table 2.2), density (0.68 ± 0.65 ind cm^{-2}; Supplementary table 2.5), and surface and canopy coverage ($10.7 \pm 13.3\%$ and $10.1 \pm 14.8\%$ respectively; Figure 2.6; Supplementary Table 2.6). While orders of magnitude fewer, foraminifers were the second most abundant phylum (262 ind), followed by arthropods (131 ind), molluscs (35 ind), radiolarians (8 ind), poriferans (5 ind), and annelids (4 ind; Table 2.2). Density of all other phyla was below 0.01 ind cm^{-2}, in order of decreasing density foraminifers, molluscs, arthropods, radiolarians,

annelids, and poriferans (Supplementary table 2.5). Negligible percent cover at the block-face level characterized all non-cnidarian phyla (1.6 ± 1.5% at the base and 0.3 ± 1.1% at the canopy; Supplementary table 2.6, 2.7, 2.8). Across block faces, the cover was consistently higher at the base than at the canopy (Figure 2.5).

2.4.2 Effect of substratum type

When analysing substratum type irrespective of geographic site and independent of substratum block, plastic was the most colonized substratum with a total of 41 763 individuals (morphospecies pooled; Table 2.2), and a density of 50.5 ± 28.8 ind cm^{-1} (Supplementary table 2.5). It was followed by stone (41 549 ind, 31.7 ± 27.7 ind cm^{-1}), mesh (41 260 ind, 26.0 ± 31.1 ind cm^{-1}), and wood (3 152 ind, 4.8 ± 6.2 ind cm^{-1}). Total abundance differed significantly among substratum types (pseudo-F = 8.15; $p < 0.001$; Supplementary table 2.9), as did density (pseudo-F = 6.74; $p < 0.001$). Plastic exhibited the clearest clustering in total abundance, whereas mesh and stone exhibited two clusters and wood was grouped more loosely (Figure 2.7). Specifically, total abundance significantly differed between mesh vs. plastic ($\rho = 0.657$; $p < 0.001$) and vs. stone ($\rho = 0.593$; $p = 0.001$), as well as between plastic vs. wood ($\rho = 0.704$; $p = 0.047$) (Supplementary table 2.9). Density was also significantly higher on mesh than on plastic ($\rho = 0.500$; $p = 0.006$) or stone ($\rho = 0.463$; $p = 0.006$) as well as higher on plastic than on wood ($\rho = 0.704$; $p = 0.047$). Plastic also exhibited the highest abundance and density of any one morphospecies, i.e., Campanulariidae sp. 3 (37 347 ind, 7.6 ± 4.3 ind cm^{-1}; Supplementary table 2.4, 2.5).

Coverage differed significantly among substratum types at both the base (pseudo-F = 5.29; $p < 0.001$) and canopy (pseudo-F = 3.39; $p < 0.001$) levels (Supplementary table 2.9). Wood was the most heavily covered when combining all morphospecies, both at the base (50.3 ±

42.6%) and canopy (42.8 ± 37.5%), followed by plastic (23.6 ± 14.9% and 21.1 ± 22.6%; Figure 2.6). Stone was covered more than mesh at the base (18.6 ± 8.4% and 17.5 ± 12.9%, respectively), whereas the inverse occurred at the canopy (15.2 ± 8.2% and 17.7 ± 19.2%, respectively). Base coverage differed significantly between mesh vs. plastic ($\rho = 0.583$; $p < 0.001$), mesh vs. stone ($\rho = 0.556$; $p = 0.004$), and mesh vs. wood ($\rho = 0.704$; $p = 0.047$) as well as between plastic vs. wood ($\rho = 0.852$; $p = 0.002$; Supplementary table 2.9). Canopy coverage significantly differed between mesh vs. plastic ($\rho = 0.370$; $p = 0.005$) and vs. stone ($\rho = 0.463$; $p = 0.002$) as well as plastic vs. stone ($\rho = 0.389$; $p = 0.006$; Supplementary table 2.9).

Overall, mesh supported the highest total richness, with 26 mspp spanning seven phyla (and two unknown mspp). Thirteen mspp from five phyla colonized both plastic and stone (and one unknown msp), with six mspp from three phyla colonizing wood (as well as one unknown msp). Mesh also harbored the highest morphospecies and phylum richness per substratum block, averaging of 7.3 ± 2.3 mspp from 5.3 ± 0.5 phyla per block, followed by stone (4.2 ± 1.8 spp block^{-1} and 2.8 ± 1.0 ph block^{-1}), plastic (4.0 ± 1.7 spp block^{-1} and 2.5 ± 1.0 ph block^{-1}), and wood (3.0 ± 1.7 spp block^{-1} and 1.7 ± 0.6 ph block^{-1}; Figure 2.4). Morphospecies richness differed significantly among substratum types (pseudo-$F = 8.62$; $p < 0.001$) as did phylum richness (pseudo-$F = 9.19$; $p < 0.001$; Supplementary table 2.9). Mesh significantly differed from all other substratum types in both morphospecies (plastic: $\rho = 0.569$, $p = 0.001$; stone: $\rho = 0.514$, $p < 0.001$; wood: $\rho = 1.00$, $p = 0.016$) and phylum richness (plastic: $\rho = 0.625$, $p < 0.001$; stone: $\rho = 0.366$, $p = 0.01$; wood: $\rho = 0.852$, $p = 0.031$). Shannon diversity was highest on mesh ($H' = 0.62 \pm 0.46$), followed by stone ($H' = 0.39 \pm 0.18$), wood ($H' = 0.34 \pm 0.49$) and plastic ($H' = 0.33 \pm 0.25$); it did not significantly differ among substratum types overall (pseudo-$F = 1.07$; $p =$

0.4), but did differ significantly among substratum types within geographic sites (pseudo-F = 2.31; p = 0.010; Supplementary table 2.9).

Four ubiquitous mspp occurred on all substratum types: Campanulariidae sp. 2 and sp. 3, *Eudendrium* sp. 1, and Foraminifera sp. 1 (i.e., 13% of all mspp combined; Table 2.1). Conversely, 15 mspp occurred on only one substratum (i.e., 48% of all mspp), chiefly on mesh (n = 13; 42%), and stone (n = 2; 6%), whereas no morphospecies occurred exclusively on plastic or wood (Figure 2.4).

2.4.2.1 Spatial recruitment and colonization patterns

2.4.2.1.1 Sessile morphospecies

Twenty mspp colonized surface locations and microhabitats (Figure 2.6). Eleven mspp colonized just one surficial location per substratum type; of these, 4 mspp colonized just one location globally (described below; Table 2.3). Eleven mspp occurred in just one microhabitat per substratum type; 6 mspp colonized just one microhabitat globally (four singletons, and two which occurred multiple times in the same microhabitat). Overall, 16 mspp colonized the centre location, irrespective of substratum type and site (~89%) and 12 mspp colonized edges (~60%). Sixteen mspp colonized the unsheltered microhabitat irrespective of substratum type and site (~80%), whereas 18 colonized the sheltered microhabitats (90%; Figure 2.6; Table 2.3). Only one msp, Unknown sp. 3, bored into the wood substratum (i.e., sheltered microhabitat).

Three colonial hydrozoans (Campanulariidae sp. 3, sp. 2, and *Eudendrium* sp. 1) colonized almost all locations and microhabitats available on the substrata (Figure 2.6A). The most abundant and opportunistic colonizer (Campanulariidae sp. 3) did not display location preferences, and colonies extended across unsheltered and sheltered microhabitats, except for

sheltered microhabitats on stone at Site 2, mesh at Site 1, and wood. Campanulariidae sp. 2 also showed little location preference, except for mesh edges at Site 3. Biota colonized almost all microhabitats, except for sheltered microhabitats on stone at Site 3 and wood. *Eudendrium* sp. 1 colonized corner, edge, and centre locations with no exceptions; all microhabitats available were colonized except the sheltered microhabitat on wood.

An additional four mspp colonized broad locations and microhabitats across multiple substratum types and sites: Octocorallia sp. 1, Foraminifera sp. 1, Radiolaria sp. 1, and Unknown sp. 1 (Figure 2.6B). Six mspp occurred in few locations and microhabitats across two sites, and seven mspp recruited to or colonized one or both locations and microhabitats but were restricted to just one site (Figure 2.6C). For a detailed description of location and microhabitat utilization, refer to Supplementary (2.10.1.1).

2.4.2.1.2 Motile morphospecies

Ten motile mspp utilized specific surface locations and microhabitats. Seven mspp occurred in the centre location, irrespective of substratum type and site (~78%), four on edges (~44%), and two in corners (~22%; Table 2.3). Five mspp occurred in unsheltered microhabitats irrespective of substratum type or site (~56%), and nine mspp in sheltered microhabitats (90%).

Copepoda sp. 1 occurred across sites, predominantly on various surficial locations of the mesh substratum, secondarily in the centre location of plastic, and in the centre of the wood substratum at Site 4 (Table 2.3). Sheltered locations dominated microhabitat utilization. Gammaridea sp. 1 occurred in multiple locations of the mesh substratum and in the centre of both plastic and stone, predominately in unsheltered mesh and stone microhabitats, though more often in sheltered plastic microhabitats. Gammaridea sp. 2 utilized mesh centre and edge

locations at Site 1 and, though present in both, occurred more often in unsheltered than sheltered microhabitats. Caprellidae sp. 1 colonized mesh edges at Site 4 in equal presence in both sheltered and unsheltered microhabitats. All other arthropods occurred in just one location and microhabitat: Halacaridae sp. 1 occurred solely on mesh edge at Site 1 and in sheltered microhabitat; Isopoda sp. 1 and Ostracoda sp. 1 both occurred in mesh centres at Site 4; the former utilized unsheltered microhabitats whereas the latter utilized sheltered microhabitat. Polychaeta sp. 2 occurred in the centre of mesh at Site 1 and stone at Site 4, and always in sheltered microhabitat. The molluscs each occurred in just one location and/or microhabitat. Gastropoda sp. 1 and sp. 3 both colonized the mesh centre at Site 4 in sheltered microhabitat (Table 2.3).

2.4.3 Effect of geographic site

Settlement frames were positioned at differing depths and altitudes across sites (Figure 2.2). When combining all substrata within each geographic site, Site 1 had the highest abundance of recruits/colonizers (57 101 ind; Table 2.2; Supplementary table 2.4) and highest density (52.1 ± 35.8 ind cm^{-1}; Supplementary Table 2.5). Site 4 (49 393 ind, 40.0 ± 20.7 ind cm^{-1}), Site 2 (12 375 ind, 11.2 ± 21.1 ind cm^{-1}), and Site 3 (8 856 ind, 10.6 ± 8.6 ind cm^{-1}) followed. Total abundance differed significantly among sites (pseudo-F = 10.99; $p < 0.001$), as did density (pseudo-F = 9.31; $p < 0.001$; Supplementary table 2.9). In nMDS, Sites 1 and 4 clustered closely, while Sites 2 and 3 clustered more loosely into two clusters (Figure 2.7). Site 1 differed significantly from Site 2 (abundance: $\rho = 0.889$, $p = 0.001$; density: $\rho = 0.877$, $p = 0.001$) and Site 3 ($\rho = 0.753$, $p = 0.002$; $\rho = 0.778$, $p = 0.001$); Site 2 differed significantly from Site 3 (abundance: $\rho = 0.926$, $p = 0.001$; density: $\rho = 0.901$, $p = 0.001$) and Site 4 (abundance: $\rho =$

0.827, p = 0.001; density: ρ = 0.605, p = 0.002); and Site 3 differed significantly from Site 4 (abundance: ρ = 0.457, p = 0.002; density: ρ = 0.259, p = 0.034; Supplementary table 2.9).

Site 4 had the most covered substrata (morphospecies pooled; 45.9 ± 27.1% at the surface and 48.0 ± 21.4% at the canopy), followed by Site 1 (35.0 ± 19.0% and 28.4 ± 17.0%), Site 3 (10.6 ± 7.7% and 9.0 ± 8.9%), and Site 2 (8.5 ± 4.6% and 3.0 ± 2.0%; Figure 2.5). The difference in surface and canopy cover between sites was statistically significant (pseudo-F = 10.05-10.11, $p < 0.001$). All significantly differed from one another ($p < 0.05$) except for Site 1 and Site 4 (base: ρ = 0.025, p = 0.405; canopy: ρ = 0.012, p = 0.456; Supplementary table 2.9).

Total richness across substratum types was highest at Site 4 (22 mspp from 6 phyla), followed by Site 1 (16 mspp from 5 phyla), Site 3 (13 mspp from 6 phyla), and Site 2 (10 mspp from 5 phyla). Morphospecies richness per substratum block remained highest at Site 4 (6.5 ± 2.0 spp $block^{-1}$) followed by Site 3 (5.4 ± 2.0 spp $block^{-1}$), Site 1 (4.7 ± 2.5 spp $block^{-1}$), and Site 2 (2.4 ± 1.1 spp $block^{-1}$; Figure 2.4). Morphospecies richness differed significantly among sites (pseudo-F = 9.87, $p < 0.001$; Supplementary table 2.9). Site 1 significantly differed from Site 2 (ρ = 0.543, p = 0.01), and Site 2 differed from both Site 3 (ρ = 0.580, p = 0.004) and Site 4 (ρ = 0.765, p = 0.001). Phylum richness across substrata was highest at Site 3 (4.0 ± 1.7 ph $block^{-1}$), followed by Site 4 (3.5 ± 1.3 ph $block^{-1}$), Site 2 (2.8 ± 1.7 ph $block^{-1}$), and Site 1 (2.5 ± 1.7 ph $block^{-1}$). Phylum richness did not differ significantly among sites (pseudo-F = 2.51, p = 0.07; Supplementary table 2.9). Shannon diversity was highest at Site 3 (H’ = 0.74 ± 0.47), followed by Site 4 (H’ = 0.53 ± 0.27), Site 2 (H’ = 0.32 ± 0.31), and finally Site 1 (H’ = 0.18 ± 0.13). Shannon diversity differed significantly among sites (pseudo-F = 3.82, $p < 0.001$), with Site 1 differing significantly from Site 2 (ρ = 0.267, p = 0.033) and Site 3 (ρ = 0.346, p = 0.01), and

Site 2 differing significantly from Site 3 ($\rho = 0.558$, $p = 0.001$) and Site 4 ($\rho = 0.304$, $p = 0.04$; Supplementary table 2.9).

The four geographic sites had three mspp in common: Campanulariidae sp. 3, Copepoda sp. 1, and Foraminifera sp. 1 (i.e., 10% of all mspp; Table 2.1). Conversely, 14 mspp (i.e., 45% of all mspp) occurred at only one site, with the highest number of unique morphospecies at Site 4 (n = 8, 25% of all mspp, 505 m) and the fewest at Site 2 (n = 1, 3% of all mspp, 960 m; Figure 2.4). Highest total abundance of Campanulariidae sp. 3 (54 563 ind) and density (9.3 ± 4.7 ind cm^{-1}) occurred at Site 1, followed by Site 4 (37 533 ind, 6.0 ± 1.6 ind cm^{-1}), Site 2 (12 328 ind, 2.3 ± 4.6 ind cm^{-1}), and finally Site 3 (6 921 ind, 1.6 ± 1.3 ind cm^{-1}; Table 2.2; Supplementary table 2.4, 2.5). Abundance and density of Campanulariidae sp. 3 was significantly different between sites ($p < 0.001$).

We recorded arthropods, cnidarians, and foraminifers at all sites (Figure 2.4). Radiolarians were absent from Site 1, annelids from Site 2, poriferans from Site 4, and molluscs from all sites except Site 4. Site 4 had the highest number of cnidarian morphospecies (4.2 ± 0.2 spp $block^{-1}$), followed by Site 1 (3.1 ± 1.4 spp $block^{-1}$), Site 3 (2.8 ± 0.4 spp $block^{-1}$) and then Site 2 (1.1 ± 0.2 spp $block^{-1}$). Highest morphospecies richness of foraminifers, annelids, and arthropods occurred at Site 3 (0.8 ± 0.5, 0.2 ± 0.4, and 1.2 ± 0.2 spp $block^{-1}$, respectively), in contrast to highest richness of radiolarians (0.3 ± 0.2 spp $block^{-1}$) and molluscs (0.2 ± 0.3 spp $block^{-1}$) at Site 4 and highest richness of poriferans at Sites 1 and 2 (0.2 ± 0.3 and 0.2 ± 0.2 spp $block^{-1}$, respectively; Figure 2.4).

2.4.4 Growth patterns and lifestyles

Colonial forms dominated at the substratum level, averaging between 1.7 ± 1.2 and 3.3 ± 1.3 mspp, with correspondingly lower averages for unitary morphospecies between 0.7 ± 0.6 and 3.8 ± 1.0 per block. Within each site, colonial morphospecies consistently dominated as well, averaging between 1.3 ± 0.2 and 3.5 ± 0.6 per block, in contrast to a range of 0.8 ± 1.2 to 2.4 ± 1.4 per block for unitary morphospecies.

Sessile morphospecies dominated at the substratum level, averaging between 2.3 ± 1.5 and 5.2 ± 1.5 per block whereas correspondingly lower averages between 0.3 ± 0.6 and 1.9 ± 0.7 per block characterized motile morphospecies. Sessile morphospecies dominated at the site level as well, averaging from 1.8 ± 0.9 to 5.1 ± 1.1 per block whereas motile morphospecies ranged from 0.3 ± 0.5 to 1.3 ± 1.0 per block.

2.4.5 Reproductive status

A few individuals harboured oocytes and embryos. A mature female Caprellidae sp. 1 with a brood pouch carried visible embryos (Figure 2.3E). Individuals of two mspp of colonial hydrozoans, Campanulariidae sp. 3 and *Eudendrium* sp. 1, had mature gonozooids containing visible development (Figure 2.3A).

2.4.6 Epibiosis

We observed 16 occurrences of epibiosis, all on three colonial hydrozoan hosts (Campanulariidae sp. 2, *Eudendrium* sp. 1 and sp. 2). The associations occurred primarily at Site 4 (n = 12), with some at Sites 1 and 3 (n = 2 each). One gastropod mollusc that occurred only as egg masses, Gastropoda sp. 2 occurred exclusively as an epibiont of Campanulariidae sp. 2. Five mspp occurred occasionally as epibionts: the benthic Foraminifera sp. 1, two colonial

hydrozoans (Campanulariidae sp. 3 and *Eudendrium* sp. 1), the Caprellidae sp. 1, and individual eggs of Unknown sp. 1. The most common epibiont, Foraminifera sp. 1, was observed twice each on Campanulariidae sp. 2, *Eudendrium* sp. 1, and sp. 2. *Eudendrium* sp. 1 also occurred commonly as an epibiont on Campanulariidae sp. 2 (n = 4). Similarly, Campanulariidae sp. 2 also occurred once as an epibiont on *Eudendrium* sp. 1. Individual eggs (Unknown sp. 1) occurred once on Campanulariidae sp. 2. Of the motile morphospecies, we observed Caprellidae sp. 1 on *Eudendrium* sp. 1 three times.

2.5 Discussion

At the temporal scales studied (about one year), colonial hydrozoans emerged as the dominant recruits on all substratum types and at all sites, contributing almost the entirety of overall abundance and cover of substratum surfaces and canopies. Numerous studies document colonial hydrozoans as pioneer recruits to artificial settlement frames and anthropogenic structures in tropical, temperate, and polar shallow waters (Boero 1984; Ronowicz 2007; Ronowicz et al. 2008; Ronowicz et al. 2013; Calder et al. 2021). Arctic deep-sea taxa apparently follow this pattern, based on our findings and those of Meyer-Kaiser et al. (2019), who reported a colonial hydrozoan (*Halisiphonia arctica*) among the earliest recruits to brick and plastic substrata at 2500 m depth in the Fram Strait (west of Svalbard, Norway). The fast growth rate of hydrozoans could have allowed settling larvae to develop and spread rapidly across the substrata in our study through stolonization (i.e., horizontal growth). Colonial hydrozoans also occurred on the settlement frame itself and the bolts (both plastic) holding the blocks. Hydrozoans were also the only sessile morphospecies to display reproductive maturity and to host epibionts, attesting to their rapid development and sexual maturation. Kristen-Meyer et al. (2022) also reported reproductive maturation of three species of hydrozoans on settlement plates deployed over a

similar time span in the Fram Strait. Considering the near absence of these same hydrozoan morphospecies on well-established hard bottoms in nearby habitats (see Chapter 3), these erect hydrozoan colonies may act as a crucial first stage of succession in the establishment of hard bottom deep-sea benthic communities; other taxa may rely on their presence for recruitment and might graze or overtake them over the longer term. In line with this explanation, we observed gastropod eggs at the base of a hydrozoan colony, and epibiotic foraminifers, caprellids, and unidentifiable eggs on hydrozoan stalks. Gastropod nudibranchs prey on hydrozoans (Martin 2003), which would align with deposition of gastropod egg masses on the base of a hydrozoan colony as a source of food for the juveniles. Similarly, Lutze and Thiel (1989) reported that some foraminifer species preferentially position themselves on elevated substrata for better access to food, and caprellids use or even preferentially select biogenic structures such as hydrozoans as substrata in shallow North Atlantic studies (McCain 1968; Caine 1998). Such preferences in epibiotic relationships could define the first steps of succession in such an early community.

2.5.1 Effect of substratum type

We observed differences in morphospecies and phylum richness, as well as density between substratum types, indicating that substratum-specific features such as the surface material, locations, and microhabitats available to larvae play a role in recruitment and colonization patterns. Of all substrates, higher richness characterized the complex three-dimensional structure of the mesh substratum at both the morphospecies and phylum levels. Mesh substratum also hosted the most unique morphospecies, although it did not dominate in morphospecies abundance, density, or coverage. The comparatively loose and flexible structure of the mesh, with its fragmented surface and many folds, may accommodate more morphospecies simultaneously but impede growth and expansion by recruits. For instance,

recruits utilized the unique features of mesh in different ways, including copepods, tube-dwelling amphipods, and free-living polychaetes stretching the flexible strands and folds to get inside, and colonial hydrozoans extending stolons throughout the internal area, presumably to anchor more strongly. Accordingly, Girard et al. (2016) reported that no single taxon dominated on complex substrata (comparable to mesh in the present study), and lower hydrozoan biomass (i.e., abundance and coverage in the present study) on complex than simple substrata (stone) in their 4-y study in the Gulf of Maine (USA) at sites between 600–900 m. Potentially, the lower morphospecies and phylum richness on other substratum types tested in our study reflects preference, as emphasized by fewer unique morphospecies occupying other substrata even at the same site. Case in point, Burkett et al. (2016) deployed a recruitment experiment containing three substratum types at 595–777 m depth in Hydrate Canyon (Oregon, USA), and reported that epibenthic foraminifers never settled on wood, whereas polypropylene (comparable to plastic) hosted only 3% of total foraminifer abundance relative to mesh (97%). In our study, foraminifers colonized other substrata, but only mesh harbored all four morphospecies of recorded foraminifers, underscoring an attraction to this more complex and pliable substratum type.

While not highest in richness, plastic in our study supported the highest total abundance and density of morphospecies per surface area. The most likely potential driver of this could be the larger, unbroken surface area of plastic with the added three-dimensionality of a large, sheltered microhabitat (i.e., between plastic projections). Apparently, more morphospecies could utilize the mesh surface simultaneously (increasing richness), and the plastic substratum allowed recruits to grow more quickly. Similarly, Lacharité and Metaxas (2013) reported greater recruitment of corals (*P. resedaeformis* and *P. arborea*) to the structurally complex plastic components of the collector frame than to the flat surfaces of the collectors, which they attributed

to sheltering effects of the three-dimensional components (comparable to sheltered microhabitat) that could result in minute changes in flow, food availability, and vulnerability to predators. Most other recruitment experiments listing plastic as a substratum type used flat panels (no projections), which yielded results opposite to ours. For instance, Meyer-Kaiser et al. (2019) reported higher abundance of recruits on brick panels (~stone) than on plastic panels deployed for 19 years, attributing it to more complex microhabitats on the former than the latter. This interpretation aligns with our conclusion that high recruit abundance on the plastic could reflect microhabitat complexity rather than substratum material.

Despite lower recruit densities than plastic and lower scores in all other recruitment metrics, wood had the highest coverage (all morphospecies combined) at both the base and canopy levels. Its smooth (nonporous) surface area may have allowed expansion of recruits more easily than on complex three-dimensional structures in other substrata, which may constrain vertical and horizontal growth. Fine-scale flow around certain sheltered components of the settlement frame could affect recruitment (Lacharité and Metaxas 2013), so that unsheltered wood potentially improved the vertical and horizontal expansion by taxa preferring that feature. In addition, we offered wood as a single larger panel rather than as replicated blocks, possibly facilitating horizontal expansion of colonial hydrozoans, which dominated its base and canopy coverage. Consistent with this explanation, we observed greater abundance on wood with one of the ubiquitous morphospecies of colonial hydrozoan that occurred both as an erect, branching colony and horizontally-stolonizing polyps that surrounded them (Campanulariidae sp. 2A, 2B respectively), indicating this substratum improves colonization success. This morphospecies could be the morphologically similar and common deep-water Arctic hydrozoan *Stegopoma plicatile*, which densely covered settlement plates deployed at 215 m in Kongsfjorden (western

Spitsbergen, Norway) (Meyer et al. 2017). The latter study used flat acrylic panels, i.e. a plastic material whose other features provided a flat (unsheltered) surface similar to the wood substratum in our study. We note the loss of the wood panel from Site 3, excluding a site with lower recruit coverage overall for this substratum (discussed below). Wood otherwise harbored just two morphospecies not among the four generalists: the motile Copepoda sp. 1 and a biological aggregate of unknown phylum (Unknown sp. 3), though both also occurred on other substratum types. The presence of copepods aligns with a recruitment experiment at the Lucky Strike Hydrothermal Field (near Azores, Portugal), which reported two species of wood-boring bivalves and a surface-dwelling copepod exclusive to wood, in contrast to greater abundances of another surface-dwelling copepod and three gastropod species on wood than slate (Cuvelier et al. 2014). The copepods in our study were also more abundant on wood than on stone (where they were absent) but less abundant on wood than on mesh and plastic, two substrata not tested by Cuvelier et al. (2014). Interestingly, we found no wood-boring bivalves, although the unknown biological aggregate apparently bored into the wood. Potentially, wood specialist taxa were absent regionally, given that our study occurred at a latitude above the tree line, presumably offering a very limited supply of natural wood to the marine environment. Previous studies conducted at latitudes below the tree line report wood-boring bivalves in other regions of the deep sea, using similar depths and time frames, attributing their absence to unfavourable environmental conditions or overall lack of wood to support a population (Cuvelier et al. 2014; Romano et al. 2014).

Stone did not dominate in any colonization metric, but it was one of two substrata that attracted unique morphospecies (Campanulariidae sp. 1 and Hydrozoa sp. 1), suggesting that some taxa preferentially recruit to stone. That the latter are hydrozoans aligns with previous

studies in shallow waters of the Arctic, wherein Ronowicz et al (2013) reported that some species of stolonate and erect hydrozoans (*Bougainvillia* cf. *superciliaris* and *Sarsia* sp.) occur more commonly on rocks, and higher richness of hydrozoans overall on rocks than on some other structurally similar substrata but lower than on algae. Potentially, the features of the stone used in our study, such as a predominately flat surface with only minute, sheltered areas (i.e., the pores), attract more resilient suspension feeders, noting that the colonizing hydrozoans were stolonate or had a high flexibility that would enable them to withstand the stronger flow associated with unsheltered substrata. Notably, Hydrozoa sp. 1 anchored in a sheltered microhabitat (pore) but grew vertically into the water column, suggesting the larvae sought it out. Smaller recruits such as foraminifers, primary polyps of octocorals, and small actinarians also took advantage of the pores. Consistent with this interpretation, Girard et al (2016) reported the presence of actiniarians only on simple substrata (comparable to stone in this study) and not on complex mesh, though they did not test other substratum types. Given that we found actiniarians on both stone and plastic in sheltered areas, these habitats may offer similarly attractive characteristics (e.g. flat, inert surface with micro-shelter).

Four morphospecies overall apparently showed no substratum preference, including three colonial hydrozoans, two of which were campanulariids (Campanulariidae sp. 2A, 2B and 3), well-known to display little substratum preference during colonization (Cornelius 1982). Ronowicz (2008) reported that, of the 17 hydrozoans in coastal waters of Spitsbergen (Svalbard, Norway), campanulariids occurred across a multiple of available substrata in a kelp forest; Ronowicz et al. (2013) also reported that many species of hydrozoans utilize rocks, algae, and secondary substrata (bryozoans, hydrozoans) in the shallow Arctic. The third substratum-generalist hydrozoan in our study (*Eudendrium* sp. 1) contrasted the findings of Ronowicz

(2008), who reported eudendriids on just one substratum type per species, though they later reported other species of eudendriid colonizing more than one substratum type (Ronowicz 2013). Wasserthal and Wasserthal (1973) indicated that eudendriids reproduce using slime ropes along which planulae travel, increasing gregariousness with the parent colony, and they grow through horizontal stolonization (Schuchert 2008). These characteristics could have driven expansion of a substratum-specific recruit onto less preferred substrata within the same frame. Because the hydrozoan colonies had developed beyond the first recruit by the time of frame retrieval, the planulae potentially settled preferentially, similarly to Hydrozoa sp. 1 in stone pores noted above, but subsequent horizontal growth obscured these results.

Foraminifera sp. 1, the fourth substratum-generalist morphospecies we recorded, could be the morphologically similar *Cibicidoides wuellersdorfi*, a well-known, common, and opportunistic epibenthic foraminifer, which Meyer-Kaiser et al. (2019) reported as a dominant recruit on both brick and plastic panels deployed in the deep sea of the Fram Strait. Earlier studies characterized *C. wuellersdorfi* as a substratum generalist, colonizing hydroids, stones, tube worms, sponge skeletons, crinoids (Lutze and Thiel 1989; Linke and Lutze 1993) as well as mesh and plastic substrata at Hydrate Ridge, Oregon, USA (Burkett et al. 2016). Foraminifera sp. 1 commonly colonized centre locations and unsheltered areas of all substratum types, suggesting a preference for elevated or relatively exposed surfaces of any material. This interpretation aligns with a previous study: Veillette et al. (2008) reported that most suspension-feeding foraminifers colonizing polymetallic nodules at ~5000 m depth in the Clarion-Clipperton Fracture Zone (central Pacific) preferred raised over depressed microhabitats (~unsheltered and sheltered respectively). Potentially, the larvae of these more ubiquitous taxa do not have strict recruitment preferences, allowing them to colonize more substrata.

Most other morphospecies occupied block centres rather than edges, regardless of substratum material; this pattern confirms most recruitment studies that often exclude edges because of concerns regarding erosion and edge effects (Bowden 2005; Barnes 2017). Primary coral polyps (Octocorallia sp. 1) mostly colonized centres, as did actiniarians, radiolarians, foraminifers, and poriferans. Flows at settlement block edges may be too strong or unpredictable for many taxa; alternatively, perhaps the fauna at the edges eroded over time, noting that we observed some degradation on the edges of the stone substratum. However, some morphospecies occurred exclusively (e.g., Campanulariidae sp. 4 on mesh at Site 4) or more commonly (e.g., *Eudendrium* sp. 1 on plastic and stone at Site 1) on edge locations of some substratum types, which suggests that excluding edges could underestimate the richness, diversity, or abundance measures. More resilient or flexible suspension feeders, such as hydrozoans, may benefit from the flow dynamics and fluctuations that decreases competition for the resources.

Conversely, we observed more varied colonization preferences between sheltered and unsheltered microhabitats. The patterns in poriferans and foraminifers were morphospecies-specific. Actiniarians, radiolarians, and all three unknown morphospecies colonized sheltered microhabitats, whereas octocoral primary polyps commonly occurred in unsheltered microhabitats, as did some hydrozoans, in contrast to Lacharite and Metaxas (2013), who reported higher abundances of the coral *P. resedaeformis* in complex (~sheltered) habitat rather than on flat (~unsheltered) surfaces; this difference may reflect geographic or environmental differences between study areas. Importantly, we cannot fully separate the substratum materials, locations, and microhabitats from each other because their complex interplay affects fine-scale larval recruitment patterns; in addition, a seeming preference for these features could be more a

function of the benefits they convey towards successful recruitment through post-settlement processes than a true preference.

2.5.2 Effect of geographic site

Inter-site differences in abundance, density, coverage (at the base and canopy), and morphospecies richness suggest structuring roles for depth, geographic site, year, and frame altitude above bottom, either independently or in combination. Phylum richness, a notable exception, did not differ across sites. In Antarctic shallow-water recruitment experiments that included several sites, Bowden et al. (2006) also reported that variability in local conditions could heavily influence recruitment and colonization. Many recruitment experiments in the deep sea have also reported variation among sites that could reflect contributions of factors such as depth, frame altitude, and local water-mass characteristics (Romano et al. 2014; Meyer-Kaiser et al. 2019; Meyer-Kaiser et al. 2022).

Interestingly, highest morphospecies and phylum richness and coverage characterized Site 4, as well as the most unique morphospecies, and the most radiolarians and molluscs. Site 4 was closest to Sites 1 and 2 geographically, approximately 170 km off the northernmost coast of Labrador, but water depth (505 m) and frame altitude (16 m) were comparable to Site 1. This site was also one of two with a settlement frame unobstructed by flat placement (see Methods), which could have increased accessibility to pelagic larvae. However, the fact that Site 3 frame ranked second in richness, casts doubt on the dominating importance of flow (through a frame) for this variable. Previous studies have established the importance of food availability, local larval supply, and fine-scale hydrodynamics in larval recruitment and success (Wahl 2009); potentially these variables contributed to richness and abundance of recruits at Site 4.

Site 3 displayed the highest Shannon diversity and highest number of annelid, arthropod, and foraminifer morphospecies. This finding aligns with Meyer-Kaiser et al. (2019), who compared settlement plates deployed at different altitudes (0.25, 0.60, and 0.90 m above bottom) and inferred that annelids drove abundance on plates just above the sea floor. Moreover, Foraminifera sp. 4 and Gammaridea sp. 1 were unique to Site 3, which stood out as the shallowest (409 m) site with an unobstructed frame closest to the bottom (1 m). Potentially that nearness to the bottom played a critical role, given that Shannon diversity indicated a high number of morphospecies in low abundance. Foraminifers have species-specific preferences or limitations to where they can settle; *Cibicidoides wuellersdorfi* (possibly Foraminifera sp. 1) prefers elevation above the bottom (Lutze and Thiel 1989; Sen Gupta 2007) whereas limited dispersal distance characterizes other species (Sen Gupta 2007). Thus, bottom proximity might explain why Foraminifera sp. 4 only occurred at Site 3; conversely, the higher altitude for the frame at Site 4 (11 m) could explain why Foraminifera sp. 2 occurred only there.

Possibly, benthic predators might visit frames close to the sea floor more frequently, thus reducing coverage, abundance, and density of recruits, all of which were lowest at Site 3. Free-living polychaetes at Site 3 (also at Site 1), along with Gammaridea sp. 1, may have been feeding on recruits or dislodging them, thereby reducing numbers of colonizers. Multiple studies document the role of predation in limiting larval recruitment (Osman et al. 1992; Jenkins et al. 2009) and in shallow-water studies in the west Antarctic Peninsula, Bowden et al. (2006) reported higher colonization rates in sheltered settlement frames, attributing differences to fewer predators such as errant polychaetes. Additionally, omnivorous amphipods play an important role in the deep sea, particularly at hydrothermal vents, where four species of lysianassoid amphipods alternated between scavenging, predation, and necrophagy as dominant feeding

modes (Blankenship and Levin 2007). The interplay of an unobstructed frame (i.e., fewer sheltered surfaces) and proximity of benthic predators could have contributed to the high Shannon diversity but low-density community of recruits at Site 3.

Consistent with this explanation, the highest morphospecies abundance and density occurred at Site 1, which was comparable in frame altitude (11 m) and water depth (499 m) to Site 4 but was mounted flat against the mooring structure (i.e., obstructed). This site was also where the highest abundance of any one morphospecies was found (the stolonate colonial hydrozoan Campanulariidae sp. 3), further suggesting that the mounting method alone was not a major driver of recruitment patterns in all metrics, and that it likely acts in combination with other factors such as proximity to the sea floor. Previous studies documented higher recruitment rates near more sheltered components or sides of settlement plates as a result of fine-scale hydrodynamic fluctuations and protection against predators (Bowden et al. 2006; Lacharité and Metaxas 2013); and that some species preferentially position themselves relative to water flow (Mullineaux and Butman 1990; Meyer-Kaiser et al. 2019). Although we did not measure directional positioning relative to water flow over and through the differently mounted frames, such preferences may have influenced recruitment to these settlement frames.

No biological metric dominated at Site 2, the other obstructed frame, which had the lowest morphospecies and phylum richness, number of unique morphospecies, and coverage overall. Annelid and mollusc recruits were absent, and we documented just a single morphospecies of arthropod (Copepoda sp. 1). The frame at this site also had the highest altitude (60 m) and greatest water depth (960 m). Potentially, the greater frame altitude and depth limited the number of recruits that could access the substrata, noting that the site lacked otherwise ubiquitous morphospecies (e.g. Campanulariidae sp. 2, *Eudendrium* sp. 1).

Larval dispersal can strongly affect recruitment, often as a function of planktonic larval duration. The gregariousness of eudendriids (Wasserthal and Wasserthal 1973) likely limits their ability to colonize frames well above bottom deployed for a relatively short time period. Interestingly, annelids and amphipods occurred at all three shallower sites but not at Site 2. This pattern aligns with a study in the Siberian Arctic deep sea, where Vedenin et al (2021) reported annelids and amphipods crowding (e.g., overlapping of upper and lower species' limits) at 400–800 m (~Sites 1, 3, and 4 here), but no crowding from 800 to 1000 m (~Site 2). Similarly, a study of amphipod diversity as function of depth around Iceland reported species richness peaking at ~500 m before declining (Lörz et al. 2021). While impossible to tease out these factors and others (i.e., intra-annual variation) at play, overall site- and substratum-specific factors clearly affect recruitment in complex, interconnected ways.

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2.7 References

Al-Habahbeh AK, Kortsch S, Bluhm BA, Beuchel F, Gulliksen B, Ballantine C, Cristini D, Primicerio R. 2020. Arctic coastal benthos long-term responses to perturbations under climate warming. Philos Trans R Soc Lond Ser Math Phys Eng Sci. 378(2181):20190355-. doi:10.1098/rsta.2019.0355.

Barnes DK. 2017. Marine colonization and biodiversity at Ascension Island and remote islands. J Mar Biol Assoc UK. 97(4):771–782. doi:10.1017/S0025315415001526.

Barnes, Kukliński P. 2005. Low colonisation on artificial substrata in arctic Spitsbergen. Polar Biol. 29(1):65–69. doi:10.1007/s00300-005-0044-y.

Beaulieu SE. 2001. Colonization of habitat islands in the deep sea: recruitment to glass sponge stalks. Deep Sea Res Part I: Oceanogr Res Pap. 48(4):1121–1137. doi:10.1016/S0967-0637(00)00055-8.

Blankenship LE, Levin LA. 2007. Extreme food webs: foraging strategies and diets of scavenging amphipods from the ocean's deepest 5 kilometers. Limnol Oceanogr. 52(4):1685–1697. doi:10.4319/lo.2007.52.4.1685.

Boero F. 1984. The ecology of marine hydroids and effects of environmental factors: a review. Mar Ecol. 5(2):93–118. doi:10.1111/j.1439-0485.1984.tb00310.x.

Bowden DA. 2005. Seasonality of recruitment in Antarctic sessile marine benthos. Mar Ecol Prog Ser 297:101–118. doi:10.3354/meps297101.

Bowden DA, Clarke A, Peck LS, Barnes DKA. 2006. Antarctic sessile marine benthos: colonisation and growth on artificial substrata over three years. Mar Ecol Prog Ser. 316:1–16. doi:10.3354/meps316001.

Brown KM, Fraser KPP, Barnes DKA, Peck LS. 2004. Links between the structure of an Antarctic shallow-water community and ice-scour frequency. Oecologia. 141(1):121–129. doi:10.1007/s00442-004-1648-6.

Burkett AM, Rathburn AE, Elena Pérez M, Levin LA, Martin JB. 2016. Colonization of over a thousand *Cibicidoides wuellerstorfi* (Foraminifera: Schwager, 1866) on artificial substrates in seep and adjacent off-seep locations in dysoxic, deep-sea environments. Deep Sea Res Part I: Oceanogr Res Pap. 117:39–50. doi:10.1016/j.dsr.2016.08.011.

Caine EA. 1998. First case of caprellid amphipod-hydrozoan mutualism. J Crustac Biol. 18(2):317–320. doi:10.2307/1549325.

Calder D, Carlton J, Keith I, Larson K, McCann L, Geller J, Wheelock M, Choong H, Ruiz G. 2021. Additions to the hydroids (Cnidaria, Hydrozoa) of marine fouling communities on the mainland of Ecuador and in the Galapagos Islands. Aquat Invasions. 16(2):208–252. doi:10.3391/ai.2021.16.2.02.

Canning-Clode J. 2009. Latitudinal patterns of species richness in hard-bottom communities. In: Wahl M, editor. Marine Hard Bottom Communities: Patterns, Dynamics, Diversity, and Change. Berlin, Heidelberg: Springer. (Ecological Studies). p. 81–87. https://doi.org/10.1007/b76710_5.

Chalmer PN. 1982. Settlement patterns of species in a marine fouling community and some mechanisms of succession. J Exp Mar Biol Ecol. 58(1):73–85. doi:10.1016/0022-0981(82)90098-3.

Clarke K, Gorley R, Somerfield P, Warwick R. 2014. Change in Marine Communities: An Approach to Statistical Analysis.

Cornelius PFS. 1982. Hydroids and medusae of the family Campanulariidae recorded from the eastern north Atlantic, with a world synopsis of genera. Bull Br Mus Nat Hist Zool. 42:37--148.

Cuvelier D, Beesau J, Ivanenko VN, Zeppilli D, Sarradin P-M, Sarrazin J. 2014. First insights into macro- and meiofaunal colonisation patterns on paired wood/slate substrata at Atlantic deep-sea hydrothermal vents. Deep Sea Res Part I: Oceanogr Res Pap. 87:70–81. doi:10.1016/j.dsr.2014.02.008.

Davis AR. 2009. The role of mineral, living and artificial substrata in the development of subtidal assemblages. In: Wahl M, editor. Marine Hard Bottom Communities: Patterns, Dynamics, Diversity, and Change. Berlin, Heidelberg: Springer. (Ecological Studies). p. 19–37. https://doi.org/10.1007/b76710_2.

Dayton PK. 1989. Interdecadal variation in an Antarctic sponge and its predators from oceanographic climate shifts. Science 245(4925):1484–1486. doi:10.1126/science.245.4925.1484.

Denitto F, Terlizzi A, Belmonte G. 2007. Settlement and primary succession in a shallow submarine cave: spatial and temporal benthic assemblage distinctness: Settlement and primary succession in a submarine cave. Mar Ecol. 28:35–46. doi:10.1111/j.1439-0485.2007.00172.x.

Dumont CP, Gaymer CF, Thiel M. 2011. Predation contributes to invasion resistance of benthic communities against the non-indigenous tunicate *Ciona intestinalis*. Biol Invasions. 13(9):2023–2034. doi:10.1007/s10530-011-0018-7.

Gaines SD, Bertness MD. 1992. Dispersal of juveniles and variable recruitment in sessile marine species. Nature 360(6404):579–580. doi:10.1038/360579a0.

Gates AR, Benfield MC, Booth DJ, Fowler AM, Skropeta D, Jones DOB. 2017. Deep-sea observations at hydrocarbon drilling locations: Contributions from the SERPENT Project after 120 field visits. Deep Sea Res Part II: Top Stud Oceanogr. 137:463–479. doi:10.1016/j.dsr2.2016.07.011.

Gilg MR, Hoffman EA, Schneider KR, Ryabinov J, El-Khoury C, Walters LJ. 2010. Recruitment preferences of non-native mussels: interaction between marine invasions and land-use changes. J Molluscan Stud. 76(4):333–339. doi:10.1093/mollus/eyq017.

Girard F, Lacharité M, Metaxas A. 2016. Colonization of benthic invertebrates in a submarine canyon in the NW Atlantic. Mar Ecol Prog Ser. 544:53–64. doi:10.3354/meps11555.

Gollner S, Kaiser S, Menzel L, Jones DOB, Brown A, Mestre NC, van Oevelen D, Menot L, Colaço A, Canals M, et al. 2017. Resilience of benthic deep-sea fauna to mining activities. Mar Environ Res. 129:76–101. doi:10.1016/j.marenvres.2017.04.010.

Goode SL, Rowden AA, Bowden DA, Clark MR. 2020. Resilience of seamount benthic communities to trawling disturbance. Mar Environ Res. 161:105086. doi:10.1016/j.marenvres.2020.105086.

Guy G, Metaxas A. 2022. Recruitment of deep-water corals and sponges in the Northwest Atlantic Ocean: implications for habitat distribution and population connectivity. Mar Biol. 169(8):107. doi:10.1007/s00227-022-04089-w.

Hadfield MG. 2011. Biofilms and marine invertebrate larvae: what bacteria produce that larvae use to choose settlement sites. Annu Rev Mar Sci. 3(1):453–470. doi:10.1146/annurev-marine-120709-142753.

Hilário A, Metaxas A, Gaudron SM, Howell KL, Mercier A, Mestre NC, Ross RE, Thurnherr AM, Young C. 2015. Estimating dispersal distance in the deep sea: challenges and applications to marine reserves. Front Mar Sci. 2:1–14. doi:10.3389/fmars.2015.00006.

Hunt HL, Scheibling RE. 1997. Role of early post-settlement mortality in recruitment of benthic marine invertebrates. Mar Ecol Prog Ser 155:269–301. doi:10.3354/meps155269.

Jenkins SR, Marshall D, Fraschetti S. 2009. Settlement and recruitment. In: Wahl M, editor. Marine Hard Bottom Communities: Patterns, Dynamics, Diversity, and Change. Berlin, Heidelberg: Springer. (Ecological Studies). p. 177–190. https://doi.org/10.1007/b76710_12.

Johnson CH, Woollacott RM. 2010. Larval settlement preference maximizes genetic mixing in an inbreeding population of a simultaneous hermaphrodite (*Bugula stolonifera*, Bryozoa). Mol Ecol. 19(24):5511–5520. doi:10.1111/j.1365-294X.2010.04887.x.

Konar B. 2007. Recolonization of a high latitude hard-bottom nearshore community. Polar Biol. 30(5):663–667. doi:10.1007/s00300-007-0261-7.

Konar B. 2013. Lack of recovery from disturbance in high-arctic boulder communities. Polar Biol. 36(8):1205–1214. doi:10.1007/s00300-013-1340-6.

Kukliński P, Berge J, McFadden L, Dmoch K, Zajaczkowski M, Nygård H, Piwosz K, Tatarek A. 2013. Seasonality of occurrence and recruitment of Arctic marine benthic invertebrate larvae in relation to environmental variables. Polar Biol. 36(4):549–560. doi:10.1007/s00300-012-1283-3.

Lacharité M, Metaxas A. 2013. Early life history of deep-water gorgonian corals may limit their abundance. PLOS One. 8(6):e65394–e65394. doi:10.1371/journal.pone.0065394.

Linke P, Lutze GF. 1993. Microhabitat preferences of benthic Foraminifera—a static concept or a dynamic adaptation to optimize food acquisition? Mar Micropaleontol. 20(3):215–234. doi:10.1016/0377-8398(93)90034-U.

Lörz A-N, Kaiser S, Oldeland J, Stolter C, Kürzel K, Brix S. 2021. Biogeography, diversity and environmental relationships of shelf and deep-sea benthic Amphipoda around Iceland. PeerJ. 9:e11898. doi:10.7717/peerj.11898.

Lutze GF, Thiel H. 1989. Epibenthic Foraminifera from elevated microhabitats; *Cibicidoides wuellerstorfi* and *Planulina ariminensis*. J Foraminifer Res. 19(2):153–158. doi:10.2113/gsjfr.19.2.153.

Martin R. 2003. Management of nematocysts in the alimentary tract and in cnidosacs of the aeolid nudibranch gastropod *Cratena peregrina.* Mar Biol. 143(3):533–541. doi:10.1007/s00227-003-1078-8.

McCain JC. 1968. The Caprellidae (Crustacea: Amphipoda) of the western North Atlantic. Bulletin. 278:1--47. doi:10.5962/bhl.part.8960.

Metaxas A, Kelly NE. 2010. Do larval supply and recruitment vary among chemosynthetic environments of the deep sea? PLOS One. 5(7):e11646–e11646. doi:10.1371/journal.pone.0011646.

Metaxas A, Ramirez-Llodra E, Hilário A. 2022. Working Group 3: Population connectivity | INDEEP. www.indeep-project.org

Meyer KS, Li Y, Young CM. 2018. Oceanographic and biological influences on recruitment of benthic invertebrates to hard substrata on the Oregon shelf. Estuar Coast Shelf Sci. 208:1–8. doi:10.1016/j.ecss.2018.04.037.

Meyer KS, Sweetman AK, Kukliński P, Leopold P, Vogedes D, Berge J, Griffiths C, Young CM, Renaud PE. 2017. Recruitment of benthic invertebrates in high Arctic fjords: Relation to temperature, depth, and season. Limnol Oceanogr. 62(6):2732–2744. doi:10.1002/lno.10602.

Meyer-Kaiser K, Bergmann M, Soltwedel T, Klages M. 2019. Recruitment of Arctic deep-sea invertebrates: Results from a long-term hard-substrate colonization experiment at the Long-Term Ecological Research observatory HAUSGARTEN. Limnol Oceanogr. 64(5):1924–1938. doi:10.1002/lno.11160.

Meyer-Kaiser KS, Schrage KR, von Appen W-J, Hoppmann M, Lochthofen N, Sundfjord A, Soltwedel T. 2022. Larval dispersal and recruitment of benthic invertebrates in the Arctic Ocean. Prog Oceanogr. 203:102776. doi:10.1016/j.pocean.2022.102776.

Migotto AE, Marques AC, Flynn MN. 2001. Seasonal recruitment of hydroids (Cnidaria) on experimental panels in the São Sebastião Channel, southeastern Brazil. Bull Mar Sci. 68(2):287–298.

Morse ANC, Iwao K, Baba M, Shimoike K, Hayashibara T, Omori M. 1996. An Ancient Chemosensory Mechanism Brings New Life to Coral Reefs. The Biological Bulletin. 191(2):149–154. doi:10.2307/1542917.

Mullineaux LS, Butman CA. 1990. Recruitment of encrusting benthic invertebrates in boundary-layer flows: a deep-water experiment on cross seamount. Limnol Oceanogr. 35(2):409–423.

Osman RW, Whitlatch RB, Malatesta RJ. 1992. Potential role of micro-predators in determining recruitment into a marine community. Mar Ecol Prog Ser. 83(1):35–43.

Palardy JE, Witman JD. 2013. Flow, recruitment limitation, and the maintenance of diversity in marine benthic communities. Ecol Letters 95(2):286–297. doi:10.1890/12-1612.1.

Pawlik JR. 1986. Chemical induction of larval settlement and metamorphosis in the reef-building tube worm *Phragmatopoma californica* (Sabellariidae: Polychaeta). Mar Biol. 91(1):59–68. doi:10.1007/BF00397571.

Ramirez-Llodra E, Tyler PA, Baker MC, Bergstad OA, Clark MR, Escobar E, Levin LA, Menot L, Rowden AA, Smith CR, et al. 2011. Man and the last great wilderness: human impact on the deep sea. PLOS One. 6(8):e22588-. doi:10.1371/journal.pone.0022588.

Romano C, Voight JR, Pérez-Portela R, Martin D. 2014. Morphological and genetic diversity of the wood-boring Xylophaga (Mollusca, Bivalvia): new species and records from deep-sea Iberian canyons. PLOS One. 9(7):1–20. doi:10.1371/journal.pone.0102887.

Ronowicz. 2007. Benthic hydroids (Cnidaria: Hydrozoa) from Svalbard waters-biodiversity and distribution. J Mar Biol Assoc UK. 87(5):1089–1094.

Ronowicz M, Wlodarska-Kowalczuk M, Kukliński P. 2008. Factors influencing hydroids (Cnidaria: Hydrozoa) biodiversity and distribution in Arctic kelp forest. J Mar Biol Assoc UK. 88(8):1567–1575. doi:10.1017/S0025315408001495.

Ronowicz M, Włodarska-Kowalczuk M, Kukliński P. 2013. Hydroid epifaunal communities in Arctic coastal waters (Svalbard): effects of substrate characteristics. Polar Biol. 36(5):705–718. doi:10.1007/s00300-013-1297-5.

Schuchert P. 2008. The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Filifera Part 4. Rev Suisse Zool. 115:677–757. doi:10.5962/bhl.part.80453.

Sen Gupta BK. 2007. Modern Foraminifera. 1st ed. Dordrecht: Springer Nature.

Shannon CE. 1948. A mathematical theory of communication. Bell Syst Tech J. 27(3):379–423. doi:10.1002/j.1538-7305.1948.tb01338.x.

Stanwell-Smith D, Barnes DKA. 1997. Benthic community development in Antarctica: recruitment and growth on settlement panels at Signy Island. J Exp Mar Biol Ecol. 212(1):61–79. doi:10.1016/S0022-0981(96)02754-2.

Sun Z, Hamel J-F, Mercier A. 2010. Planulation periodicity, settlement preferences and growth of two deep-sea octocorals from the northwest Atlantic. Mar Ecol Prog Ser. 410:71–87. doi:10.3354/meps08637.

Sun Z, Hamel J-F, Mercier A. 2011. Planulation, larval biology, and early growth of the deep-sea soft corals Gersemia fruticosa and Duva florida (Octocorallia: Alcyonacea). Invertebr Biol. 130(2):91–99. doi:10.1111/j.1744-7410.2011.00229.x.

Teichert S, Woelkerling W, Rüggeberg A, Wisshak M, Piepenburg D, Meyerhöfer M, Form A, Büdenbender J, Freiwald A. 2012. Rhodolith beds (Corallinales, Rhodophyta) and their physical and biological environment at 80°31′N in Nordkappbukta (Nordaustlandet, Svalbard Archipelago, Norway). Phycologia. 51(4):371–390. doi:10.2216/11-76.1

Wahl M. 2009. Marine Hard Bottom Communities: Patterns, Dynamics, Diversity, and Change. 1. Aufl. Berlin, Heidelberg: Springer-Verlag (Ecological Studies).

Walters LJ, Wethey DS. 1996. Settlement and early post-settlement survival of sessile marine invertebrates on topographically complex surfaces: the importance of refuge dimensions and adult morphology. Mar Ecol Prog Ser. 137(1/3):161–171. doi:10.3354/meps137161.

Wasserthal LT, Wasserthal W. 1973. Ökologische bedeutung der schleimsekretion bei den planula-larven der hydroidengattung *Eudendrium*. Mar Biol. 22(4):341–345. doi:10.1007/BF00391391.

Wisshak M, Meyer N, Kuklinski P, Rüggeberg A, Freiwald A. 2022. ‘Ten Years After’—a long-term settlement and bioerosion experiment in an Arctic rhodolith bed (Mosselbukta, Svalbard). Geobiology. 20(1):112–136. doi:10.1111/gbi.12469

2.8 Tables

Table 2.1 Frequency of occurrence of all morphospecies found across the four substratum types deployed at four geographic sites. For substratum type, the number indicates at how many sites the morphospecies occurred on that substratum. For geographic site, the number indicates on how many substratum types the morphospecies occurred at that site. A blank indicates morphospecies was not present.

Morphospecies	**Substratum Type**				**Geographic site**			
	Mesh	*Plastic*	*Stone*	*Wood*	*Site 1*	*Site 2*	*Site 3*	*Site 4*
Polychaeta sp. 1	1		1				1	1
Polychaeta sp. 2	2				1		1	
Caprellidae sp. 1	2	1			1			2
Copepoda sp. 1	4	3		1	1	2	2	3
Gammaridea sp. 1	1	1	1				3	
Gammaridea sp. 2	1				1			
Halacaridae sp. 1	1				1			
Isopoda sp. 1	1							1
Ostracoda sp. 1	1							1
Actiniaria sp. 1	2	1	1		2			2
Campanulariidae sp. 1			1			1		
Campanulariidae sp. 2A	3	3	3	1	3		3	4
Campanulariidae sp. 2B		3	2	1	2		1	3
Campanulariidae sp. 3	4	4	4	3	4	4	3	4
Campanulariidae sp. 4	2				1			1
Eudendrium sp. 1	3	3	3	1	3		3	4
Eudendrium sp. 2	1							1
Hydrozoa sp. 1			1					1
Octocorallia sp. 1	2	2	2		3			3
Foraminifera sp. 1	4	1	3	1	3	1	3	2
Foraminifera sp. 2	1		1					2
Foraminifera sp. 3	2					1		1
Foraminifera sp. 4	1	1					2	
Gastropoda sp. 1	1							1
Gastropoda sp. 2	1							1
Porifera sp. 1	1	1				1	1	
Porifera sp. 2	2				1	1		
Porifera sp. 3	1				1			
Radiolaria sp. 1	3	1	2			2	1	3
Unknown sp. 1		1	3		2	1		1
Unknown sp. 2	1							1
Unknown sp. 3	1			1		1	1	

Table 2.2 Morphospecies abundance examined as total number of individuals or colonies. Zero indicates morphospecies was not present. Errors are standard deviation (if absent, morphospecies occurred only once).

Morphospecies	Global	Substratum Type				Geographic site			
	Total	*Mesh*	*Plastic*	*Stone*	*Wood*	*Site 1*	*Site 2*	*Site 3*	*Site 4*
Annelida	**4**	**2**	**0**	**1**	**0**	**0**	**0**	**2**	**1**
Polychaeta sp. 1	2	1	0	1	0	0	0	1	1
Polychaeta sp. 2	2	1	0	0	0	0	0	1	0
Arthropoda	**131**	**98**	**15**	**13**	**1**	**22**	**21**	**31**	**53**
Caprellidae sp. 1	21	20	1	0	0	1	0	0	20
Copepoda sp. 1	67	58	4	0	1	16	21	3	23
Gammaridea sp. 1	28	5	10	13	0	0	0	28	0
Gammaridea sp. 2	4	4	0	0	0	4	0	0	0
Halacaridae sp. 1	1	1	0	0	0	1	0	0	0
Isopoda sp. 1	9	9	0	0	0	0	0	0	9
Ostracoda sp. 1	1	1	0	0	0	0	0	0	1
Cnidaria	**130859**	**40875**	**41745**	**41422**	**3149**	**56841**	**12342**	**8728**	**49281**
Actiniaria sp. 1	5	3	1	0	0	1	0	0	3
Campanulariidae sp. 1	16	0	0	13	0	0	13	0	0
Campanulariidae sp. 2A	553	168	186	113	73	160	0	16	364
Campanulariidae sp. 2B	3913	0	1840	1224	850	951	0	139	2822
Campanulariidae sp. 3	114821	33721	37347	38145	2135	54563	12329	6922	37533
Campanulariidae sp. 4	17	16	0	0	0	1	0	0	15
Eudendrium sp. 1	7123	2567	2368	1922	91	1160	0	1650	4138
Eudendrium sp. 2	4396	4396	0	0	0	0	0	0	4396
Hydrozoa sp. 1	2	0	0	2	0	0	0	0	2
Octocorallia sp. 1	12	4	3	4	0	4	0	0	7
Foraminifera	**262**	**238**	**2**	**8**	**1**	**137**	**6**	**91**	**15**
Foraminifera sp. 1	255	233	1	7	1	137	5	89	11
Foraminifera sp. 2	2	1	0	1	0	0	0	0	2
Foraminifera sp. 3	3	3	0	0	0	0	1	0	2
Foraminifera sp. 4	2	1	1	0	0	0	0	2	0
Mollusca	**35**	**35**	**0**	**0**	**0**	**0**	**0**	**0**	**35**
Gastropoda sp. 1	1	1	0	0	0	0	0	0	1
Gastropoda sp. 2	34	34	0	0	0	0	0	0	34
Porifera	**5**	**4**	**0**	**0**	**0**	**2**	**1**	**1**	**0**
Porifera sp. 1	2	1	0	0	0	0	0	1	0
Porifera sp. 2	2	2	0	0	0	1	1	0	0
Porifera sp. 3	1	1	0	0	0	1	0	0	0
Radiolaria	**8**	**5**	**1**	**2**	**0**	**0**	**2**	**2**	**4**
Radiolaria sp. 1	8	5	1	2	0	0	2	2	4
Unknown	**108**	**3**	**0**	**103**	**1**	**99**	**3**	**1**	**4**
Unknown sp. 1	104	0	0	103	0	99	2	0	2
Unknown sp. 2	2	2	0	0	0	0	0	0	2
Unknown sp. 3	2	1	0	0	1	0	1	1	0

Table 2.3 Recruitment location and microhabitat preferences of motile morphospecies. Measurements are percentage of occurrences in each recruitment location out of total number of occurrences. Zero indicates no occurrences in that location.

Phylum	**Morphospecies**	**Site**	**Substratum Type**	**Location (%)**		**Microhabitat (%)**	
				Centre	*Edge*	*Unsheltered*	*Sheltered*
Annelida	Polychaeta sp. 2	1	Mesh	100	0	0	100
	Polychaeta sp. 2	3	Mesh	0	0	0	100
	Polychaeta sp. 2	4	Stone	100	0	0	100
Arthropoda	Caprellidae sp. 1	4	Mesh	0	50	50	50
	Copepoda sp. 1	1	Mesh	80	20	0	100
	Copepoda sp. 1	2	Mesh	50	36	50	100
	Copepoda sp. 1	2	Plastic	100	0	0	100
	Copepoda sp. 1	3	Mesh	0	0	60	100
	Copepoda sp. 1	3	Plastic	100	0	0	100
	Copepoda sp. 1	4	Mesh	80	20	0	100
	Copepoda sp. 1	4	Plastic	100	0	0	100
	Copepoda sp. 1	4	Wood	100	0	100	0
	Gammaridea sp. 1	3	Mesh	60	20	60	33
	Gammaridea sp. 1	3	Plastic	100	0	13	88
	Gammaridea sp. 1	3	Stone	100	0	100	0
	Gammaridea sp. 2	1	Mesh	33	67	100	67
	Halacaridae sp. 1	1	Mesh	0	100	0	100
	Isopoda sp. 1	4	Mesh	100	0	100	0
	Ostracoda sp. 1	4	Mesh	100	0	0	100
Mollusca	Gastropoda sp. 1	4	Mesh	100	0	0	100
	Gastropoda sp. 3	4	Mesh	0	0	0	100

2.9 Figures

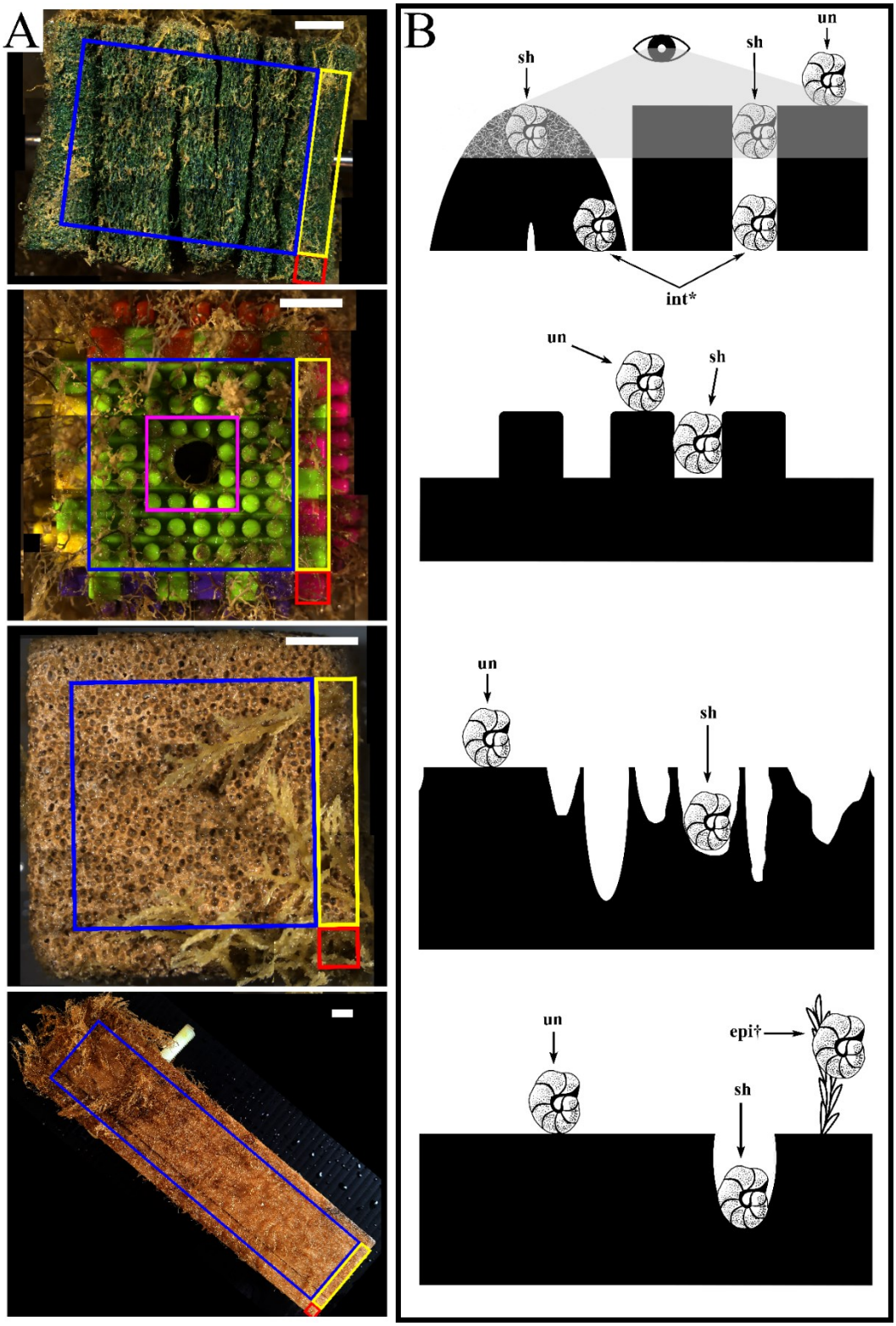


Figure 2.1 (previous page) The four substratum types deployed at each geographic site with illustration of microhabitats; diagrams defined in Table 2.3. (A) For all substratum types, recruitment locations used during this study are highlighted as “edge” (within 5 mm of any meeting point between 2 or 3 faces): including corners (red) and edges (yellow); and centres (blue). Excluded were bolt areas (pink), with the white arrows indicating the bolt hole through which the substratum block was attached. From top to bottom: mesh, plastic, stone, and wood recruitment locations analysed. (B) For all substratum types, recruitment microhabitats used are indicated with arrows as sheltered (sh) and unsheltered (un) and the diagram scale is 1 cm. Recruitment as epibionts (epi) and internal (int) were excluded from microhabitat calculations. From top to bottom: mesh (grey area indicates visible field), plastic, stone, and wood microhabitats analyzed. All scale bars represent 10 mm.

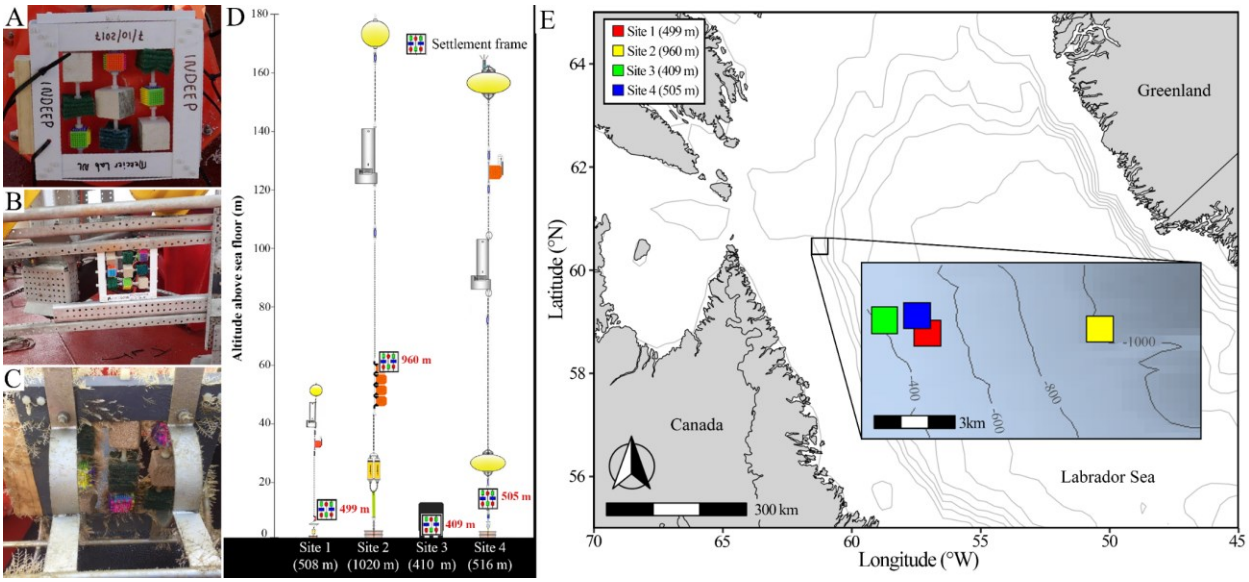
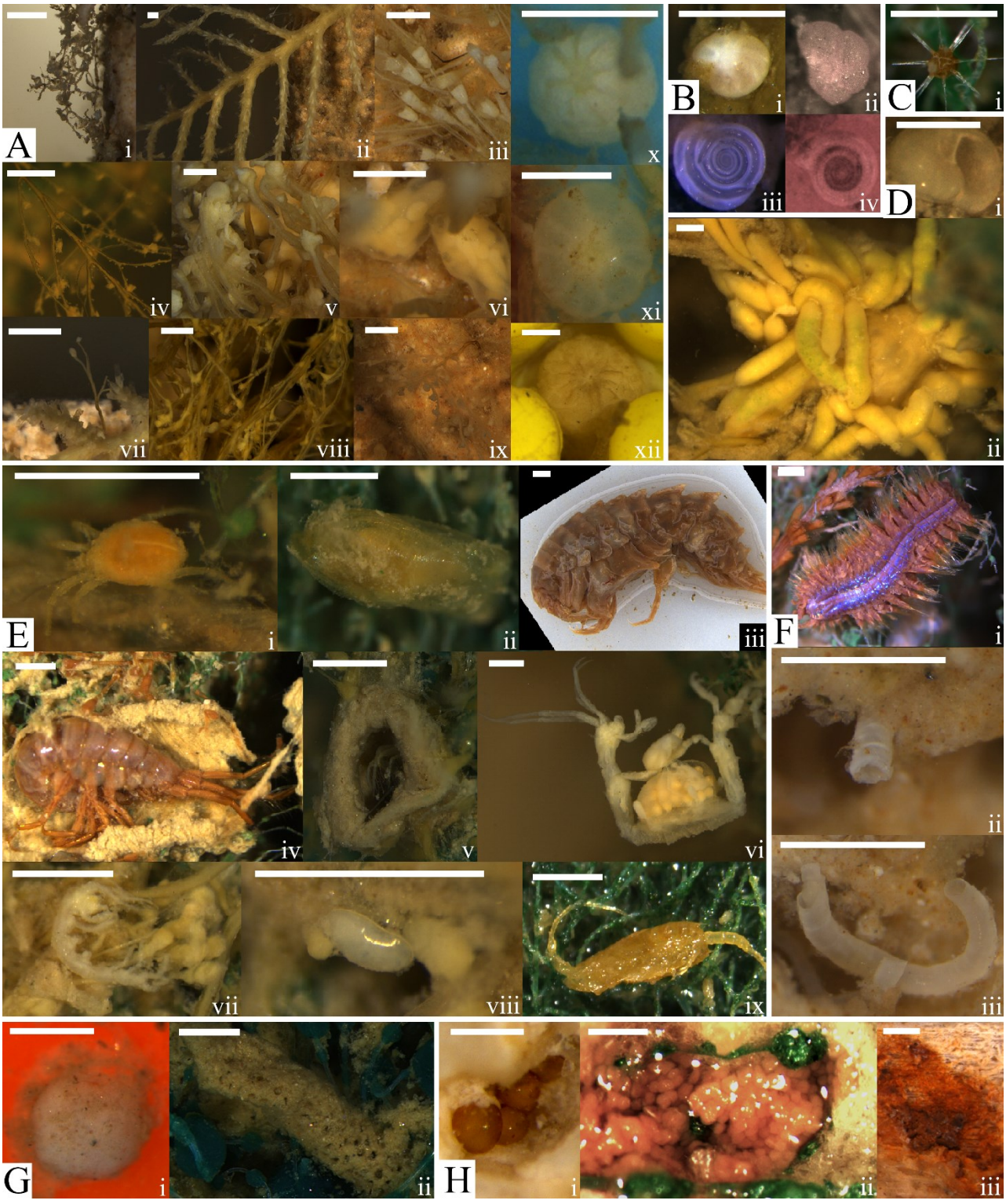


Figure 2.2 Deployment and geographic location of settlement frames. (A) Pre-deployment settlement frame, showing the standardized distribution of substratum blocks, deployed attached to a buoy on a scientific mooring as in Site 1 and 2. (B) Pre-deployment settlement frame deployed on a lander as in Site 3. (C) Post-retrieval settlement frame deployed in an open cage on a scientific mooring as in Site 4. (D) Scientific mooring and lander deployment diagrams showing position of the settlement frame on the apparatus, altitude above bottom, and its approximate depth in red, with the site name and total depth of sea floor below each deployment apparatus diagram in white (Table 2.1; diagrams courtesy of Shawn Meredyk, Amundsen Science, and ArcticNet). (E) Map of the deployment locations of the four successfully retrieved settlement frames. Exact location, depth, and altitude above the sea floor details can be found in Supplementary Table 2.1.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(Previous page) Figure 2.3 Recruits found on all deployed substratum types in the Labrador Sea (Newfoundland and Labrador, Canada) arranged by phylum. Scale bars (white) represent 1 mm for A, E, F; 0.5 mm for B, C, D, G, H. (A) Cnidaria, Hydrozoa (i-ix) and Anthozoa (x-xii): (i) Campanulariidae sp. 1, (ii) Campanulariidae sp. 2, (iii) Campanulariidae sp. 3, (iv) Campanulariidae sp. 4, (v) *Eudendrium* sp. 1 colony, (vi) *Eudendrium* sp. 1 gonozooids, (vii) Epibiotic *Eudendrium* sp. 1 on Campanulariidae sp. 2 (see ii), (viii) *Eudendrium* sp. 2 colony, (ix) Hydrozoa sp. 1 colony, (x) Octocorallia sp. 1 primary polyp, (xi) Octocorallia sp. 1 , (xii) Actiniaria sp. 1. (B) Foraminifera: (i) Foraminifera sp. 1, (ii) Foraminifera sp. 2, (iii) Foraminifera sp. 3, and (iv) Foraminifera sp. 4. Scale bar (white) is applicable to i – iv. (C) Radiolaria: (i) Radiolaria sp. 1. (D) Mollusca: (i) Gastropoda sp. 1, and (ii) Gastropoda sp. 2 egg masses on the base of a Campanulariidae sp. 2 colony (A-ii). (E) Arthropoda: (i) Halacaridae sp. 1, mite within mesh substratum, (ii) Ostracoda sp. 1, from between the mesh substratum sheets, (iii) Gammaridea sp. 1, amphipod (iv) Gammaridea sp. 2, tube-dwelling amphipod, after removal of tube on one side (v) Same morphospecies but different individual from G, without removal from tube, (vi) Caprellidae sp. 1, gravid female with brood pouch, (vii) Caprellidae sp. 1 cluster of smaller individuals, (viii) Isopoda sp. 1, and (ix) Copepoda sp. 1, found within mesh. (F) Annelida: (i) Polychaeta sp. 1, free living polychaete photographed after removal from mesh substratum sheets, (ii) Polychaeta sp. 2, tube-dwelling polychaete (tube only), and (iii) Same as F-ii, after removal from stone substratum. (G) Porifera: (i) Porifera sp. 1, and (ii) Porifera sp. 3. (H) Morphospecies of unknown phylum: (i) Unknown sp. 1 cluster, subsurface on stone substratum type, (ii) Unknown sp. 2, a possible egg mass on mesh substratum, and (iii) Unknown sp. 3, a biological aggregate in a divot on wood substratum type.

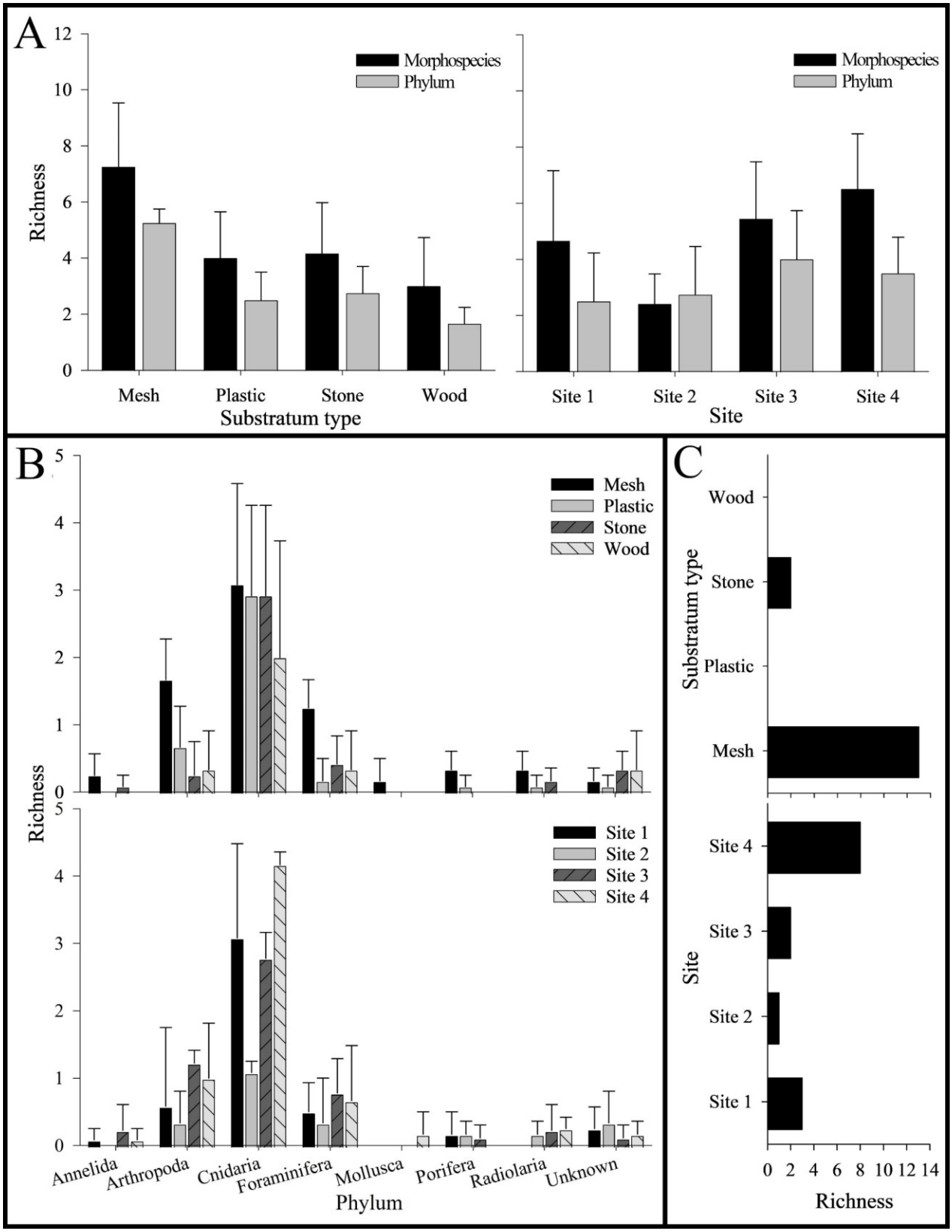

A
Richness
Morphospecies
Phylum
Mesh
Plastic
Stone
Wood
Substratum type
Site 1
Site 2
Site 3
Site 4
Site
B
Mesh
Plastic
Stone
Wood
Site 1
Site 2
Site 3
Site 4
Annelida
Arthropoda
Cnidaria
Foraminifera
Mollusca
Porifera
Radiolaria
Unknown
Phylum
C
Substratum type
Site
Richness

Figure 2.4 (previous page) Number of morphospecies, phyla, and unique morphospecies (i.e., richness) across the four settlement frame substratum types (see Figure 2.2) and four deployment sites (see Figure 2.1) in Labrador Sea (Newfoundland and Labrador, Canada). No bar indicates none present. Error bars represent standard deviation. A. Morphospecies and phylum richness. Left: by substratum type. Right: by site. B. Morphospecies richness within each phylum. Top: by substratum type. Bottom: by site. C. Unique morphospecies richness. Top: by substratum type. Bottom: by site.

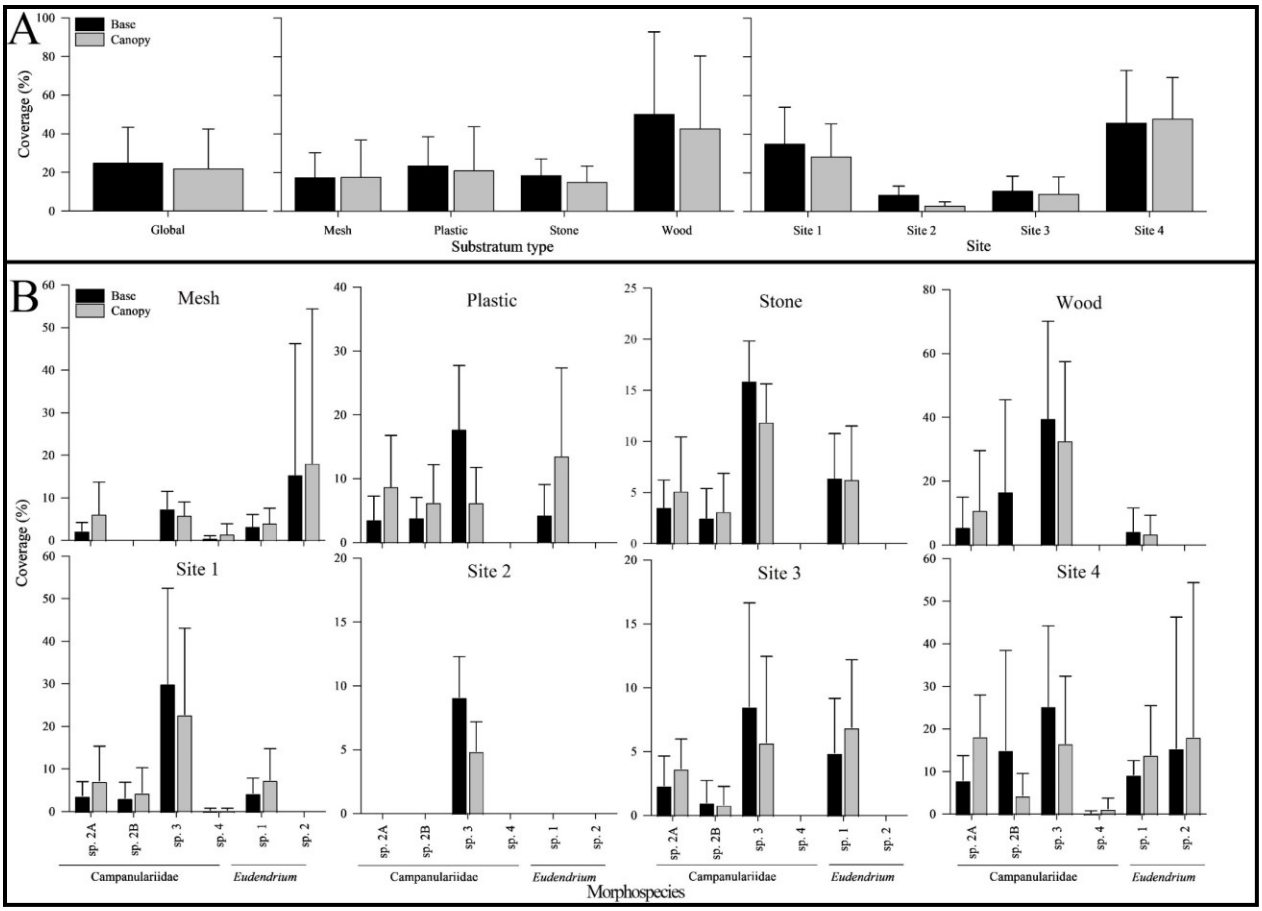


Figure 2.5 Base and canopy cover exhibited by five common hydrozoans, examined by settlement frame substratum types (mesh, plastic, stone, wood) and by deployment site (Site 1, 2, 3, 4) in the Labrador Sea (Newfoundland and Labrador, Canada). Error bars indicate standard deviation. Note the differing scales of y-axes.

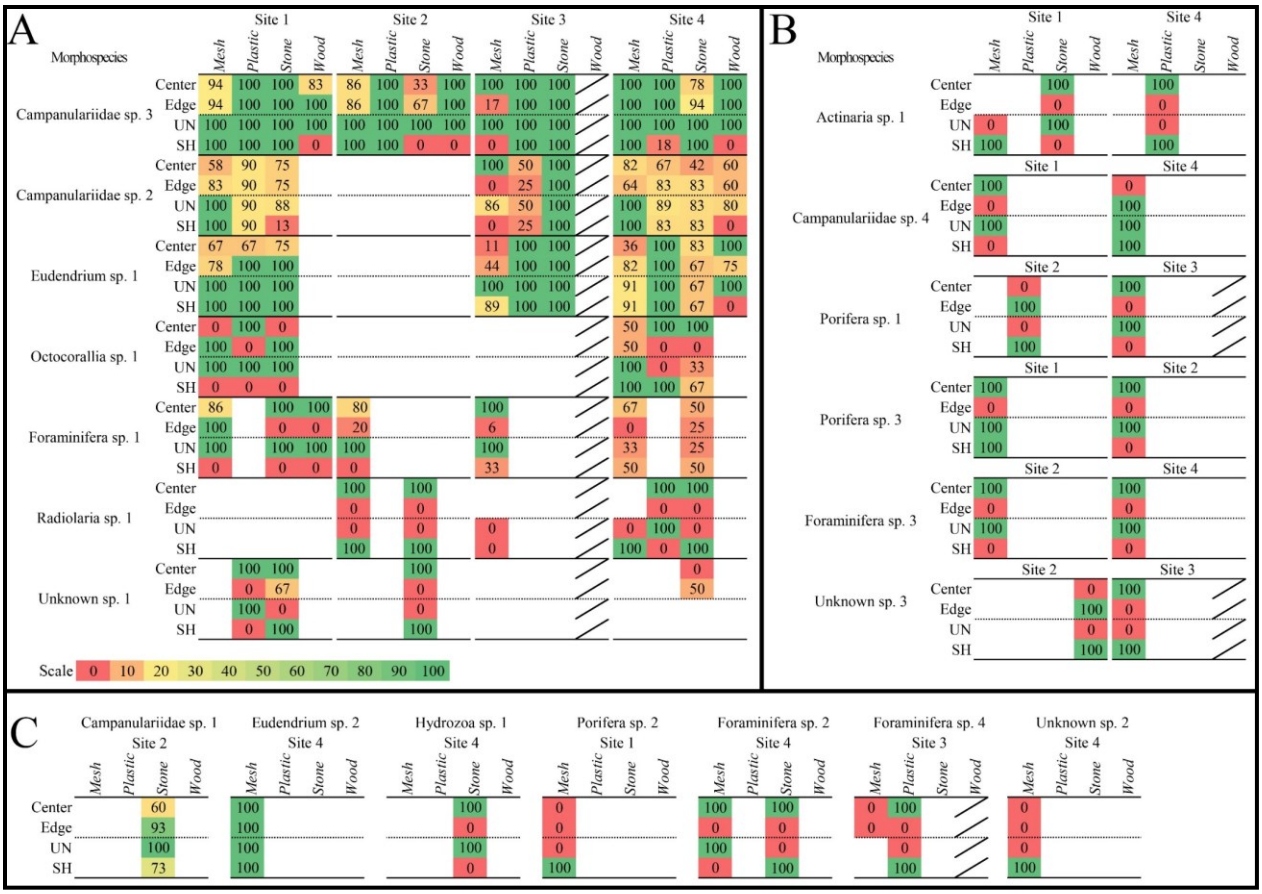


Figure 2.6 Heat maps of recruitment locations and microhabitats of all sessile morphospecies examined, expressed as a percentage of the total number of occurrences. (A) Morphospecies that recruited broadly to surface locations and microhabitats, on three or more substratum types or sites. (B) Morphospecies that recruited more narrowly to locations and microhabitats at two sites. (C) Morphospecies that recruited to one location or microhabitat and/or at one site. Diagonal bar indicates substratum types that were not analyzed.

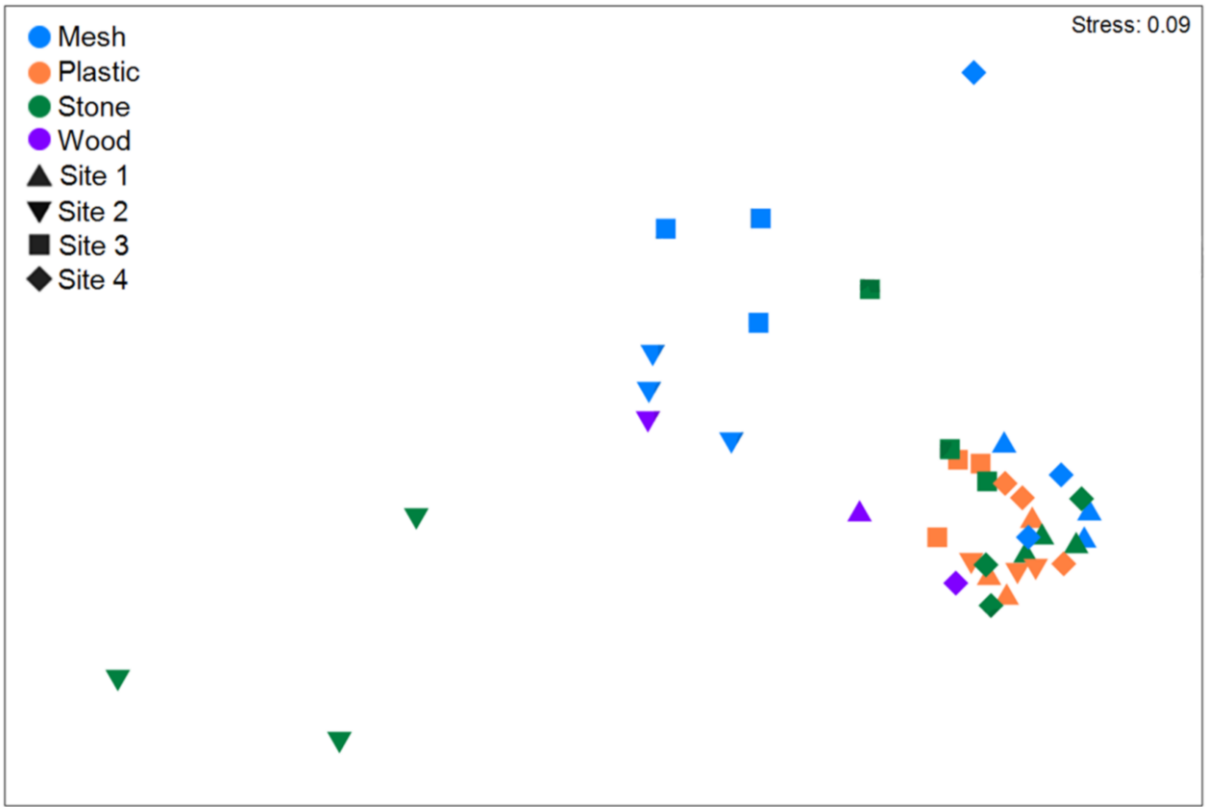


Figure 2.7 Non-metric multidimensional scaling (nMDS) using Bray-Curtis similarity coefficients of total abundance of recruits of all morphospecies to the four substratum types present at four geographic sites in the Labrador Sea (Canada).

2.10 Appendix

2.10.1 Supplementary results

2.10.1.1 Surface location and microhabitat colonization pattern detail

Three colonial hydrozoans (Campanulariidae sp. 3, sp. 2, and *Eudendrium* sp. 1) colonized almost all locations and microhabitats available on the substrata (Figure 2.6A). The most abundant and opportunistic colonizer (Campanulariidae sp. 3) did not display location preferences, except for corners of stone and wood at Site 2. In terms of microhabitat colonization, colonies extended through most microhabitats available, except into the pores of stone at Site 2 or below the outermost surface of mesh at Site 3. Colonies also extended stolons internally in mesh (Sites 1, 2 and 3). Low colonization was observed below the outermost surface of plastic at Site 4. Campanulariidae sp. 2 consistently colonized corners, edges, and centre of the blocks except for edges and corners on mesh at Site 3. Microhabitats were almost all colonized, except below the outermost surface on mesh at Site 3. *Eudendrium* sp. 1 colonized the corner, edge, and centre locations with no exceptions; all microhabitats available were colonized.

An additional four morphospecies exhibited broad colonization of locations and microhabitats across multiple substratum types and sites (Figure 2.6A). The colonial cnidarian Octocorallia sp. 1 had variable settling locations across geographic site and substratum type but occurred in one location per block; the exception was broader colonization of mesh at Site 4 where the morphospecies occurred in two recruitment locations. It colonized the outer microhabitat only at Site 1 across three substratum types (mesh, plastic, and stone) and only the inner microhabitat on plastic at Site 4, while again exhibiting broader colonization on mesh as well as stone, where it colonized all microhabitats available. The benthic Foraminifera sp. 1 also

occurred in multiple locations on mesh at Site 1 (3 locations), mesh at Sites 2 and 3 (2 locations each), and stone at Site 4 (2 locations). At Site 1 it also occurred on stone and wood in the centre, and at Site 4 on mesh in the centre. Microhabitat colonization was variable: it occurred in the outer microhabitats of mesh, stone, and wood at Site 1 as well as mesh at Sites 2 and 3, while more broadly colonizing most available microhabitats on mesh and stone at Site 4. The only exception was internal occurrence on mesh at Site 1 and 3. The benthic radiolarian Radiolaria sp. 1 conversely was limited to one location per substratum type: it occurred just in the centre of mesh and stone at Site 2 as well as plastic and stone at Site 4. At Sites 3 and 4 it occurred in two microhabitats, inner and internally, while all other occurrences it was in just one microhabitat per substratum type. It was in the middle microhabitat of mesh at Site 2, the outer of plastic at Site 4, and the inner microhabitats of stone at both Site 2 and 4. Individual eggs (Unknown sp. 1) occurred in the centre of plastic at Site 1 and stone at Site 2 as well on the edges of stone at Site 4, while showing up in all locations of stone at Site 1. Its microhabitat colonization was limited, as it occurred in the outer microhabitat of plastic at Site 1, and the inner of stone at Sites 1 and 2.

Six mspp recruited to or colonized few locations and microhabitats across two sites (Figure 2.6B). The unitary cnidarian Actiniaria sp. 1 had no specific location trend but occurred in one location per substratum type; it was present in the centre of stone at Site 1 and in the centre of plastic at Site 4. Similarly, it occurred in one microhabitat per substratum type: internally on mesh and outer on stone at Site 1, and middle on plastic at Site 4. The colonial hydrozoan Campanulariidae sp. 4 colonized the centre of mesh at Site 1 but more broadly including the edges and corners of mesh at Site 4. Its microhabitat colonization followed a similar pattern, occurring in the outer microhabitat on mesh at Site 1 and all available microhabitats on mesh at Site 4 including extending stolons from the colony internally. Porifera

sp. 1 occurred in one location per site, on the edge of plastic at Site 2 and the centre of mesh at Site 3; microhabitat colonization was the inner microhabitat on plastic at Site 2 and outer on mesh at Site 3. Porifera sp. 3 colonized just one location: centre of mesh at both Site 1 and 2. Broader microhabitat colonization occurred on mesh at Site 1 in both outer and middle microhabitats, while on mesh at Site 2 it colonized just the outer. A biological aggregate (Unknown sp. 3) was present on the edge of wood at Site 2; inner microhabitat colonization occurred on wood at Site 2 and it was present internally on mesh at Site 3.

The remaining seven mspp recruited to or colonized one or more locations and microhabitats but restricted to just one site (Figure 2.6C). This included two colonial hydrozoans colonizing locations and microhabitats broadly (Campanulariidae sp. 1 and *Eudendrium* sp. 2). Campanulariidae sp. 1 occurred in all locations and microhabitats available on stone at Site 1; *Eudendrium* sp. 2, similarly colonized all locations and microhabitats available on mesh at Site 4. Conversely, another colonial hydrozoan Hydrozoa sp. 1 occurred solely in centre location of stone at Site 1, colonizing the outer microhabitat alone. Foraminifera sp. 2 was present in the centre locations of mesh and stone at Site 4, colonizing the outer microhabitat on the former and the inner on the latter. Foraminifera sp. 4 occurred in the centre of plastic at Site 3, as well as being found internally on mesh at the same site. Its microhabitat colonization of the former occurred in the middle.

2.10.2 Supplementary tables

Supplementary table 2.1 Recruitment location on the substratum (see Figure 2.2 for details).

Location	Description
Center	Substratum area excluding Corner, Edge, and bolt holes*
Edge	Within 5 mm of sides
Corner	5 x 5 mm box including corner
Epibiota	Using another morphospecies as substratum

*Holes through the center of two opposite faces of the panels where they were bolted to the frame.

Supplementary table 2.2 Recruitment features or "microhabitats" on the substratum types (see Figure 2.2 for details)

Microhabitat		Description
Mesh		
	Unsheltered	Outermost area
	Sheltered	Below outermost surface, between and inside sheets of mesh
Plastic		
	Unsheltered	Outermost area at top of plastic protuberances
	Sheltered	Side or between plastic protuberances, and surface at base
Stone		
	Unsheltered	Outermost area
	Sheltered	Inside crevices and indentations below surface
Wood		
	Unsheltered	Outermost area
	Sheltered	Found below surface of substratum (boring)

Supplementary table 2.3 Deployment information for all settlement frames on moorings and landers.

Name	Site ID	Method	Depth (m)	Altitude (m)	Deployed	Recovered	Latitude	Longitude
Site 1	HiBioA	Mooring	499	10	Oct 2017	Jul 2018	60.46083° N	– 61.26217° W
Site 2	HiBioC	Mooring	960	60	Aug 2018	Jul 2019	60.46406° N	– 61.15908° W
Site 3	SpongeSite3	Lander	410	1	Jul 2018	Jul 2019	60.46738° N	– 61.28785° W
Site 4	HiBioA	Mooring	505	16	Jul 2019	Aug 2020	60.47417° N	– 60.26944° W
Site 5*	HiBioB	Mooring	1855	30	Aug 2018	-	60.47365° N	– 60.37526° W
Site 6*	HiBioC	Mooring	1025	12	Jul 2019	-	60.46405° N	– 61.15780° W

*Not recovered

Supplementary table 2.4 Total abundance of all individuals or colonies of all morphospecies present on four substratum types at four sites in the Labrador Sea (Canada).

Phylum/ Species	Site 1 Mesh	Plastic	Stone	Wood	*Site 1 Total*	Site 2 Mesh	Plastic	Stone	Wood	*Site 2 Total*	Site 3 Mesh	Plastic	Stone	Wood	*Site 3 Total*	Site 4 Mesh	Plastic	Stone	Wood	*Site 4 Total*	*Mesh Total*	*Plastic Total*	*Stone Total*	*Wood Total*	*All blocks pooled*
Annelida	**0**	**0**	**0**	**0**	***0***	**0**	**0**	**0**	**0**	***0***	**2**	**0**	**0**	**0**	***2***	**0**	**0**	**1**	**0**	***1***	***2***	***0***	***1***	***0***	*3*
Polychaeta sp. 1	0	0	0	0	*0*	0	0	0	0	*0*	1	0	0	0	*1*	0	0	1	0	*1*	*1*	*0*	*1*	*0*	*2*
Polychaeta sp. 2	0	0	0	0	*0*	0	0	0	0	*0*	1	0	0	0	*1*	0	0	0	0	*0*	*1*	*0*	*0*	*0*	*1*
Arthropoda	**22**	**0**	**0**	**0**	***22***	**20**	**1**	**0**	**0**	***21***	**7**	**11**	**13**	**0**	***31***	**49**	**3**	**0**	**1**	***53***	***98***	***15***	***13***	***1***	*127*
Caprellidae sp. 1	1	0	0	0	*1*	0	0	0	0	*0*	0	0	0	0	*0*	19	1	0	0	*20*	*20*	*1*	*0*	*0*	*21*
Copepoda sp. 1	16	0	0	0	*16*	20	1	0	0	*21*	2	1	0	0	*3*	20	2	0	1	*23*	*58*	*4*	*0*	*1*	*63*
Gammaridea sp. 1	0	0	0	0	*0*	0	0	0	0	*0*	5	10	13	0	*28*	0	0	0	0	*0*	*5*	*10*	*13*	*0*	*28*
Gammaridea sp. 2	4	0	0	0	*4*	0	0	0	0	*0*	0	0	0	0	*0*	0	0	0	0	*0*	*4*	*0*	*0*	*0*	*4*
Halacaridae sp. 1	1	0	0	0	*1*	0	0	0	0	*0*	0	0	0	0	*0*	0	0	0	0	*0*	*1*	*0*	*0*	*0*	*1*
Isopoda sp. 1	0	0	0	0	*0*	0	0	0	0	*0*	0	0	0	0	*0*	9	0	0	0	*9*	*9*	*0*	*0*	*0*	*9*
Ostracoda sp. 1	0	0	0	0	*0*	0	0	0	0	*0*	0	0	0	0	*0*	1	0	0	0	*1*	*1*	*0*	*0*	*0*	*1*
Cnidaria	**24497**	**11296**	**20462**	**585**	***56841***	**154**	**12132**	**16**	**40**	***12342***	**93**	**4902**	**3732**	**0**	***8728***	**16130**	**13414**	**17212**	**2524**	***49281***	***40875***	***41745***	***41422***	***3149***	*127191*
Actinaria sp. 1	1	0	0	0	*1*	0	0	0	0	*0*	0	0	0	0	*0*	2	1	0	0	*3*	*3*	*1*	*0*	*0*	*4*
Campanulariidae sp. 1	0	0	0	0	*0*	0	0	13	0	*13*	0	0	0	0	*0*	0	0	0	0	*0*	*0*	*0*	*13*	*0*	*13*
Campanulariidae sp. 2A	64	67	29	0	*160*	0	0	0	0	*0*	7	3	6	0	*16*	97	116	78	73	*364*	*168*	*186*	*113*	*73*	*540*
Campanulariidae sp. 2B	0	625	327	0	*951*	0	0	0	0	*0*	0	139	0	0	*139*	0	1076	897	850	*2822*	*0*	*1840*	*1224*	*850*	*3913*
Campanulariidae sp. 3	23696	10489	19793	585	*54563*	154	12132	3	40	*12329*	56	4043	2823	0	*6922*	9815	10683	15525	1510	*37533*	*33721*	*37347*	*38145*	*2135*	*111347*
Campanulariidae sp. 4	1	0	0	0	*1*	0	0	0	0	*0*	0	0	0	0	*0*	15	0	0	0	*15*	*16*	*0*	*0*	*0*	*16*
Eudendrium sp. 1	734	114	312	0	*1160*	0	0	0	0	*0*	30	717	903	0	*1650*	1802	1538	707	91	*4138*	*2567*	*2368*	*1922*	*91*	*6948*
Eudendrium sp. 2	0	0	0	0	*0*	0	0	0	0	*0*	0	0	0	0	*0*	4396	0	0	0	*4396*	*4396*	*0*	*0*	*0*	*4396*
Hydrozoa sp. 1	0	0	0	0	*0*	0	0	0	0	*0*	0	0	0	0	*0*	0	0	2	0	*2*	*0*	*0*	*2*	*0*	*2*
Octocorallia sp. 1	1	2	1	0	*4*	0	0	0	0	*0*	0	0	0	0	*0*	3	1	3	0	*7*	*4*	*3*	*4*	*0*	*11*
Foraminifera	**134**	**0**	**2**	**1**	***137***	**6**	**0**	**0**	**0**	***6***	**88**	**2**	**1**	**0**	***91***	**10**	**0**	**5**	**0**	***15***	***238***	***2***	***8***	***1***	*249*
Foraminifera sp. 1	134	0	2	1	*137*	5	0	0	0	*5*	87	1	1	0	*89*	7	0	4	0	*11*	*233*	*1*	*7*	*1*	*242*
Foraminifera sp. 2	0	0	0	0	*0*	0	0	0	0	*0*	0	0	0	0	*0*	1	0	1	0	*2*	*1*	*0*	*1*	*0*	*2*
Foraminifera sp. 3	0	0	0	0	*0*	1	0	0	0	*1*	0	0	0	0	*0*	2	0	0	0	*2*	*3*	*0*	*0*	*0*	*3*
Foraminifera sp. 4	0	0	0	0	*0*	0	0	0	0	*0*	1	1	0	0	*2*	0	0	0	0	*0*	*1*	*1*	*0*	*0*	*2*
Mollusca	**0**	**0**	**0**	**0**	***0***	**0**	**0**	**0**	**0**	***0***	**0**	**0**	**0**	**0**	***0***	**35**	**0**	**0**	**0**	***35***	***35***	***0***	***0***	***0***	*35*
Gastropoda sp. 1	0	0	0	0	*0*	0	0	0	0	*0*	0	0	0	0	*0*	1	0	0	0	*1*	*1*	*0*	*0*	*0*	*1*
Gastropoda sp. 2	0	0	0	0	*0*	0	0	0	0	*0*	0	0	0	0	*0*	34	0	0	0	*34*	*34*	*0*	*0*	*0*	*34*
Porifera	**2**	**0**	**0**	**0**	***2***	**1**	**0**	**0**	**0**	***1***	**1**	**0**	**0**	**0**	***1***	**0**	**0**	**0**	**0**	***0***	***4***	***0***	***0***	***0***	*4*
Porifera sp. 1	0	0	0	0	*0*	0	0	0	0	*0*	1	0	0	0	*1*	0	0	0	0	*0*	*1*	*0*	*0*	*0*	*1*
Porifera sp. 2	1	0	0	0	*1*	1	0	0	0	*1*	0	0	0	0	*0*	0	0	0	0	*0*	*2*	*0*	*0*	*0*	*2*
Porifera sp. 3	1	0	0	0	*1*	0	0	0	0	*0*	0	0	0	0	*0*	0	0	0	0	*0*	*1*	*0*	*0*	*0*	*1*
Radiolaria	**0**	**0**	**0**	**0**	***0***	**1**	**0**	**1**	**0**	***2***	**2**	**0**	**0**	**0**	***2***	**2**	**1**	**1**	**0**	***4***	***5***	***1***	***2***	***0***	*8*
Radiolaria sp. 1	0	0	0	0	*0*	1	0	1	0	*2*	2	0	0	0	*2*	2	1	1	0	*4*	*5*	*1*	*2*	*0*	*8*
Unknown	**0**	**0**	**99**	**0**	***99***	**0**	**0**	**2**	**1**	***3***	**1**	**0**	**0**	**0**	***1***	**2**	**0**	**2**	**0**	***4***	***3***	***0***	***103***	***1***	*107*
Unknown sp. 1	0	0	99	0	*99*	0	0	2	0	*2*	0	0	0	0	*0*	0	0	2	0	*2*	*0*	*0*	*103*	*0*	*103*
Unknown sp. 2	0	0	0	0	*0*	0	0	0	0	*0*	0	0	0	0	*0*	2	0	0	0	*2*	*2*	*0*	*0*	*0*	*2*
Unknown sp. 3	0	0	0	0	*0*	0	0	0	1	*1*	1	0	0	0	*1*	0	0	0	0	*0*	*1*	*0*	*0*	*1*	*2*
Species pooled	*24655*	*11296*	*20563*	*586*	*57101*	*182*	*12133*	*19*	*41*	*12375*	*194*	*4915*	*3746*	*0*	*8856*	*16228*	*13418*	*17221*	*2525*	*49393*	*41260*	*41763*	*41549*	*3152*	*127724*

Supplementary table 2.5 Density of all individuals or colonies per cm^2 of all morphospecies present on four substratum types at four sites in the Labrador Sea (Canada).

Phylum/ Species	Site 1 Mesh	Plastic	Stone	Wood	*Site 1 Total*	Site 2 Mesh	Plastic	Stone	Wood	*Site 2 Total*	Site 3 Mesh	Plastic	Stone	Wood	*Site 3 Total*	Site 4 Mesh	Plastic	Stone	Wood	*Site 4 Total*	*Mesh Total*	*Plastic Total*	*Stone Total*	*Wood Total*	*All blocks pooled*
Annelida	**0**	**0**	**0**	**0**	***0***	**0**	**0**	**0**	**0**	***0***	**0.002472**	**0**	**0**	**0**	***0.00062***	**0**	**0**	**0.001459**	**0**	***0.00036***	***0.00062***	***0***	***0.00036***	***0***	*0.0002457*
Polychacta sp. 1	0	0	0	0	*0*	0	0	0	0	*0*	0.002593	0	0	0	*0.00065*	0	0	0.002917	0	*0.00073*	*0.00065*	*0*	*0.00073*	*0*	*0.0003444*
Polychaeta sp. 2	0	0	0	0	*0*	0	0	0	0	*0*	0.002351	0	0	0	*0.00059*	0	0	0	0	*0*	*0.00059*	*0*	*0*	*0*	*0.0001469*
Arthropoda	**0.004693**	**0**	**0**	**0**	***0.00117***	**0.003751**	**0.000504**	**0**	**0**	***0.00106***	**0.001829**	**0.002268**	**0.002575**	**0**	***0.00167***	**0.009338**	**0.001461**	**0**	**0.002461**	***0.00332***	***0.0049***	***0.00106***	***0.00064***	***0.00062***	*0.001805*
Caprellidae sp. 1	0.002589	0	0	0	*0.00065*	0	0	0	0	*0*	0	0	0	0	*0*	0.023258	0.003341	0	0	*0.00665*	*0.00646*	*0.00084*	*0*	*0*	*0.0018243*
Copepoda sp. 1	0.020978	0	0	0	*0.00524*	0.026258	0.003531	0	0	*0.00745*	0.005185	0.003363	0	0	*0.00214*	0.017701	0.006886	0	0.017229	*0.01045*	*0.01753*	*0.00344*	*0*	*0.00431*	*0.0063207*
Gammaridea sp. 1	0	0	0	0	*0*	0	0	0	0	*0*	0.00762	0.012514	0.018022	0	*0.00954*	0	0	0	0	*0*	*0.0019*	*0.00313*	*0.00451*	*0*	*0.0023848*
Gammaridea sp. 2	0.006694	0	0	0	*0.00167*	0	0	0	0	*0*	0	0	0	0	*0*	0	0	0	0	*0*	*0.00167*	*0*	*0*	*0*	*0.0004184*
Halacaridae sp. 1	0.002589	0	0	0	*0.00065*	0	0	0	0	*0*	0	0	0	0	*0*	0	0	0	0	*0*	*0.00065*	*0*	*0*	*0*	*0.0001618*
Isopoda sp. 1	0	0	0	0	*0*	0	0	0	0	*0*	0	0	0	0	*0*	0.022034	0	0	0	*0.00551*	*0.00551*	*0*	*0*	*0*	*0.0013771*
Ostracoda sp. 1	0	0	0	0	*0*	0	0	0	0	*0*	0	0	0	0	*0*	0.002371	0	0	0	*0.00059*	*0.00059*	*0*	*0*	*0*	*0.0001482*
Cnidaria	**1.257467**	**1.701541**	**1.094506**	**0.245626**	***1.07478***	**0.02398**	**0.85651**	**0.001109**	**0.058737**	***0.23508***	**0.009506**	**0.3348**	**0.285714**	**0**	***0.1575***	**0.717661**	**1.123788**	**1.091242**	**2.055479**	***1.24704***	***0.50215***	***1.00416***	***0.61814***	***0.58996***	*0.6786041*
Actinaria sp. 1	0.002589	0	0	0	*0.00065*	0	0	0	0	*0*	0	0	0	0	*0*	0.004513	0.00338	0	0	*0.00197*	*0.00178*	*0.00085*	*0*	*0*	*0.0006552*
Campanulariidae sp. 1	0	0	0	0	*0*	0	0	0.008357	0	*0.00209*	0	0	0	0	*0*	0	0	0	0	*0*	*0*	*0*	*0.00209*	*0*	*0.0005223*
Campanulariidae sp. 2	0.059277	0.150447	0.022595	0	*0.05808*	0	0	0	0	*0*	0.008916	0.010246	0.016547	0	*0.00893*	0.05048	0.065779	0.056696	0.314438	*0.12185*	*0.02967*	*0.05662*	*0.02396*	*0.07861*	*0.0472139*
Campanulariidae sp. 2 low	0	3.786513	0.759296	0	*1.13645*	0	0	0	0	*0*	0	0.469585	0	0	*0.1174*	0	3.635953	2.635653	14.64507	*5.22917*	*0*	*1.97301*	*0.84874*	*3.66127*	*1.6207546*
Campanulariidae sp. 3	12.00276	12.72666	9.919103	2.456263	*9.27619*	0.239797	8.565101	0.002734	0.587372	*2.34875*	0.065495	2.364879	2.309856	0	*1.18506*	4.268253	6.65449	7.781203	5.203308	*5.97681*	*4.14408*	*7.57778*	*5.00322*	*2.06174*	*4.6967043*
Campanulariidae sp. 4	0.002426	0	0	0	*0.00061*	0	0	0	0	*0*	0	0	0	0	*0*	0.011283	0	0	0	*0.00282*	*0.00343*	*0*	*0*	*0*	*0.0008568*
Eudendrium sp. 1	0.505194	0.339527	0.241741	0	*0.27162*	0	0	0	0	*0*	0.020647	0.503288	0.530738	0	*0.26367*	1.102654	0.874899	0.427002	0.391971	*0.69913*	*0.40712*	*0.42943*	*0.29987*	*0.09799*	*0.3086038*
Eudendrium sp. 2	0	0	0	0	*0*	0	0	0	0	*0*	0	0	0	0	*0*	1.736979	0	0	0	*0.43424*	*0.43424*	*0*	*0*	*0*	*0.1085612*
Hydrozoa sp. 1	0	0	0	0	*0*	0	0	0	0	*0*	0	0	0	0	*0*	0	0	0.005835	0	*0.00146*	*0*	*0*	*0.00146*	*0*	*0.0003647*
Octocorallia sp. 1	0.002426	0.012264	0.002323	0	*0.00425*	0	0	0	0	*0*	0	0	0	0	*0*	0.002448	0.00338	0.006028	0	*0.00296*	*0.00122*	*0.00391*	*0.00209*	*0*	*0.0018044*
Foraminifera	**0.015812**	**0**	**0.001157**	**0.005248**	***0.00555***	**0.003475**	**0**	**0**	**0**	***0.00087***	**0.009836**	**0.001784**	**0.000679**	**0**	***0.00307***	**0.003251**	**0**	**0.002258**	**0**	***0.00138***	***0.00809***	***0.00045***	***0.00102***	***0.00131***	*0.0027188*
Foraminifera sp. 1	0.063249	0	0.004626	0.020994	*0.02222*	0.011584	0	0	0	*0.0029*	0.036669	0.003521	0.002715	0	*0.01073*	0.006043	0	0.005921	0	*0.00299*	*0.02939*	*0.00088*	*0.00332*	*0.00525*	*0.0097076*
Foraminifera sp. 2	0	0	0	0	*0*	0	0	0	0	*0*	0	0	0	0	*0*	0.002257	0	0.00311	0	*0.00134*	*0.00056*	*0*	*0.00078*	*0*	*0.0003354*
Foraminifera sp. 3	0	0	0	0	*0*	0.002317	0	0	0	*0.00058*	0	0	0	0	*0*	0.004705	0	0	0	*0.00118*	*0.00176*	*0*	*0*	*0*	*0.0004389*
Foraminifera sp. 4	0	0	0	0	*0*	0	0	0	0	*0*	0.002676	0.003617	0	0	*0.00157*	0	0	0	0	*0*	*0.00067*	*0.0009*	*0*	*0*	*0.0003933*
Mollusca	**0**	**0**	**0**	**0**	***0***	**0**	**0**	**0**	**0**	***0***	**0**	**0**	**0**	**0**	***0***	**0.041428**	**0**	**0**	**0**	***0.01036***	***0.01036***	***0***	***0***	***0***	*0.0025892*
Gastropoda sp. 1	0	0	0	0	*0*	0	0	0	0	*0*	0	0	0	0	*0*	0.002257	0	0	0	*0.00056*	*0.00056*	*0*	*0*	*0*	*0.000141*
Gastropoda sp. 2	0	0	0	0	*0*	0	0	0	0	*0*	0	0	0	0	*0*	0.080599	0	0	0	*0.02015*	*0.02015*	*0*	*0*	*0*	*0.0050374*
Porifera	**0.001824**	**0**	**0**	**0**	***0.00046***	**0.000772**	**0**	**0**	**0**	***0.00019***	**0.000892**	**0**	**0**	**0**	***0.00022***	**0**	**0**	**0**	**0**	***0***	***0.00087***	***0***	***0***	***0***	*0.000218*
Porifera sp. 1	0	0	0	0	*0*	0	0	0	0	*0*	0.002676	0	0	0	*0.00067*	0	0	0	0	*0*	*0.00067*	*0*	*0*	*0*	*0.0001673*
Porifera sp. 2	0.002737	0	0	0	*0.00068*	0.002317	0	0	0	*0.00058*	0	0	0	0	*0*	0	0	0	0	*0*	*0.00126*	*0*	*0*	*0*	*0.0003158*
Porifera sp. 3	0.002737	0	0	0	*0.00068*	0	0	0	0	*0*	0	0	0	0	*0*	0	0	0	0	*0*	*0.00068*	*0*	*0*	*0*	*0.000171*
Radiolaria	**0**	**0**	**0**	**0**	***0***	**0.002317**	**0**	**0.002804**	**0**	***0.00128***	**0.005269**	**0**	**0**	**0**	***0.00132***	**0.004513**	**0.00338**	**0.00311**	**0**	***0.00275***	***0.00302***	***0.00085***	***0.00148***	***0***	*0.0013371*
Radiozoa sp. 1	0	0	0	0	*0*	0.002317	0	0.002804	0	*0.00128*	0.005269	0	0	0	*0.00132*	0.004513	0.00338	0.00311	0	*0.00275*	*0.00302*	*0.00085*	*0.00148*	*0*	*0.0013371*
Unknown	**0**	**0**	**0.038944**	**0**	***0.00974***	**0**	**0**	**0.001869**	**0.004895**	***0.00169***	**0.000892**	**0**	**0**	**0**	***0.00022***	**0.001504**	**0**	**0.000972**	**0**	***0.00062***	***0.0006***	***0***	***0.01045***	***0.00122***	*0.0030673*
Unknown sp. 1	0	0	0.116833	0	*0.02921*	0	0	0.005607	0	*0.0014*	0	0	0	0	*0*	0	0	0.002917	0	*0.00073*	*0*	*0*	*0.03134*	*0*	*0.0078349*
Unknown sp. 2	0	0	0	0	*0*	0	0	0	0	*0*	0	0	0	0	*0*	0.004513	0	0	0	*0.00113*	*0.00113*	*0*	*0*	*0*	*0.0002821*
Unknown sp. 3	0	0	0	0	*0*	0	0	0	0.014684	*0.00367*	0.002676	0	0	0	*0.00067*	0	0	0	0	*0*	*0.00067*	*0*	*0*	*0.00367*	*0.001085*
Species pooled	*65.5377*	*85.9198*	*55.1222*	*1.9028*	*52.1206*	*1.42423*	*42.8486*	*0.09775*	*0.50575*	*11.2191*	*0.81089*	*16.7915*	*14.2945*	*0*	*10.6323*	*36.3966*	*56.5126*	*54.9234*	*12.0201*	*39.9632*	*26.0423*	*50.5182*	*31.7337*	*4.80956*	*28.4838*

Supplementary table 2.6 Surface and canopy coverage by all non-hydrozoan morphospecies and phyla across substratum types (mesh, plastic, stone, wood) and geographic sites (1, 2, 3, 4). A * indicates that the Cnidaria cover includes hydrozoans (see Figure 3.6 for detail).

Phylum/ Morphospecies	Surface cover (%)									Canopy cover (%)								
		Substratum type				Geographic location					Substratum type				Geographic location			
	Overall	Mesh	Plastic	Stone	Wood	Site 1	Site 2	Site 3	Site 4	*Overall*	Mesh	Plastic	Stone	Wood	Site 1	Site 2	Site 3	Site 4
Annelida	***3.0***	**3.7**	**0.0**	**1.0**	**0.0**	**5.0**	**0.0**	**3.0**	**1.0**	***0.0***	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**
Polychaeta sp. 1	*3.0*	5.0	0.0	1.0	0.0	0.0	0.0	5.0	1.0	*0.0*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polychaeta sp. 2	*3.0*	3.0	0.0	0.0	0.0	5.0	0.0	1.0	0.0	*0.0*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Arthropoda	***1.7***	**2.2**	**0.9**	**1.0**	**1.0**	**2.1**	**1.8**	**1.0**	**2.4**	***0.5***	**0.6**	**0.4**	**0.5**	**0.0**	**0.5**	**0.0**	**0.1**	**1.3**
Caprellidae sp. 1	*1.3*	1.7	0.0	0.0	0.0	0.0	0.0	0.0	1.7	*5.0*	5.0	5.0	0.0	0.0	5.0	0.0	0.0	5.0
Copepoda sp. 1	*2.1*	2.4	1.0	0.0	1.0	1.8	1.8	1.0	2.5	*0.0*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gammaridea sp. 1	*1.0*	1.0	1.0	1.0	0.0	0.0	0.0	1.0	0.0	*0.1*	0.0	0.0	0.5	0.0	0.0	0.0	0.1	0.0
Gammaridea sp. 2	*3.7*	3.7	0.0	0.0	0.0	3.7	0.0	0.0	0.0	*0.0*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Halacaridae sp. 1	*1.0*	1.0	0.0	1.0	0.0	1.0	0.0	0.0	0.0	*0.0*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Isopoda sp. 1	*5.0*	5.0	0.0	0.0	0.0	0.0	0.0	0.0	5.0	*0.0*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ostracoda sp. 1	*1.0*	1.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	*0.0*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cnidaria*	***11.7***	**8.2**	**11.8**	**10.8**	**37.1**	**13.6**	**9.0**	**6.4**	**13.7**	***11.1***	**10.1**	**10.5**	**9.1**	**32.1**	**11.2**	**2.8**	**5.9**	**15.8**
Actiniaria sp. 1	*1.0*	1.0	1.0	1.0	0.0	1.0	0.0	0.0	1.0	*0.3*	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5
Octocorallia sp. 1	*1.0*	1.0	1.0	1.0	0.0	1.0	0.0	0.0	1.0	*2.6*	0.0	0.0	2.6	0.0	0.0	2.6	0.0	0.0
Foraminifera	***1.4***	**1.5**	**1.0**	**0.9**	**1.0**	**3.2**	**1.0**	**1.0**	**0.8**	***11.4***	**9.2**	**12.5**	**8.5**	**32.5**	**8.9**	**0.0**	**2.3**	**14.9**
Foraminifera sp. 1	*1.4*	1.5	1.0	0.8	1.0	3.2	1.0	1.0	0.7	*10.3*	6.6	5.9	12.8	42.7	15.3	2.9	5.3	12.1
Foraminifera sp. 2	*1.0*	1.0	0.0	1.0	0.0	0.0	0.0	0.0	1.0	*3.4*	3.4	0.0	0.0	0.0	1.0	0.0	0.0	5.0
Foraminifera sp. 3	*1.0*	1.0	0.0	0.0	0.0	0.0	1.0	0.0	1.0	*12.2*	5.5	21.0	9.7	10.3	7.5	0.0	7.7	18.5
Foraminifera sp. 4	*1.0*	0.0	1.0	0.0	0.0	0.0	0.0	1.0	0.0	*72.5*	72.5	0.0	0.0	0.0	0.0	0.0	0.0	72.5
Mollusca	***0.5***	**0.5**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.5**	***1.0***	**0.0**	**0.0**	**1.0**	**0.0**	**0.0**	**0.0**	**0.0**	**1.0**
Gastropoda sp. 1	*1.0*	1.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	*0.0*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gastropoda sp. 2	*0.0*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*6.7*	0.0	8.0	6.7	0.0	10.0	0.0	2.5	6.3
Porifera	***2.0***	**2.3**	**1.0**	**0.0**	**0.0**	**1.0**	**1.0**	**5.0**	**0.0**	***0.1***	**0.1**	**0.0**	**0.1**	**0.0**	**0.1**	**0.0**	**0.0**	**0.2**
Porifera sp. 1	*3.0*	5.0	1.0	0.0	0.0	0.0	1.0	5.0	0.0	*0.1*	0.1	0.0	0.2	0.0	0.1	0.0	0.0	0.3
Porifera sp. 2	*1.0*	1.0	0.0	0.0	0.0	1.0	1.0	0.0	0.0	*0.0*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Porifera sp. 3	*0.0*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*0.0*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Radiolaria	***1.0***	**1.0**	**1.0**	**1.0**	**0.0**	**0.0**	**1.0**	**0.0**	**1.0**	***0.0***	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**
Radiolaria sp. 1	*1.0*	1.0	1.0	1.0	0.0	0.0	1.0	0.0	1.0	*2.5*	2.5	0.0	0.0	0.0	0.0	0.0	0.0	2.5
Unknown	***1.9***	**0.0**	**1.0**	**2.2**	**1.0**	**3.0**	**1.0**	**0.0**	**0.5**	***0.0***	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**
Unknown sp. 1	*2.0*	0.0	1.0	2.2	0.0	3.0	1.0	0.0	0.5	*5.0*	5.0	0.0	0.0	0.0	0.0	0.0	0.0	5.0
Unknown sp. 2	*0.0*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*0.0*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Unknown sp. 3	*1.0*	0.0	0.0	0.0	1.0	0.0	1.0	0.0	0.0	*0.0*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Supplementary table 2.7 Base coverage (%) of all individuals or colonies of all morphospecies present on four substratum types at four sites in the Labrador Sea (Canada).

	Site 1				Site 2				Site 3			Site 4			
Species	Mesh	Plastic	Stone	Wood	Mesh	Plastic	Stone	Wood	Mesh	Plastic	Stone	Mesh	Plastic	Stone	Wood
Polychaeta sp. 1	0	0	0	0	0	0	0	0	5	0	0	0	0	1	0
Polychaeta sp. 2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Caprellidae sp. 1	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
Copepoda sp. 1	1	0	0	0	2	1	0	0	0	1	0	3	1	0	1
Gammaridea sp. 1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0
Gammaridea sp. 2	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Halacaridae sp. 1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Isopoda sp. 1	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0
Ostracoda sp. 1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Actinaria sp. 1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Campanulariidae sp. 1	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0
Campanulariidae sp. 2	4	8	3	0	0	0	0	0	1	1	5	4	5	6	17
Campanulariidae sp. 2B	0	8	5	0	0	0	0	0	0	3	0	0	5	5	50
Campanulariidae sp. 3	11	28	18	62	9	13	10	5	2	6	18	8	24	18	52
Campanulariidae sp. 4	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Eudendrium sp. 1	6	3	8	0	0	0	0	0	2	3	10	5	11	8	13
Eudendrium sp. 2	0	0	0	0	0	0	0	0	0	0	0	62	0	0	0
Hydrozoa sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Octocorallia sp. 1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0
Foraminifera sp. 1	4	0	1	1	1	0	0	0	1	1	1	1	0	1	0
Foraminifera sp. 2	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Foraminifera sp. 3	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
Foraminifera sp. 4	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Gastropoda sp. 1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Gastropoda sp. 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Porifera sp. 1	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0
Porifera sp. 2	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Porifera sp. 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Radiolaria sp. 1	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0
Unknown sp. 1	0	0	4	0	0	0	1	0	0	0	0	0	0	1	0
Unknown sp. 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unknown sp. 3	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0

Supplementary table 2.8 Canopy coverage (%) of all individuals or colonies of all morphospecies present on four substratum types at four sites in the Labrador Sea (Canada).

	Site 1				Site 2				Site 3			Site 4			
Species	Mesh	Plastic	Stone	Wood	Mesh	Plastic	Stone	Wood	Mesh	Plastic	Stone	Mesh	Plastic	Stone	Wood
Polychaeta sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polychaeta sp. 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Caprellidae sp. 1	5	0	0	0	0	0	0	0	0	0	0	5	5	0	0
Copepoda sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gammaridea sp. 1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Gammaridea sp. 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Halacaridae sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Isopoda sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ostracoda sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Actinaria sp. 1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Campanulariidae sp. 1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
Campanulariidae sp. 2	7	19	3	0	0	0	0	0	1	5	5	16	11	13	33
Campanulariidae sp. 2B	0	13	5	0	0	0	0	0	0	3	0	0	10	8	0
Campanulariidae sp. 3	9	13	15	53	6	2	7	5	2	2	14	6	8	12	40
Campanulariidae sp. 4	1	0	0	0	0	0	0	0	0	0	0	5	0	0	0
Eudendrium sp. 1	7	18	5	0	0	0	0	0	2	6	13	7	31	7	10
Eudendrium sp. 2	0	0	0	0	0	0	0	0	0	0	0	73	0	0	0
Hydrozoa sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Octocorallia sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Foraminifera sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Foraminifera sp. 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Foraminifera sp. 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Foraminifera sp. 4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gastropoda sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gastropoda sp. 2	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0
Porifera sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Porifera sp. 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Porifera sp. 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Radiolaria sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unknown sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Unknown sp. 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unknown sp. 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

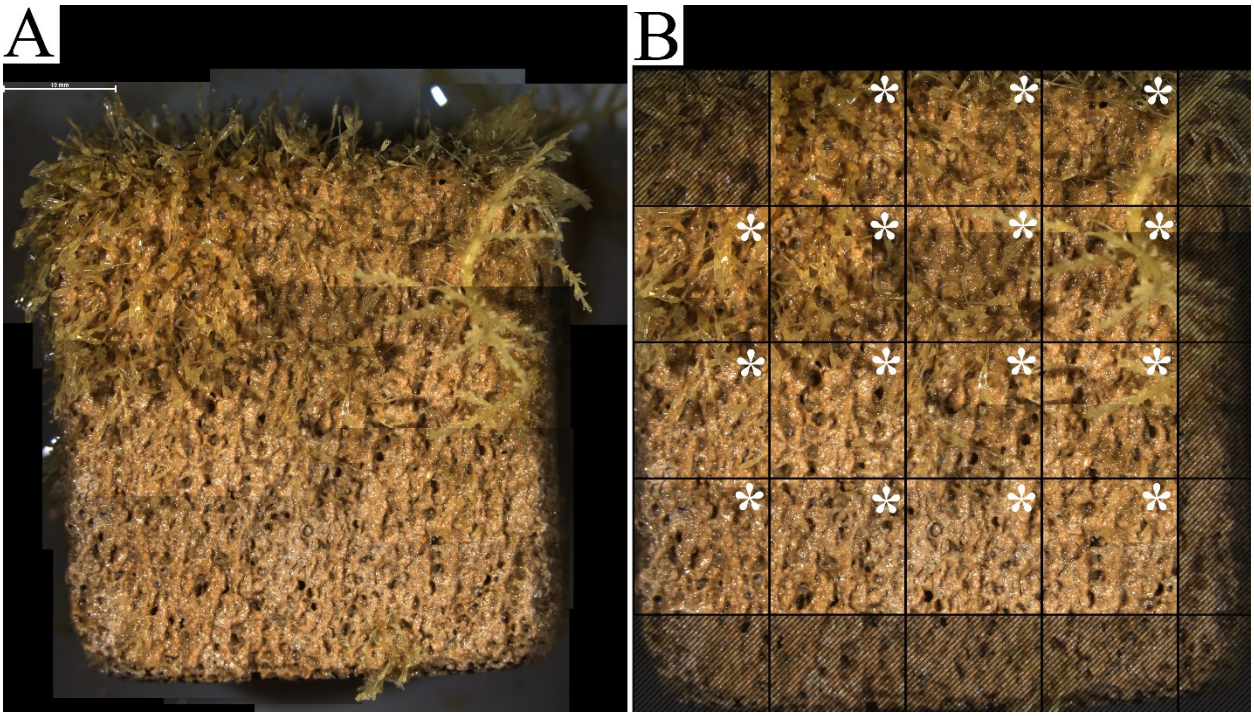
Supplementary table 2.9 Results of PERMANOVA and two-way crossed analysis of similarity (ANOSIM) tests on Bray-Curtis resemblance matrices on the four substratum types and four geographic sites in Labrador Sea (Canada). Global results are indicated in bold.

	PERMANOVA		ANOSIM	
Substratum Type	**Pseudo-F**	**Significance (p)**	**Dissimilarity (ρ)**	**Significance (p)**
Base coverage	**5.28**	**<0.001**	**0.441**	**<0.001**
Mesh, Plastic			0.583	<0.001
Mesh, Stone			0.556	0.004
Mesh, Wood			0.704	0.047
Plastic, Stone			0.213	0.067
Plastic, Wood			0.852	0.016
Stone, Wood			0.259	0.172
Canopy coverage	**3.39**	**<0.001**	**0.352**	**<0.001**
Mesh, Plastic			0.37	0.005
Mesh, Stone			0.463	0.002
Mesh, Wood			0.111	0.422
Plastic, Stone			0.389	0.006
Plastic, Wood			0.704	0.016
Stone, Wood			0.333	0.125
Abundance	**8.15**	**<0.001**	**0.471**	**<0.001**
Mesh, Plastic			0.657	<0.001
Mesh, Stone			0.593	0.001
Mesh, Wood			0.63	0.063
Plastic, Stone			0.185	0.125
Plastic, Wood			0.704	0.047
Stone, Wood			0.556	0.109
Density	**6.74**	**<0.001**	**0.405**	**<0.001**
Mesh, Plastic			0.5	0.006
Mesh, Stone			0.463	0.006
Mesh, Wood			0.556	0.078
Plastic, Stone			0.157	0.163
Plastic, Wood			0.704	0.047
Stone, Wood			0.407	0.188
Shannon diversity	**1.07**	**0.374**	**0.212**	**0.025**
Mesh, Plastic			0.339	0.019
Mesh, Stone			0.139	0.172
Mesh, Wood			0.556	0.078
Plastic, Stone			0.021	0.374
Plastic, Wood			0.407	0.094
Stone, Wood			0.185	0.266
Species richness	**8.62**	**<0.001**	**0.326**	**0.005**
Mesh, Plastic			0.569	0.001
Mesh, Stone			0.514	<0.001
Mesh, Wood			1	0.016
Plastic, Stone			-0.046	0.58
Plastic, Wood			0.037	0.484
Stone, Wood			-0.296	1
Phylum richness	**9.19**	**<0.001**	**0.247**	**0.019**
Mesh, Plastic			0.625	<0.001
Mesh, Stone			0.366	0.01
Mesh, Wood			0.852	0.031
Plastic, Stone			-0.13	0.761
Plastic, Wood			-0.222	1
Stone, Wood			-0.333	0.969

	PERMANOVA		ANOSIM	
Geographic site	**Pseudo-F**	**Significance (p)**	**Dissimilarity (ρ)**	**Significance (p)**
Base coverage	**10.05**	**<0.001**	**0.67**	**<0.001**
Site 1, Site 2			0.951	0.001
Site 1, Site 3			0.58	0.006
Site 1, Site 4			0.025	0.405
Site 2, Site 3			0.901	0.001
Site 2, Site 4			0.84	0.001
Site 3, Site 4			0.63	0.002
Canopy coverage	**10.11**	**<0.001**	**0.592**	**<0.001**
Site 1, Site 2			0.938	0.001
Site 1, Site 3			0.383	0.032
Site 1, Site 4			0.012	0.456
Site 2, Site 3			0.704	0.003
Site 2, Site 4			0.963	0.001
Site 3, Site 4			0.494	0.003
Abundance	**10.99**	**<0.001**	**0.617**	**<0.001**
Site 1, Site 2			0.889	0.001
Site 1, Site 3			0.753	0.002
Site 1, Site 4			-0.062	0.599
Site 2, Site 3			0.926	0.001
Site 2, Site 4			0.827	0.001
Site 3, Site 4			0.457	0.002
Density	**9.31**	**<0.001**	**0.553**	**<0.001**
Site 1, Site 2			0.877	0.001
Site 1, Site 3			0.778	0.001
Site 1, Site 4			-0.025	0.49
Site 2, Site 3			0.901	0.001
Site 2, Site 4			0.605	0.002
Site 3, Site 4			0.259	0.034
Shannon diversity	**3.82**	**<0.001**	**0.292**	**<0.001**
Site 1, Site 2			0.267	0.033
Site 1, Site 3			0.346	0.01
Site 1, Site 4			0.074	0.324
Site 2, Site 3			0.558	0.001
Site 2, Site 4			0.304	0.04
Site 3, Site 4			0.259	0.077
Species richness	**9.87**	**<0.001**	**0.328**	**0.002**
Site 1, Site 2			0.543	0.01
Site 1, Site 3			0.006	0.436
Site 1, Site 4			0.08	0.814
Site 2, Site 3			0.58	0.004
Site 2, Site 4			0.765	0.001
Site 3, Site 4			0.012	0.507
Phylum richness	**2.51**	**0.07**	**0.066**	**0.237**
Site 1, Site 2			-0.167	1
Site 1, Site 3			0.296	0.056
Site 1, Site 4			0.056	0.472
Site 2, Site 3			0.222	0.13
Site 2, Site 4			0.111	0.262
Site 3, Site 4			-0.117	0.73

	PERMANOVA	
Site x Substratum type	**Pseudo-F**	**Significance (p)**
Base coverage	**3.01**	**<0.001**
Canopy coverage	3.01	<0.001
Abundance	3.46	<0.001
Density	3.64	<0.001
Shannon diversity	2.35	0.002
Species richness	0.89	0.549
Phylum richness	0.55	0.82

2.10.3 Supplementary figures



Supplementary figure 2.1 Sample of a mosaic image and the grid overlays used for morphospecies abundance measurements from “Face #2” of “Stone #1” of Site 4, e.g., the second face examined on one of the three carbonate block replicates at Site 4. Cross-hatching indicates squares excluded on all substratum types due to erosion (corners), or an incomplete grid square. Scale bar is 10 mm. (A) The mosaic image generated using individual photographs taken of each section of the surface using the Leica M205 stereo microscope and LAS-X software, then stitched together in Adobe Photoshop CS6. (B) A grid overlay of 1 cm squares on the mosaic image, used for surfaces with more sparse colonization.

Chapter 3: Rock bottom: colonization of dropstones in bathyal zones of the subarctic and Arctic[1]

3.1 Abstract

Hard substrata of allochthonous origin, such as ice-rafted dropstones, can provide essential habitat for benthic communities in the polar and subpolar deep sea, acting as "islands" in otherwise finer-grained sedimentary environments. The present study explored the diversity and distribution patterns of morphospecies (msp / mspp) present on dropstones collected at bathyal depths in the Labrador Sea (LAB) and Baffin Bay (BAF), respectively spanning subarctic and Arctic regions of eastern Canada. Specifically, the zonation, intra- and interspecific interactions, and succession of all colonizers were examined. Based on in-situ images, dropstones exhibited ~94% greater epibenthic megafaunal richness than similar surfaces of the substratum immediately surrounding them. Analysis of three dropstones collected from each of six sites documented a total of 101 sessile and motile taxa spanning 10 phyla. Across sites, bryozoans dominated at all depths and locations (27 mspp, plus 3 dead) followed by poriferans (27 mspp), 19 cnidarians, eight arthropods, eight annelids, five chordates (tunicates), three echinoderms, three molluscs, and one foraminifer. There were 19 mspp that spanned both LAB and BAF, with greater overall richness in the subarctic region (62 vs 26 mspp). A total of 64 sessile mspp occurred above the stone-sediment interface (e.g., cnidarians and poriferans), whereas 22 mspp (mostly bryozoans) occurred at the stone-sediment interface; one morphospecies of polychaete occurred below. The most abundant morphospecies was an

[1] A version of this manuscript is currently undergoing revision in Deep Sea Research Part I: Oceanographic Research Papers.

arborescent bryozoan, while two encrusting bryozoans covered the most surface area. Eight morphospecies occurred as just one individual or colony per stone, and 35 mspp appeared to maintain an exclusion zone between conspecifics (e.g., tube-dwelling annelids, hydrozoans, and anthozoans). Conversely, in 51 mspp conspecifics occurred abutting one another (e.g., bryozoans and poriferans). Allospecific exclusion zones appeared to occur in 27 mspp (e.g., bryozoans and annelids), whereas 59 allospecifics (e.g., poriferans, cnidarians, and chordates) occurred within touching distance. Secondary colonization (including cases of epibiosis) in 83 mspp, documenting 204 unique pairings of hosts and colonizers were observed. The number and diversity of morphospecies colonizing dropstones in the deep sea of the eastern Canadian Arctic and subarctic support the role of dropstones as oases that facilitate connectivity in an otherwise poorly diversified epibenthic environment.

3.2 Introduction

Hard substrata composed of stones of different sizes, though less common than soft sediments in many bathyal and abyssal depths, provide essential anchors for numerous epibenthic species and the base to establish and connect other more distant hard-bottom communities (reviewed by Davis 2009) including coral or sponge gardens that sustain local biodiversity (Metaxas and Davis 2005; Roberts et al. 2009; Baillon et al. 2014; Buhl-Mortensen and Buhl-Mortensen 2018; Dunham et al. 2018). Stony substrata likely increase access to pelagic food by sessile or sedentary organisms through increased height into the water column, and allows a better opportunity for spawning and dispersion of gametes within and beyond the benthic boundary layer (reviewed by Jenkins et al. 2009). Established hard-bottom communities also create complex heterogeneous microhabitats in which prey can hide and predators can feed (Beaulieu 2001a; Miller et al. 2012; Baillon et al. 2014; Pierrejean et al. 2020).

Continental margins of polar and subpolar regions offer a rich supply of hard substrata in the form of terrigenous stones transported by glaciers or glacial runoff, and ice-rafted stones carried even farther offshore by icebergs, collectively called dropstones (Bennett et al. 1996). In the eastern Canadian North Atlantic and Arctic, melt-out at the ice margin in the last major deglaciation event beginning ~18,000–13,000 years ago likely enhanced dropstone supply, followed by successive, seasonal ice-rafting events (Bennett et al. 1996; Edinger et al. 2011; Dalton et al. 2020). Dropstones play an important role in deep-sea habitats by depositing small islands of hard substrata into an otherwise finer-grained sedimentary bottom, increasing environmental heterogeneity and, in some cases, creating an island-like habitat or at least one that offers higher elevation on a gravelly substratum (Schulz et al. 2010; Ziegler et al. 2017). Researchers hypothesize that, like terrestrial islands, these dropstones increase local biodiversity and facilitate different patterns of colonization based on available surface area, distance from larval supply, and surrounding local environmental conditions (Syvitski et al. 1989; Meyer et al. 2016).

Until recently, few studies have focused on deep-sea dropstone communities, primarily because of the difficulty in both accessing and collecting dropstones. Globally, most studies have focused on the Greenland Sea, as well as western Antarctica. In the Greenland Sea, photographic and video transects using remotely operated vehicles (ROVs) showed that dropstones harbour numerous epibenthic macrofauna not found on the surrounding soft sediment (Schulz et al. 2010). These dropstones reportedly host uniquely rich communities composed of foraminifers, bryozoans, polychaetes, anthozoans, and ascidians (Kukliński and Bader 2007). In the Fram Strait, photographic surveys of dropstones identified taxonomic morphotypes with distribution patterns similar to those of terrestrial islands; for example, species richness, species abundance,

and species diversity correlated positively with dropstone size and proximity to other colonized hard substrata such as rocky reefs, though with inferred driving mechanisms specific to the deep sea (e.g., epibiosis may increase co-occurrence of species; Meyer et al. 2016). In the fjords of the Western Antarctic Peninsula, photographic transects identified dropstone-associated species, of which more than one third were absent in surrounding sediments, so that their assemblages contributed 20% of overall species richness, despite comprising <1% of the substratum surface in the survey area (Ziegler et al. 2017).

In the Pacific abyssal plains, fields of polymetallic nodules resemble dropstones in how they sit within an otherwise muddy substratum. These partially-buried and slow-growing manganese precipitates also generate localized patterns of higher biodiversity in epibenthic macrofauna dominated by suspension-feeding species not found on the surrounding soft substratum (Mullineaux 1987). In the Clarion-Clipperton Zone of the Pacific, ROV surveys documented seven species and four genera previously unknown to science in the nodule field, and half of all species discovered were associated exclusively with the nodules (Amon et al. 2016). Another study in the same region found 19 new species, nine new genera, and two new families of bryozoans associated with nodules (Grischenko et al. 2018).

Beyond biodiversity assessments, no study has documented the colonization of dropstones or nodules at a fine scale to evaluate zonation, exclusion, cooperation, or succession patterns. Furthermore, no study to date has investigated the role of dropstones (at any scale) in the deep waters of the Canadian Arctic and subarctic. However, studies of assemblages on hard substrata in specific localities of the Northwest Atlantic have highlighted the general importance of hard bottoms for recruitment of many taxa, including habitat-forming corals and sponges (Edinger et al. 2011; Guy and Metaxas 2022).

The present study sought to expand the understanding of the diversity and complexity of dropstone-associated assemblages by examining species distributions and composition on dropstones from the deep sea of the North Atlantic and Eastern Canadian Arctic. Photographs were taken of dropstones from bathyal depths at two northern locations (Labrador Sea and Baffin Bay) to explore their broad contributions to local megafaunal biodiversity. A subset of these dropstones was collected to assess their macrofaunal species diversity and spatial distribution and infer whether inter- or intraspecific interactions occur (i.e., between allospecifics and conspecifics, respectively), both within and across sites and depths. The primary aim was to test the hypotheses that (1) the community assemblages on dropstones collected from sites within a geographic region are more similar than those collected across distant geographic regions; and (2) species exhibit consistent patterns of zonation (i.e., vertical distance above or below the sediment surface) through their preferential positioning on stone surfaces. The study also explored the potential influence of ecological interactions (e.g., epibiosis) on positioning both at fine scales and at regional assemblages.

3.3 Methods

3.3.1 Study sites

The study was carried out across six sites divided between two broad geographic regions; three sites were in the Labrador Sea (Newfoundland and Labrador) and three in Baffin Bay (Nunavut) (Figure 1). All three Labrador Sea (LAB) sites were in the subarctic, i.e., below the Arctic Circle, with two on Saglek Bank (LAB 1 and 2) at 766 and 822 m depths, respectively, and one farther offshore (LAB 3) at 1308 m. Baffin Bay (BAF) sites were in the Arctic, i.e., above the Arctic Circle, with all three near Scott Inlet (BAF 1, 2 and 3) at 220, 497, and 239 m depths. All dropstones were labeled according to site and order of collection (e.g., at LAB 1 site,

the three dropstones are LAB 1-1, LAB 1-2, and LAB 1-3). Detailed coordinates and depth of each stone collection and site are available in Supplementary Table 3.1.

We characterized notable features of the sites by reviewing known literature (e.g., publications or cruise reports) (Cramm et al. 2021; Desmarais et al. 2021; Vogt et al. 2023) as well as using ROV footage to document all soft and hard substrata sediment sizes, dominant visible taxa, and any geological and hydrological features.

3.3.2 Dropstone collections and associated video surveys

We collected dropstones showing signs of established epibenthic communities and measuring ~5–10 cm across (to standardize the size of dropstones, within at-depth storage constraints) using the ROV *Astrid* on the CCGS *Amundsen* between July and August of 2021. Collection of three dropstones at each of the six sites yielded a total of 18 dropstones. We defined each site as a transect of ~100 m around the dropstone collections throughout which the ROV took in-situ photographic and video footage using its two main cameras (Insite Pacific Mini Zeus MKIII High-Definition CMOS color zoom video camera "MiniZeus" and SubC imaging 1Cam Alpha "Alpha1Cam") (Figure 1). The ROV photographed dropstones and their immediate surroundings to coarsely compare the epibenthic megafaunal assemblages present on the dropstone to those on the surrounding sediment, before being transferred to the storage boxes. Upon retrieval of the ROV, we photographed the dropstones in a benthic laboratory aboard the ship using an Olympus Tough TG-6 digital camera and then preserved in 20-l buckets in 70–100% ethanol (depending on the biomass present). Motile fauna present in the ROV storage boxes that had released during surfacing (confirmed using ROV footage to be epifauna present on dropstones in situ) were also preserved separately in 50-ml containers. Upon collection, we photographed and documented morphometrics of large biogenic structures (e.g.,

coral colonies), their position on the dropstone, and associated fauna; we then removed them and froze them separately because of freezer space constraints. All dropstones and associated fauna were transferred to fresh ethanol (100%) upon arrival at the Ocean Sciences Centre (Memorial University, Newfoundland).

We also characterized dropstones using ROV footage in an opportunistic, coarse comparison for species richness (number of unique species) and abundance (number of individuals or colonies) between dropstones and the surrounding substratum; see Supplementary Methods for details.

3.3.3 Fine-scale analysis of dropstone colonization in the laboratory

We measured dropstones in three dimensions based on how they were buried in the sediment: length (longest distance parallel with the sediment line), width (widest distance perpendicular to the length while still parallel with the sediment line), and total height (distance between lowest and highest points perpendicular to the stone-sediment interface). We treated them as ellipsoids based on these three measurements to calculate total surface area (cm2). Each collected dropstone was then divided into two zones, above and below the visible line along which they were buried in the sediment upon collection (sediment line), corresponding to the exposed and buried surfaces, respectively (Figure 2). The exposed height (mm) and surface area (cm2) were also measured for comparison. We examined each zone to establish the proportion of exposed versus buried surface, calculated as a percentage of the total surface area (cm2), documenting any evidence suggesting that the dropstone had rotated or tilted in the past (e.g., dead coral skeletons on the buried surface), though the sediment line remained defined by position at time of collection. We confirmed any ambiguous delineation using the high-definition ROV images taken in situ.

Our analyses documented all metrics (described below) at four levels: first per individual dropstone; second by site, as an average across the three dropstones collected at each site; third by region, across the three sites in each region (LAB and BAF); and finally at the global overall scale of the study, across all samples, irrespective of site and region.

3.3.3.1 Richness and categorization of colonizing species

We identified each individual (ind) or colony (col) of epibenthic mega- and macrofauna present on each dropstone to the lowest taxonomic level possible within the limitations of morphological identification using visual analysis and assigned to a morphospecies (abbreviated to msp / mspp). Due to the size of the dropstones, photo identification relied on a Leica M205 stereo microscope with a Leica DFC 7000T camera (and LAS-X software; magnification range 0.75x to 321x), where possible, or else on a handheld Olympus Tough TG-6 digital camera. Limits of the visual analysis of collected dropstones also forced the grouping of all benthic foraminifers together into one taxon. We carried out identifications using morphological comparisons and relevant publications (e.g. Powell 1968; Kluge 1975; Pollock 1998; Kukliński et al. 2007), with the assistance of collaborators for the identification of chordates (tunicates) (K.C.K. Ma; de Rocha et al. 2012; Ma et al. 2017), poriferans (B. Caines, DFO, St. John's), and cnidarians (V. Wareham-Hayes, DFO, St. John's). We calculated richness as the number of morphospecies or phyla present, and also assessed morphospecies richness by phylum.

We further categorized each morphospecies as either unitary (i.e., solitary) or colonial and noted its growth style and morphology (e.g., sessile encrusting, sessile erect, motile), as well as whether it was dead or alive at the time of collection. Dead individuals and colonies were excluded from analyses unless otherwise noted.

3.3.3.2 Abundance, coverage, and diversity

If a morphospecies was unitary, sessile erect, or motile, we measured its abundance as a total abundance, i.e., sum of all individuals at a given level, and density, i.e., the number of individuals or colonies present per surface area of the zone they colonized (ind cm-2 or col cm-2), while only the presence or absence of encrusting colonial morphospecies was noted. We calculated the coverage (%) of each morphospecies relative to the surface area of the zone it colonized (either exposed or buried) at the surface level (within 1 cm of the stone surface) and in the canopy (greater than 1 cm above the stone surface).

3.3.3.3 Spatial mapping of colonizing species

We schematized (hand drew) dropstones to map the positioning of all colonizers, which were generally categorized as colonizing the exposed (epibenthic) or buried (endobenthic) zone (Figure 2). We determined zonation of morphospecies by establishing the exact vertical position of colonizing individuals and colonies in elevation above or below the sediment line, measured as their distance from the stone-sediment boundary (i.e., vertical position), measured as the shortest vertical straight line between the individual and the sediment line. A zonation of zero, i.e., the individual or colony had no measurable distance from the sediment line, was termed to be “at the sediment line”. We examined proportional zonation as a percentage of morphospecies above (exposed), at, or below (buried) the sediment line. For sessile morphospecies only, establishing relative positioning of colonizer based on gregariousness and colonization strategy used the distance between conspecifics (i.e., intraspecific distance) and allospecifics (i.e., interspecific distance). We used digital calipers to measure distances.

3.3.3.4 Secondary colonization and epibiosis

We examined succession by quantifying both secondary colonization and epibiosis. At the individual and colony level, we categorized each occurrence as a primary colonizer (i.e., colonizing the surface of the dropstone), a secondary colonizer (i.e., colonizing the remains of another individual or colony), or an epibiont (i.e., colonizing still-living host tissue). When found still attached firmly to another individual or colony post collection, we considered motile morphospecies as epibionts. Documenting secondary colonization and epibiotic pairings between a colonized morphospecies (host) and colonizer (i.e., on a dead host) or epibiont (i.e., on a live host) enabled examination of the contribution of these relationships to the assemblages.

3.3.3.5 Statistical analyses

We calculated species diversity using morphospecies abundance in the Shannon Index H' (Shannon 1948):

$$H' = \sum_{i=1}^{s} (\rho_i) \ln \rho_i$$

where ρi is the proportion of individuals or colonies of one morphospecies divided by the total number of individuals or colonies found, ln is the natural log, and s is the number of morphospecies.

We used one-way analyses of variance (ANOVA) and a Tukey post-hoc multiple comparison test in SigmaPlot 15.0 which enabled testing of differences in species diversity indices (H') between regions, along with Shapiro-Wilk test for normality and a Brown-Forsythe for equal variance.

We completed multivariate analyses using Primer v7. Principal coordinate analysis (PCO) examined the influence of regional (depth, latitude, longitude) and physical characteristics (exposed stone height, exposed surface area, and percentage of the surface exposed) on the presence and abundance of morphospecies after normalizing both regional and physical data to zero. Application of a log(x+1) transformation to abundance enabled better consideration of both the most common and rarer morphospecies (Clarke et al. 2014); they were also examined following a presence/absence transformation to balance underrepresented encrusting colonial morphospecies. We then used a similarity percentages test (SIMPER) to identify the primary morphospecies contributing to each region's dissimilarity.

3.4 Results

3.4.1 Characterization of study sites and collected dropstones

The six collection sites had unique environments, depths, and substrata surrounding the collected dropstones (summarized in Supplementary Table 3.1). The two southernmost sites (LAB 1, 766 m depth; LAB 2, 822 m) were near a known coral hotspot in northeast Saglek Bank (Desmarais et al. 2021) (Figure 1B). This area experiences strong bottom currents (~20 cm s-1) linked to macrotidal oscillation in Frobisher Bay (Desmarais et al. 2021). LAB 3 (1308 m; Figure 1B) was farther away from the other two sites in the region (352.8 km northeast from LAB 2) and the deepest sampled, lying farther offshore and closer to Davis Strait.

BAF 1 (220 m depth) was the shallowest site, and close to a previously documented hydrocarbon seep (Desmarais et al. 2021) (Figure 1C). BAF 2 (497 m) was the northernmost site (7.8 km from BAF 1), at the top of a bedrock massif of a presumed fault in Scott Trough, and another potential hydrocarbon seep location (Desmarais et al. 2021). BAF 3 (239 m) was above

the scarp of the eroding southwest margin of Scott Trough in a turbidity current system located 10.9 km from BAF 2 (Figure 1C).

Collected dropstones were all partially buried (between 10 and 60% of their entire surface) in surrounding sediment (Supplementary Table 3.2). Overall, their exposed surface was 58 ± 17%, with slightly higher values in LAB (63 ± 9%) than in BAF region (52 ± 5%). Supplementary Table 3.2 summarizes the dimensions (i.e., length, width, height, surface area) of all dropstones collected, as well as their exposed surface area and height. Globally, individual dropstones were not significantly different in size ($p > 0.05$). Total surface areas ranged from 86 to 786 cm2, with exposed surfaces ranging from 43 to 550 cm2. Moreover, the coverage by all morphospecies combined ranged from 15 to 80% at the surface and 1 to 40% at the canopy for the exposed surface (Supplementary Table 3.2). Faunal coverage values for the buried zone ranged from 0 to 20% at the surface.

3.4.2 Fine-scale analysis of dropstone colonization in the laboratory

3.4.2.1 Richness and categorization of colonizers

Our analyses identified a total of 101 mspp spanning 10 phyla, noting that five of the morphospecies could not be identified. An additional 6 mspp were present only as dead individuals or colonies and were therefore excluded from analyses unless otherwise indicated. Bryozoans contained the highest number of morphospecies (27, plus three dead), with equal numbers of poriferans (27), followed by 18 cnidarians (plus two dead), eight arthropods, eight annelids, five chordates (tunicates), four echinoderms, three molluscs, and foraminifers (Figure 3). Of the live colonizers, 75% were colonial and 25% were unitary; 84% were sessile and 16% were motile, with 57% of the sessile morphospecies exhibiting erect growth and 43% being encrusting (Figure 4). Regionally, 62 mspp occurred exclusively in LAB, 26 exclusively in BAF,

and 19 occurred in both regions. The 21 ± 5 mspp in LAB spanned 6 ± 2 phyla, whereas the 10 ± 3 mspp in BAF spanned 4 ± 1 phyla (Figure 5). All 10 phyla listed above were represented in LAB, whereas only eight occurred in BAF (phyla Brachiopoda and Mollusca solely occurred in LAB). Bryozoa contained the highest number of BAF morphospecies with 20, whereas Porifera dominated in LAB with 21 mspp (Figure 5).

The highest richness on a single dropstone was 32 mspp from 8 phyla at LAB 2, while the lowest richness (7 mspp) occurred on four dropstones distributed across the three sites sampled in BAF (Table 3.1). The lowest number of phyla (n = 2) occurred at BAF 2. Each dropstone from LAB had higher richness than any of those from BAF (Figure 5A); analysing the dropstone means across sites (n = 3 per site) had the most morphospecies per dropstone at LAB 2 (27 ± 5 in 7 ± 1 phyla), followed by LAB 3, LAB 1, BAF 3, BAF 2, and BAF 1 with the fewest (7 ± 0 in 4 ± 2 phyla) (Table 3.1).

Phyla representation varied, with Annelida, Bryozoa, and Cnidaria represented at all six sites; Porifera and Echinodermata represented at five sites; Arthropoda and Chordata represented at four sites; Foraminifera at three; Mollusca at two; and Brachiopoda at one site only. Figure 5B summarises details of morphospecies found at each site. The three LAB sites generally had the highest number of morphospecies within each phylum, except for Bryozoa (where BAF 3 had the most morphospecies with nine), and Echinodermata (where LAB 3, BAF 1 and BAF 3 all had two morphospecies).

3.4.2.2 Abundance, coverage, and diversity

3.4.2.2.1 Abundance

The most abundant morphospecies observed was the erect bryozoan Crisiidae msp. 1, with 772 total colonies (dropstones pooled; Supplementary Table 3.3) and an overall density of 0.17 col cm-2 (Figure 6). This bryozoan had the highest density of any morphospecies on a single dropstone (1.17 col cm-2 from LAB 2) and the highest density on almost all dropstones on which it occurred (n = 8) except on one dropstone at LAB 1 where the colonial hydrozoan Campanulariidae msp. 1 surpassed it (Supplementary tables 4, 5). The same Crisiidae msp. 1 was the most abundant morphospecies site-wide at all LAB sites and one BAF site (BAF 3). At BAF 1 the most abundant morphospecies was Bryozoa msp. 1 and at BAF 2 it was Porifera msp. 14. At the regional scale, Crisiidae msp. 1 dominated both LAB and BAF (Figure 6). SIMPER analysis of morphospecies abundances identified 88.9% dissimilarity between regions, primarily attributed to Criisidae msp. 1, Aplousobranchia msp. 1 and Aglaopheniidae msp. 3. The top three morphospecies contributing to the LAB region were Crisiidae msp. 1, Aplousobranchia msp. 1, and Annelida msp. 1 (30.2% similarity), whereas Tubuliporidae msp. 1, Schizoporelloidea msp. 2, and Serpulidae msp. 1 contributed most to BAF (19.9% similarity). Of the regional and physical characteristics examined using PCO, latitude contributed positively to PCO1 (24.1%) and negatively to PCO2 (16%) whereas depth and longitude contributed predominately to PCO1 (negative) and weakly to PCO2 (positive). Surface area, exposure, and height contributed moderately to both PCO1 (negative) and PCO2 (positive; 16%) (Figure 7A). The presence/absence transformation resulted in comparable patterns, with slightly different contributions of PCO1 (27%) and PCO2 (18.5%); however, negative and positive contributions from all characteristics were inverse with regards to PCO2 (Figure 7B).

3.4.2.2.2 Surface and canopy coverage

Surface. One morphospecies dominated thirteen dropstones in surface coverage, with equal coverage by multiple morphospecies on the remaining five. Electridae msp. 1 dominated on most dropstones (n = 5) with 25% as the highest surface coverage on any individual dropstone at LAB 2-2; overall, Electridae msp. 1 covered 4.1 ± 5.9% of all dropstone surfaces. More broadly, Escharellidae msp. 2 dominated at LAB 1, Electridae msp. 1 dominated LAB 2 and LAB 3, *Haliclona (Flagellia) xenomorpha* dominated BAF 1, Porifera msp. 14 dominated BAF 2, and Schizoporelloidea msp. 2 dominated BAF 3. Regionally, Electridae msp. 1 (8.3 ± 7.3%) dominated LAB whereas Schizoporelloidea msp. 2 dominated BAF (3.5 ± 2.3%) (Table 3.2).

Canopy. One morphospecies dominated fifteen dropstones in canopy coverage, in contrast to equal coverage by multiple morphospecies for the remaining three. Different morphospecies of poriferan dominated canopy coverage (n = 6 dropstones; examples below), whereas the colonial hydrozoan Aglaopheniidae msp. 3 was the only morphospecies that dominated more than one dropstone (n = 2). The crinoid Heliometria glacialis dominated canopy coverage on any individual dropstone, with 54% at BAF 3-3; overall, H. glacialis dominated, with canopy coverage of 3.3 ± 4.4% for all dropstones. More broadly, Aglaopheniidae msp. 3 dominated LAB 1 and 2, Porifera msp. 8 dominated LAB 3, *Haliclona (Flagellia) xenomorpha* at BAF 1, Porifera msp. 14 at BAF 2, and H. glacialis at BAF 3 (Table 3.3). Regionally, Aglaopheniidae msp. 3 dominated LAB (2.9 ± 2.6%) whereas H. glacialis dominated BAF (6.4 ± 0.4%).

3.4.2.2.3 Species diversity

Morphospecies diversity differed significantly across regions for both abundance and coverage ($p < 0.001$), with higher diversity for LAB than for BAF (Table 3.1). The highest

Shannon diversity on a single dropstone was at LAB 1-2 (H' = 2.65) and the lowest was LAB 1-3 (H' = 0.79). At the site scale, LAB 3 had the highest Shannon diversity (H' = 2.33 ± 0.14) and LAB 2 the lowest (H' = 1.62) (Table 3.1).

3.4.2.3 Spatial mapping of colonizing species

3.4.2.3.1 Species zonation

Twenty-two morphospecies occurred strictly at the sediment line (~26%) and 31 mspp strictly above it (~36%); none occurred strictly below. Another 33 mspp varied in positioning across dropstones (~38%), including 31 that occurred either above or at the sediment line and two that occurred above, at, or below the sediment (Figure 8). Two morphospecies (*Escharoides* msp. 1 and Schizoporelloidea msp. 1; Supplementary Table 3.6; Figure 8) were consistently located at the sediment line (across three or more dropstones). A colony of Octocorallia msp. 1 occurred highest above the sediment (at the apex of an exposed stone 77 mm high; LAB 1-1), followed by three co-occurring morphospecies on the same dropstone: *Primnoa resedaeformis* (60 mm; n = 3), *Paragorgia* cf. *arborea* (60 mm; n = 1), and Aglaopheniidae msp. 2 (36 mm; n = 1) (Supplementary Table 3.7). Conversely, among the morphospecies present on multiple dropstones, Tubuliporidae msp. 1 occurred highest above the sediment at 64.4 mm on LAB 1-1. The two morphospecies below the sediment were Serpulidae msp. 1 (3 mm below on BAF 2-1) and Terebellidae msp. 1 (8 mm below on BAF 3-2). Site-wide analyses revealed that LAB 1 and 2 had the highest number of morphospecies at the sediment line (12 msp; representing 41 and 34% of mspp, respectively), in contrast to the highest number of morphospecies above the sediment line at LAB 2 (25 msp; 69%). The proportional zonation above and at the sediment line was consistent across the two regions: LAB had 43 mspp (68%) positioned above the sediment

line and 20 (32%) at the sediment line, whereas BAF had 27 (69%) above and 12 (31%) at the line (Figure 8).

When examined by growth pattern, encrusting morphospecies occurred higher overall than erect morphospecies; however, regionally, encrusting morphospecies occurred closer to the sediment line in BAF than in LAB, while erect morphospecies remained consistent between regions (Figure 8). Colonial morphospecies occurred higher overall in the BAF region than unitary morphospecies, while both were comparable at LAB. Examined by phylum, cnidarians occurred highest, followed by poriferans, annelids, bryozoans, and then chordates. Regionally, annelids and poriferans occurred higher in LAB than in BAF, while the inverse was true for bryozoans and chordates (Figure 8).

3.4.2.3.2 Relative distance of colonizing species

3.4.2.3.2.1 Intraspecific distance

Overall, the distance between conspecifics of all sessile morphospecies combined was 5.1 ± 12.2 mm (Figure 9). Conversely, 26 mspp were represented by a single individual or colony on at least one dropstone (e.g., no nearest conspecific). Among them, eight morphospecies occurred as a single individual or colony on each dropstone (Tubuliporidae msp. 1, *Sycon* msp. 1, *Iophon piceum*, Demospongiae msp. 2, *Haliclona (Flagellia) xenomorpha*, and Porifera spp. 3, 8, 11). When multiple conspecifics occurred on the same dropstone, 10 mspp consistently maintained distance, whereas 51 mspp did not. Twenty-five morphospecies alternatively exhibited distancing or abutting depending on the dropstone. The colonial tunicate Aplousobranchia msp. 3 yielded the highest distancing on a single dropstone with 105.0 mm (LAB 3-3) and from all conspecifics overall (71.8 ± 46.9 mm; dropstones pooled; Supplementary Table 3.8; Figure 9).

3.4.2.3.2.2 Interspecific distance

Overall, the distance between allospecifics of all sessile morphospecies combined was 1.1 ± 2.5 mm (Figure 9). Seven mspp maintained distance from all allospecifics, in contrast to 59 mspp that consistently abutted multiple allospecifics. Conversely, 20 mspp either distanced from or abutted allospecifics at different occurrences. Annelida msp. 1 yielded the highest distancing from allospecifics on an individual dropstone (19.0 mm; on BAF 2-3); however, the highest distancing overall from all allospecifics occurred in Aglaopheniidae msp. 2 at 17.6 ± 5.4 mm (dropstones pooled; Supplementary Table 3.9; Figure 9).

3.4.2.4 Secondary colonization and epibiosis

3.4.2.4.1 Secondary colonization

In total, 83 mspp were involved in secondary colonization as either host or colonizer, with a total of 204 cases documented (Supplementary Table 3.10). Among them, 40 mspp occurred as secondary colonizers (e.g., colonized another individual or colony) that were never themselves colonized by another morphospecies. Alternatively, 14 mspp occurred strictly as host while 29 occurred as both host and secondary colonizer. The most common hosts (primary colonizers directly attached to the dropstones) were two encrusting bryozoans: *Escharoides* msp. 1 hosted 19 mspp (nine poriferans, four bryozoans, three cnidarians, two chordates, and one annelid; Figure 3A) and Electridae msp. 1 hosted 25 (11 poriferans, five cnidarians, five bryozoans, two annelids, and two chordates). Only two mspp colonized dead conspecifics with new growth. Eleven mspp used a heavily damaged dead *Primnoa resedaeformis* (Figure 3C) as substratum, including colonial hydrozoans, bryozoans, and poriferans (Figure 3C). The most common secondary colonizer was the tunicate Aplousobranchia msp. 1, with 20 occurrences on

12 hosts (e.g., *Escharoides* msp. 1; Figure 3E). All other secondary colonizers (n = 49 mspp) had ≤12 occurrences on ≤10 hosts (Supplementary Table 3.10).

3.4.2.4.2 Epibiosis

We observed a total of 14 epibionts across all dropstones, occurring on 18 hosts (Supplementary Table 3.10). Sessile epibionts included the colonial hydrozoan Campanulariidae msp. 3 growing on the hydrocaulus of the colonial hydrozoan Aglaopheniidae msp. 2 (Figure 3C), and the stalked crinoid Crinoidea msp. 1 on the cuticle of the erect bryozoan Crisiidae msp. 1 (Figure 3C). Some secondary colonizers (above) also occurred as epibionts: three sessile mspp (Aglaopheniidae msp. 3, Spinularia cf. sarsii, Porifera msp. 6) occurred on a chiton grazing on primary colonizers in the exposed zone (Polyplacophora msp. 1; Figure 3H), and five others (Annelida msp. 1, *Escharoides* msp. 1, *Haliclona (Flagellia) xenomorpha*, Aplousobranchia msp. 1, 3) colonized the external surface of serpulid worm tubes in the exposed zone (Serpulidae msp. 1) (Figure 3F). However, most epibionts were motile morphospecies, and predominately arthropods. The amphipod Caprellidae msp. 1 was the most common, occurring seven times overall, across five mspp of erect and sessile hydrozoans and bryozoans (Figure 3G). Two other amphipods (Amphipoda msp. 1 and 2) occurred in the canopy of the colonial hydrozoan Aglaopheniidae msp. 3 and at the base of *Haliclona (Flagellia) xenomorpha*, respectively (Figure 3C). Finally, Isopoda msp. 1 occurred in the canopy of three sessile erect mspp: Crisiidae msp. 1, Aglaopheniidae msp. 3, and Philodoporidae msp. 1 (Figure 3G). A crinoid (Heliometria glacialis; Figure 2C) and ophiuroids (Ophiuroidea msp. 1; Figure 3I) occurred on top of numerous encrusting sessile morphospecies including one hydrozoan, four bryozoans, four poriferans, and an annelid (Supplementary Table 3.10). One gastropod (Gastropoda msp. 1) occurred on a poriferan (*Cladorhiza* msp. 1) (Figure 3H; Supplementary Table 3.10).

3.5 Discussion

The dropstones that we examined from the Labrador Sea and Baffin Bay of the Northwest Atlantic and the Eastern Canadian Arctic during this study might be considered small-scale biodiversity hotspots of epibenthic macro- and megafauna in the bathyal environments. The presence of slow-growing deep-sea corals – including the genus *Primnoa* – and extensive erect bryozoan colonies suggests that communities on these dropstones have been established for decades or more. Most dropstone surfaces were completely covered by dozens of morphospecies spanning 10 phyla. Despite the diversity of morphospecies with different lifestyles, from sessile to motile and from encrusting to erect, spatial colonizing trends were apparent on the surface of the dropstones, with some evidence of ecological (intra- and interspecific) relationships suggestive of competition or tolerance interplays. The dropstones also showed evidence of successive colonisations and incidences of epibiosis, emphasizing that their communities were long-established but nonetheless in flux.

3.5.1 Richness, abundance, coverage, and diversity of colonizing species

Visual analyses of ROV footage in both Labrador and Baffin Bay suggested higher diversity of epibenthic megafauna on dropstones than on the surrounding substrata, whether fine-grained mud or coarse gravel. This observation confirmed the few previous studies conducted in other basins that described dropstone communities as unique and more diverse than their surroundings (Syvitski et al. 1989; Schulz et al. 2010; Meyer et al. 2016; Ziegler et al. 2017). Previous studies also documented functionally similar isolated biogenic substrata such as glass sponge stalks (Beaulieu 2001a, b; Dunham et al. 2018) and polymetallic nodules (Mullineaux 1987; Veillette et al. 2007; Amon et al. 2016). Higher richness could result from dropstones providing a raised environment above the mud or gravel and a strong anchor, potentially

increasing exposure to flow and thereby access to food. The dominance of suspension-feeding and filter-feeding taxa such as bryozoans, poriferans, and cnidarians supports this interpretation.

The in-situ images hinted also at regional differences, which was later confirmed through finer analysis of collected dropstones. Differences between these two regions have been reported previously in megabenthic surveys of the Labrador Sea (Roy et al. 2015) and Baffin Bay (Rangeley et al. 2022), which found differing key species making up overall assemblages, more specifically among sponges (Curtis et al. 2020). Individual dropstones varied widely in richness, abundance, coverage, and diversity but, overall, these metrics were higher in the Labrador Sea than Baffin Bay, possibly the result of more diverse reproductive populations nearby. Accordingly, two sites in the Labrador Sea (LAB 1 and 2) were located near a known coral hotspot (Cramm et al. 2021), with colonies observed along both transects, and *Primnoa resedaeformis* directly recorded on a dropstone at LAB 1. Soft corals (either capnellid or alcyoniid malacalcyonaceans, formerly grouped as nephtheids) were also observed and found on three dropstones in the LAB transects. This could be consistent with larval dispersal from nearby stones, as malacalcyonaceans have short larval durations and a preference for settling on hard substrata (Sun et al. 2010; 2011), and it is known that nearness to larval supply increases richness on hard substrata in the deep sea (Meyer et al. 2016; Lacharité and Metaxas 2013). More generally, the regional difference may also relate to the latitudinal gradient of ~12°, with the dropstones from the Labrador Sea hosting ~36% more morphospecies than those from Baffin Bay. This aligns with the review by Canning-Clode (2009) showing lower species richness at higher latitudes for most taxa, as well as with finer-scale studies demonstrating that deep-sea communities associated with biogenic substrata decreased in diversity with latitude (Baillon et al. 2014).

The two geographic regions shared only about 20% of morphospecies on the dropstones, which suggests that environmental barriers could also be a factor. Morphospecies assemblages potentially clustered by depth limits; based on benthic grab samples from Baffin Island fjords, Syvitski et al. (1989) inferred that species assemblages were comparable at similar depths between ~200 and 800 m. However, though surface water circulates between the Labrador Sea and Baffin Bay, deep-water masses do not pass through the Davis Strait (connecting the two regions; see Figure 1) because of sill depths not exceeding 700 m, thus maintaining separation (Tang et al. 2004). Archambault et al. (2010) placed Northern Labrador in the Cold Temperate Northwest Atlantic province, with close linkage to other regions such as the Gulf of St. Lawrence and Grand Banks, in contrast to Baffin Bay located in the Canadian Arctic Archipelago approximately 650 km to the north. The same authors mentioned that more species have been described in Labrador than Baffin Bay and than in the Arctic in general (Archambault et al. 2010). Sill depth presumably prevents deep-water larval transport, exchange and recruitment across the two regions.

The dropstones from the Labrador Sea were also collected 200–500 m deeper than those from Baffin Bay, suggesting a potential link between diversity and depth; however, previous studies have reported a negative diversity-depth relationship (Rex 2010; Yasuhara et al. 2012; Baillon et al. 2014; Saeedi et al. 2019; Denisenko and Blicher 2021). Nevertheless, two phyla did align with these studies: higher morphospecies richness of Bryozoa and Echinodermata occurred on dropstones from the shallower sites (i.e., in BAF), where encrusting sessile morphospecies also dominated over erect forms, likely driven by the high number of encrusting bryozoans. This decrease in bryozoan richness with depth is consistent with other polar studies (Denisenko and Blicher 2021; Micael et al. 2022). Moreover, echinoderms have been found to cluster at different

depths in Central Arctic waters at comparable depths to BAF 2 here (~ 400 – 600 m; Vedenin et al. 2021). An interplay of broad influential factors was proposed by Meyer-Kaiser et al. (2022) who reported that species-specific recruitment, while limited to propagules within water masses, was confounded by depth and temperature in cnidarians, bryozoans, molluscs, annelids, and arthropods.

Within sites, multiple factors could contribute to variability in richness, abundance, diversity, and in surface coverage, including dropstone height, surface area, and texture, as well as surrounding environment (current speed, sedimentation rate, slope, depth, and remoteness from other hard substrata). All have been suggested as contributing factors to colonization and recruitment of hard substrata in the deep sea (Genin et al. 1986; Mullineaux 1987; Centurión and López Gappa 2011; Meyer et al. 2016; Ziegler et al. 2017). The dropstone with the highest richness (31 mspp) was also one with the largest surface exposed (90%). It also had a more complex surface texture than most other dropstones, with a rougher and more uneven surface that potentially provided more microhabitats for recruitment. This observation aligns with Meyer et al. (2016) who attributed higher richness on larger dropstones to greater surface available for colonizers, better access to food, and slower sedimentation than on smaller dropstones. Further, small-scale hydrodynamic fluctuations created by complex surfaces appears to increase larval recruitment in some deep-sea corals (Lacharité and Metaxas 2013). Here, higher currents characterized the site from which this dropstone came. Inversely, the other dropstone from the Labrador Sea with similar richness (30 mspp) did not have a comparable percentage of surface exposed and came from a site with weaker currents. However, unlike the other Labrador Sea sites, a steep slope and fine mud characterized this site. The finer-grained surroundings suggest

that fewer alternative recruitment locations for larvae requiring hard bottoms were available, so any dropstone could act as an island.

3.5.2 Zonation of colonizing species

The zonation patterns of given morphospecies on dropstones collected from the Labrador Sea and Baffin Bay were comparable across the regions, suggesting conservation of the fundamental requirements for settlement and recruitment. Taxa that occurred highest included octocorals, colonial hydrozoans, poriferans, and some bryozoans; conversely, tube-dwelling annelids were the only taxa present below the sediment line. Suspension feeders, the most common taxa on the dropstones, likely sought out or succeeded better in higher positions, which could improve their access to food. This assumption aligns with previous studies of functional groupings on polymetallic nodules (Mullineaux 1988, 1989) and positioning of larval recruits in the Fram Strait (western Svalbard, Norway; Meyer-Kaiser et al. 2019).

Erect forms in the present study generally occurred higher on the dropstones than encrusting forms. Age of the dropstone communities potentially obfuscated this pattern, in that encrusting colonies perhaps expanded down over time to the stone-sediment boundary post recruitment. Roughly a third of morphospecies showed no zonation pattern and positioned themselves above, at, or (rarely) below the stone-sediment boundary on different dropstones. Low repetition of morphospecies across different dropstones prevented any determination of whether all morphospecies positioned themselves similarly across different dropstones, but the most common morphospecies (encrusting cheilostomatid bryozoans) showed consistent positioning at the sediment line. Colonies that extended across large portions of dropstone surface overall occurred most often at the sediment line, potentially enabled by the zooids further away from the sediment (i.e., with better access to food), sharing nutrients with the rest of the

colony positioned lower. Kukliński and Bader (2007) similarly reported domination by encrusting bryozoans on shallower dropstones from depths of ~75–250 m off the NE Greenland shelf, and that all species typically favoured the top of the dropstone, presumably to access the limited amount of suspended food reaching those depths more easily. Conversely, Barnes et al. (1996) found that bryozoans colonized the sides rather than the top of stones from shallow waters (i.e., intertidal down to 42 m) whenever sediment deposition was higher. Given that sedimentation was visible on the top surfaces of several dropstones in the present study, it may also have been a driver.

3.5.3 Relative distancing of colonizing species

Ecological interactions at the intra- and interspecific levels appear to influence the presence and positioning of taxa on dropstones. Several morphospecies occurred as solitary individuals or colonies across multiple dropstones, suggesting that they might exclude conspecific competitors attempting to establish on the same dropstone. Other morphospecies maintained an exclusion zone for conspecifics but did not exclude them entirely from the same dropstone. Interference or exploitative competition between conspecifics was found in numerous benthic hard-bottom species (reviewed in Molis and da Gama 2009). In particular, the present findings align with intraspecific exclusion reported by Ayre and Grosberg (2005) in a clonal sea anemone (Anthopleura elegantissima), which exhibits distinct gaps between unrelated clonal aggregates. Conversely, some morphospecies appeared to be gregarious on dropstones. In particular, multiple conspecifics of the erect bryozoan Crisiidae msp. 1 always occurred on the same dropstone, usually in direct contact, and several juveniles (primary polyps) occurred under the only large colony of *Primnoa resedaeformis* observed. This pattern suggests that rather than excluding conspecifics, both Crisiidae sp.1 and P. resedaeformis may facilitate conspecific

recruitment, perhaps for kin selection as seen in cyprid barnacle larvae (Knight-Jones 1953; Knight-Jones and Crisp 1953).

Allospecific distances were much shorter than conspecific distances, and allospecific potential interactions more complex, given that overlaps were sometimes detected. Potentially, higher competition for resources occurs between individuals or colonies of the same morphospecies rather than those of other morphospecies that may fill a slightly different trophic niche. Though lower, some interspecific exclusion did appear to occur. For example, on a dropstone with a large actiniarian occupying the highest point and all other morphospecies positioned closer to the sediment. Adjacent growth suggests tolerance or equal competitive ability between allospecifics, whereas overgrowth of one by the other may indicate a superior competitor (Jackson 1977). Bryozoans, hydrozoans, and poriferans all engaged in adjacent growth and overgrowth of each other, suggesting stratified competitive abilities for the limited space and resources on the dropstones. Severe, hierarchical competition between bryozoan species on cobbles and pebbles at shallower depths has been shown to be characterized by overgrowth of weaker competitors by stronger competitors (Barnes and Kukliński 2003; Centurión and López Gappa 2011). However, because overgrowth typically results in the death of the individual or colony beneath, the nature of the present study as a snapshot in time could obfuscate competitive overgrowth with secondary colonization of a dead primary colonizer. Clearly, interference or tolerance of conspecifics and allospecifics influences zonation patterns on dropstones, in that an initial recruit either deters subsequent recruits or shifts their vertical positioning relative to the sediment.

3.5.4 Ecological succession including epibiosis and secondary colonization

Interspecific interactions among dropstone communities included evidence of succession through secondary colonization of a dead primary recruit and epibionts supported by a live basibiont. Cnidarians and poriferans (corals and sponges) on the dropstones both displayed secondary colonizers and epibionts, which is not surprising given that they are among the best-documented basibionts on hard substrata of any type (Beaulieu 2001a,b; Metaxas and Davis 2005; Miller et al. 2012; Baillon et al. 2014; Dunham et al. 2018; Pierrejean et al. 2020). However, corals and sponges were just a small fraction of the dropstone-associated biodiversity engaged in these interactions; bryozoans, foraminifers, annelids, molluscs, hydrozoans, and actiniarians were also secondary or primary colonizers and epi- or basibionts. Epibiosis predominately involved motile morphospecies such as amphipods and isopods on sessile hydrozoans and bryozoans; ophiuroids and crinoids using poriferans, ascidians, and bryozoans as anchors; and free-living polychaetes, pycnogonids, and molluscs using sessile morphospecies as habitat and shelter. Conversely, several poriferans and hydrozoans also occupied the shell of a chiton. The ubiquity of these interactions suggests that interspecific relationships drive much of community succession on deep-sea hard substrata; this has been reported previously as potentially obligate epibiotic relationships through regular co-occurrences of certain species (Meyer et al. 2016).

Dead portions of two encrusting bryozoans which also exhibited high surface coverage overall (*Escharoides* msp. 1 and Electridae msp. 1) were a dominant substratum for secondary colonizers, as were large dead coral skeletons (P. resedaeformis). Previous Arctic shallow-water studies reported that some hydrozoans preferentially recruit to bryozoan hosts over primary substrata such as stone or kelp (Voronkov et al. 2010; Ronowicz et al. 2013a,b) and biogenic

structures such as dead corals provide an important source of novel hard substrata for community formation (Beaulieu 2001b; Dunham et al. 2018). In particular, Kukliński (2009) noted that some encrusting bryozoans in shallow-water epilithic communities engaged in over 100 interspecific interactions, such as secondary colonization by other species. In the present study, colonized dead coral skeletons on opposing sides of dropstones also suggests that hydrodynamics (or other disturbances) can move or rotate a dropstone entirely, such that the colonization of these hard substrata could go on continually. This conclusion aligns with Tunnicliffe and Syvitski (1983) who calculated, from observations in manned submersible dives off British Columbia (Canada), that drag forces applied to large gorgonian coral fans could move boulders in high-flow currents. ROV footage obtained outside of the site transects in the present study documented tilting of dropstones, with large coral colonies laying flat on the soft sediment and bare portions of stone exposed on the opposing side. Such movement could be an important process that makes novel hard substrata available in the deep sea, where disruption of previously colonized surfaces would allow early successional species to maintain populations.

The snapshot nature of this study limits inferences on whether epibiotic relationships advance to secondary colonization as defined here by destabilizing and ending in the death of the basibiont/primary colonizer. The advanced state of deterioration in one dead P. resedaeformis suggests that colonization occurred after death; however, less clear are bryozoans with sections of the colony still living. If the portion of the colony died and was colonized afterwards, the unprotected biogenic materials would emerge as a sought-after substratum for many recruits. However, sedimentation was apparent on the top surfaces of several dropstones and between layers of bryozoan overgrowth, and a cleared patch of dropstone surface occurred beneath a predatory chiton, suggesting these disruptors are potential factors in structuring deep-sea

dropstone communities. Previous studies flag both sedimentation and predation in other regions of the deep sea where more common disruptions (i.e., strong tides and erosion) are absent (McGuinness 1987; Lacharité and Metaxas 2013; Meyer et al. 2016).

Overall, the present results suggest that the community assemblages on dropstones collected from sites within a geographic region are more similar than those collected across distant geographic regions, and that species exhibit species-specific but consistent patterns of zonation. Confounding factors beyond the environment influence both, i.e., interactions between conspecifics and allospecifics affect colonization patterns and biodiversity. Whether they supersede zonation patterns or the influence of regional environmental factors remains unclear, calling for further fine-scale studies across isolated deep-sea hard substrata such as dropstones and polymetallic nodules.

3.6 Conclusions

In this study, we found that higher epifaunal richness and more erect-growth forms occurred on dropstones sampled at lower latitudes and shallower depths, while dropstones from higher latitudes and deeper depths generally exhibited lower richness and more encrusting growth forms. The zonation patterns were taxon-specific, and colonization predominately occurred on the exposed surfaces of dropstones. Certain taxa occurred singly and others in dense aggregates. Overall, distance was greater within than among colonizing morphospecies and a small number of host taxa acted as substratum for a high number of secondary colonizers, highlighting the dynamic state of the dropstone communities. Our results suggest that environmental and ecological factors such as region, depth, and intra-and interspecific interactions influence species richness, composition, and zonation, likely in combination with local hydrodynamics, larval supply, and fine substratum characteristics. Our study provides

foundation knowledge of epifaunal assemblages growing on isolated hard substrata of exogenous origin, which are locally abundant in the deep sea of the Northwestern Atlantic and Canadian Arctic.

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3.8 References

Amon DJ, Ziegler AF, Dahlgren TG, Glover AG, Goineau A, Gooday AJ, Wiklund H, Smith CR. 2016. Insights into the abundance and diversity of abyssal megafauna in a polymetallic-nodule region in the eastern Clarion-Clipperton Zone. Sci Rep. 6:30492. doi:10.1038/srep30492.

Archambault P, Snelgrove PVR, Fisher JAD, Gagnon J-M, Garbary DJ, Harvey M, Kenchington EL, Lesage V, Levesque M, Lovejoy C, et al. 2010. From sea to sea: Canada's three oceans of biodiversity. PLOS One. 5(8):e12182. doi:10.1371/journal.pone.0012182.

Ayre DJ, Grosberg RK. 2005. Behind anemone lines: factors affecting division of labour in the social cnidarian Anthopleura elegantissima. Anim Behav. 70(1):97–110. doi:10.1016/j.anbehav.2004.08.022.

Baillon S, Hamel J-F, Mercier A. 2014. Diversity, distribution and nature of faunal associations with deep-sea pennatulacean corals in the Northwest Atlantic. PLOS One. 9(11):e111519. doi:10.1371/journal.pone.0111519.

Barnes DKA, Rothery P, Clarke A. 1996. Colonisation and development in encrusting communities from the Antarctic intertidal and sublittoral. J Exp Mar Biol Ecol. 196(1):251–265. doi:10.1016/0022-0981(95)00132-8.

Barnes DKA, Kukliński P. 2003. High polar spatial competition: extreme hierarchies at extreme latitude. Mar Ecol Prog Ser. 259:17–28. doi:10.3354/meps259017.

Beaulieu S. E. 2001. Life on glass houses: sponge stalk communities in the deep sea. Mar Biol. 138(4):803–817.

Beaulieu Stace E. 2001. Colonization of habitat islands in the deep sea: recruitment to glass sponge stalks. Deep Sea Res Part I: Oceanogr Res Pap. 48(4):1121–1137. doi:10.1016/S0967-0637(00)00055-8.

Bennett MR, Doyle P, Mather AE. 1996. Dropstones: their origin and significance. Palaeogeogr Palaeoclimatol Palaeoecol. 121(3):331–339. doi:10.1016/0031-0182(95)00071-2.

Buhl-Mortensen L, Buhl-Mortensen P. 2018. Cold Temperate Coral Habitats. In: Corals in a Changing World. IntechOpen. https://www.intechopen.com/chapters/58875.

Canning-Clode J. 2009. Latitudinal patterns of species richness in hard-bottom communities. In: Wahl M, editor. Marine Hard Bottom Communities: Patterns, Dynamics, Diversity, and Change. Berlin, Heidelberg: Springer. (Ecological Studies). p. 81–87. https://doi.org/10.1007/b76710_5.

Centurión R, López Gappa J. 2011. Bryozoan assemblages on hard substrata: species abundance distribution and competition for space. Hydrobiologia. 658(1):329–341. doi:10.1007/s10750-010-0503-5.

Clarke K, Gorley R, Somerfield P, Warwick R. 2014. Change in Marine Communities: An Approach to Statistical Analysis.

Curtis D, Xinyue Z, Edinger E, Leys SP. 2020. Sponge communities in the eastern Canadian Arctic: species richness, diversity and density determined using targeted benthic sampling and underwater video analysis. Polar Biol. 43(9):1287–1305. doi:10.1007/s00300-020-02709-z.

Dalton AS, Margold M, Stokes CR, Tarasov L, Dyke AS, Adams RS, Allard S, Arends HE, Atkinson N, Attig JW, et al. 2020. An updated radiocarbon-based ice margin chronology

for the last deglaciation of the North American Ice Sheet Complex. Quat Sci Rev. 234:106223. doi:10.1016/j.quascirev.2020.106223.

Davis AR. 2009. The role of mineral, living and artificial substrata in the development of subtidal assemblages. In: Wahl M, editor. Marine Hard Bottom Communities: Patterns, Dynamics, Diversity, and Change. Berlin, Heidelberg: Springer. (Ecological Studies). p. 19–37. https://doi.org/10.1007/b76710_2.

Denisenko NV, Blicher ME. 2021. Bryozoan diversity, biogeographic patterns and distribution in Greenland waters. Mar Biodivers. 51(5):73. doi:10.1007/s12526-021-01213-9.

Desmarais A, Merzouk A, Forest A. 2021. 2021 Expedition Report. Amundsen Science Amundsen Science Expedition Reports Report No.: 1. https://amundsenscience.com/expeditions/2021-expedition/

Dunham A, Archer SK, Davies SC, Burke LA, Mossman J, Pegg JR, Archer E. 2018. Assessing condition and ecological role of deep-water biogenic habitats: Glass sponge reefs in the Salish Sea. Mar Environ Res. 141:88–99. doi:10.1016/j.marenvres.2018.08.002.

Edinger EN, Sherwood OA, Piper DJW, Wareham VE, Baker KD, Gilkinson KD, Scott DB. 2011. Geological features supporting deep-sea coral habitat in Atlantic Canada. Cont Shelf Res. 31(2, Supplement):S69–S84. doi:10.1016/j.csr.2010.07.004.

Genin A, Dayton PK, Lonsdale PF, Spiess FN. 1986. Corals on seamount peaks provide evidence of current acceleration over deep-sea topography. Nature. 322(6074):59–61. doi:10.1038/322059a0.

Grischenko A, Gordon D, Melnik V. 2018. Bryozoa (Cyclostomata and Ctenostomata) from polymetallic nodules in the Russian exploration area, Clarion-Clipperton Fracture Zone,

eastern Pacific Ocean – taxon novelty and implications of mining. Zootaxa. 4484(1). doi:10.11646/zootaxa.4484.1.1. https://pubmed.ncbi.nlm.nih.gov/30313774/.

Guy G, Metaxas A. 2022. Recruitment of deep-water corals and sponges in the Northwest Atlantic Ocean: implications for habitat distribution and population connectivity. Mar Biol. 169(8):107. doi:10.1007/s00227-022-04089-w.

Jackson JBC. 1977. Competition on Marine Hard Substrata: The Adaptive Significance of Solitary and Colonial Strategies. Am Nat. 111(980):743–767.

Jenkins SR, Marshall D, Fraschetti S. 2009. Settlement and recruitment. In: Wahl M, editor. Marine Hard Bottom Communities: Patterns, Dynamics, Diversity, and Change. Berlin, Heidelberg: Springer. (Ecological Studies). p. 177–190. https://doi.org/10.1007/b76710_12.

Johnson CH, Woollacott RM. 2010. Larval settlement preference maximizes genetic mixing in an inbreeding population of a simultaneous hermaphrodite (Bugula stolonifera, Bryozoa). Mol Ecol. 19(24):5511–5520. doi:10.1111/j.1365-294X.2010.04887.x.

Kluge GA. 1975. Bryozoa of the northern seas of the USSR. New Delhi: Amerind Pub. Company (TT 72-52010).

Knight-Jones EW. 1953. Laboratory Experiments on gregariousness during setting in Balanus balanoides and other barnacles. J Exp Biol. 30(4):584–598. doi:10.1242/jeb.30.4.584.

Knight-Jones EW, Crisp DJ. 1953. Gregariousness in barnacles in relation to the fouling of ships and to anti-fouling research. Nature. 171(4364):1109–1110. doi:10.1038/1711109a0.

Kukliński P. 2009. Ecology of stone-encrusting organisms in the Greenland Sea—a review. Polar Res. 28(2):222–237. doi:10.1111/j.1751-8369.2009.00105.x.

Kukliński P, Bader B. 2007. Diversity, structure and interactions of encrusting lithophyllic macrofaunal assemblages from Belgica Bank, East Greenland. Polar Biol. 30(6):709–717. doi:10.1007/s00300-006-0228-0.

Kukliński P, Taylor PD, Denisenko N. 2007. Arctic cheilostome bryozoan species of the genus *Escharoides*. J Nat Hist. 41(1–4):219–228. doi:10.1080/00222930601162878.

Lacharité M, Metaxas A. 2013. Early life history of deep-water gorgonian corals may limit their abundance. PLOS One. 8(6):e65394–e65394. doi:10.1371/journal.pone.0065394.

Ma KC, Deibel D, Law KK, Aoki M, McKenzie CH, Palomares ML. 2017. Richness and zoogeography of ascidians (Tunicata: Ascidiacea) in eastern Canada. Can J Zool. 95(1):51–59. doi:10.1139/cjz-2016-0087.

McGuinness KA. 1987. Disturbance and organisms on boulders. ii. causes of patterns in diversity and abundance. Oecologia. 71(3):420–430.

Metaxas A, Davis J. 2005. Megafauna associated with assemblages of deep-water gorgonian corals in Northeast Channel, off Nova Scotia, Canada. J Mar Biol Assoc UK. 85(6):1381–1390. doi:10.1017/S0025315405012567.

Meyer KS, Young CM, Sweetman AK, Taylor J, Soltwedel T, Bergmann M. 2016. Rocky islands in a sea of mud: biotic and abiotic factors structuring deep-sea dropstone communities. Mar Ecol Prog Ser. 556:45–57. doi:10.3354/meps11822.

Meyer-Kaiser K, Bergmann M, Soltwedel T, Klages M. 2019. Recruitment of Arctic deep-sea invertebrates: Results from a long-term hard-substrate colonization experiment at the Long-Term Ecological Research observatory HAUSGARTEN. Limnol Oceanogr. 64(5):1924–1938. doi:10.1002/lno.11160.

Meyer-Kaiser KS, Schrage KR, von Appen W-J, Hoppmann M, Lochthofen N, Sundfjord A, Soltwedel T. 2022. Larval dispersal and recruitment of benthic invertebrates in the Arctic Ocean. Prog Oceanogr. 203:102776. doi:10.1016/j.pocean.2022.102776.

Micael J, Denisenko NV, Gíslason S, Guðmundsson G, Kukliński P, Rodrigues P. 2022. Diversity of Bryozoa in Iceland. Polar Biol. 45(8):1391–1402. doi:10.1007/s00300-022-03078-5.

Miller RJ, Hocevar J, Stone RP, Fedorov DV. 2012. Structure-forming corals and sponges and their use as fish habitat in Bering Sea submarine canyons. PLOS One. 7(3):e33885. doi:10.1371/journal.pone.0033885.

Molis M, da Gama BAP. 2009. Simple and complex interactions. In: Wahl M, editor. Marine Hard Bottom Communities: Patterns, Dynamics, Diversity, and Change. Berlin, Heidelberg: Springer. (Ecological Studies). p. 225–237. [accessed 2021 Oct 16]. https://doi.org/10.1007/b76710_16.

Mullineaux LS. 1987. Organisms living on manganese nodules and crusts: distribution and abundance at three North Pacific sites. Deep Sea Res Part I: Oceanogr Res Pap. 34(2):165–184. doi:10.1016/0198-0149(87)90080-X.

Mullineaux LS. 1988. The role of settlement in structuring a hard-substratum community in the deep sea. J Exp Mar Biol Ecol. 120(3):247–261. doi:10.1016/0022-0981(88)90005-6.

Mullineaux LS. 1989. Vertical distributions of the epifauna on manganese nodules: implications for settlement and feeding. Limnol Oceanogr. 34(7):1247–1262.

Pierrejean M, Grant C, de Moura Neves B, Chaillou G, Edinger E, Blanchet FG, Maps F, Nozais C, Archambault P. 2020. Influence of deep-water corals and sponge gardens on infaunal

community composition and ecosystem functioning in the Eastern Canadian Arctic. Front Mar Sci. 7.

Pollock LW. 1998. A practical guide to the marine animals of northeastern North America. New Brunswick, N.J: Rutgers University Press.

Powell NA. 1968. Bryozoa (Polyzoa) of Arctic Canada. Can J Fish Aquat Sci. 25(11):2269–2320. doi:10.1139/f68-202.

Rangeley R, de Moura Neves B, Campanyà-Llovet N, Denniston M, Laing R, Anthony K, McCarney P, McIver R, Whyte J, Vance A, et al. 2022. Megabenthic biodiversity in culturally and ecologically important coastal regions of Northern Labrador. Ecol Soc. 27(4):47-. doi:10.5751/ES-13637-270447.

Rex MA. 2010. Deep-sea biodiversity: pattern and scale. Cambridge, Mass: Harvard University Press.

Roberts JM, Wheeler A, Freiwald A, Cairns S. 2009. Habitats and ecology. In: Cold-Water Corals: The Biology and Geology of Deep-Sea Coral Habitats. Cambridge University Press. p. 142–174.

da Rocha RM, Zanata TB, Moreno TR. 2012. Keys for the identification of families and genera of Atlantic shallow water ascidians/Chaves de identificação de famílias e gêneros de ascídias de águas rasas no Atlântico. Biota Neotrop. 12(1):269–303.

Ronowicz M, Włodarska-Kowalczuk M, Kukliński P. 2013a. Hydroid epifaunal communities in Arctic coastal waters (Svalbard): effects of substrate characteristics. Polar Biol. 36(5):705–718. doi:10.1007/s00300-013-1297-5.

Ronowicz M, Włodarska-Kowalczuk M, Kukliński P. 2013b. Depth- and substrate-related patterns of species richness and distribution of hydroids (Cnidaria, Hydrozoa) in Arctic coastal waters (Svalbard). Mar Ecol. 34(s1):165–176. doi:10.1111/maec.12034.

Roy V, Iken K, Archambault P. 2015. Regional variability of megabenthic community structure across the Canadian Arctic. Arctic. 68(2):180–192. doi:10.14430/arctic4486.

Ryland JS, Sykes AM. 1972. The analysis of pattern in communities of Bryozoa. I. Discrete sampling methods. J Exp Mar Biol Ecol. 8(3):277–297. doi:10.1016/0022-0981(72)90067-6.

Saeedi H, Costello MJ, Warren D, Brandt A. 2019. Latitudinal and bathymetrical species richness patterns in the NW Pacific and adjacent Arctic Ocean. Sci Rep. 9:1–10. doi:10.1038/s41598-019-45813-9.

Schulz M, Bergmann M, von Juterzenka K, Soltwedel T. 2010. Colonisation of hard substrata along a channel system in the deep Greenland Sea. Polar Biol. 33(10):1359–1369. doi:10.1007/s00300-010-0825-9.

Shannon CE. 1948. A mathematical theory of communication. Bell Syst Tech J. 27(3):379–423. doi:10.1002/j.1538-7305.1948.tb01338.x.

Sun Z, Hamel J-F, Mercier A. 2010. Planulation periodicity, settlement preferences and growth of two deep-sea octocorals from the northwest Atlantic. Mar Ecol Prog Ser. 410:71–87. doi:10.3354/meps08637.

Sun Z, Hamel J-F, Mercier A. 2011. Planulation, larval biology, and early growth of the deep-sea soft corals Gersemia fruticosa and Duva florida (Octocorallia: Alcyonacea). Invertebr Biol. 130(2):91–99. doi:10.1111/j.1744-7410.2011.00229.x.

Syvitski JPM, Farrow GE, Atkinson RJA, Moore PG, Andrews JT. 1989. Baffin Island fjord macrobenthos: bottom communities and environmental significance. Arctic. 42(3):232–247.

Tang CCL, Ross CK, Yao T, Petrie B, DeTracey BM, Dunlap E. 2004. The circulation, water masses and sea-ice of Baffin Bay. Prog Oceanogr. 63(4):183–228. doi:10.1016/j.pocean.2004.09.005.

Tunnicliffe V, Syvitski JPM. 1983. Corals move boulders: An unusual mechanism of sediment transport. Limnol Oceanogr. 28(3):564–568. doi:10.4319/lo.1983.28.3.0564.

Vedenin A, Galkin S, Mironov AN, Gebruk A. 2021. Vertical zonation of the Siberian Arctic benthos: bathymetric boundaries from coastal shoals to deep-sea Central Arctic. PeerJ San Franc CA. 9:e11640–e11640. doi:10.7717/peerj.11640.

Veillette J, Juniper SK, Gooday AJ, Sarrazin J. 2007. Influence of surface texture and microhabitat heterogeneity in structuring nodule faunal communities. Deep Sea Res Part I: Oceanogr Res Pap. 54(11):1936–1943. doi:10.1016/j.dsr.2007.06.012.

Vogt J, Risk D, Bourlon E, Azetsu-Scott K, Edinger E, Sherwood O. 2023. Sea–air methane flux estimates derived from marine surface observations and instantaneous atmospheric measurements in the northern Labrador Sea and Baffin Bay. Biogeosciences. 20:1773–1787. doi:10.5194/bg-20-1773-2023.

Voronkov A, Stepanjants SD, Hop H. 2010. Hydrozoan diversity on hard bottom in Kongsfjorden, Svalbard. J Mar Biol Assoc UK. 90(7):1337–1352. doi:10.1017/S0025315409991573.

Yasuhara M, Hunt G, van Dijken G, Arrigo KR, Cronin TM, Wollenburg JE. 2012. Patterns and controlling factors of species diversity in the Arctic Ocean. J Biogeogr. 39(11):2081–2088.

Ziegler AF, Smith CR, Edwards KF, Vernet M. 2017. Glacial dropstones: islands enhancing seafloor species richness of benthic megafauna in West Antarctic Peninsula fjords. Mar Ecol Prog Ser. 583:1–14. doi:10.3354/meps12363.

3.9 Tables

Table 3.1 Coarse assessment of richness and total abundance (morphospecies pooled) determined for the dropstones and the sediment immediately surrounding them, using in-situ images taken with the remotely operated vehicle (ROV). More precise richness, abundance, and Shannon diversity (H') values are also provided for the dropstones that were analyzed post collection at fine-scale (FS) in the laboratory.

Level	Sediment (ROV)		Dropstone (ROV)		Dropstone (FS)		
	Richness	*Abundance*	*Richness*	*Abundance*	*Richness*	*Abundance*	*Diversity (H')*
Global	***0.4 ± 0.2***	***0.4 ± 0.2***	***2.8 ± 0.6***	***6.4 ± 0.9***	***14.9 ± 7.6***	***87.3 ± 82.7***	***1.86 ± 0.17***
LAB	**0.6 ± 0.2**	**0.6 ± 0.2**	**3.2 ± 1.0**	**7.0 ± 4.0**	**20.3 ± 5.1**	**145.9 ± 82.9**	**1.88 ± 0.40**
LAB 1	0.7 ± 0.6	0.7 ± 0.6	4.3 ± 0.6	11.3 ± 0.6	16.0 ± 7.5	180.0 ± 129.1	1.68 ± 0.94
LAB 1-1	*0.0*	*0.0*	*5.0*	*12.0*	*23.0*	*258.0*	*1.59*
LAB 1-2	*1.0*	*1.0*	*4.0*	*11.0*	*17.0*	*31.0*	*2.65*
LAB 1-3	*1.0*	*1.0*	*4.0*	*11.0*	*8.0*	*251.0*	*0.79*
LAB 2	0.3 ± 0.6	0.3 ± 0.6	2.7 ± 0.6	6.3 ± 3.1	26.0 ± 4.4	206.3 ± 64.0	1.61 ± 0.55
LAB 2-1	*0.0*	*0.0*	*3.0*	*3.0*	*23.0*	*265.0*	*1.22*
LAB 2-2	*0.0*	*0.0*	*2.0*	*9.0*	*24.0*	*138.0*	*1.39*
LAB 2-3	*1.0*	*1.0*	*3.0*	*7.0*	*31.0*	*216.0*	*2.24*
LAB 3	0.7 ± 0.6	0.7 ± 0.6	2.7 ± 0.6	3.3 ± 0.6	19.0 ± 8.9	51.3 ± 50.1	2.34 ± 0.14
LAB 3-1	*0.0*	*0.0*	*3.0*	*4.0*	*16.0*	*24.0*	*2.50*
LAB 3-2	*1.0*	*1.0*	*3.0*	*3.0*	*12.0*	*20.0*	*2.22*
LAB 3-3	*1.0*	*1.0*	*2.0*	*3.0*	*29.0*	*110.0*	*2.28*
BAF	**0.3 ± 0.3**	**0.3 ± 0.3**	**2.3 ± 0.6**	**5.8 ± 3.8**	**9.6 ± 2.8**	**28.9 ± 18.8**	**1.85 ± 0.16**
BAF 1	0.0 ± 0.0	0.0 ± 0.0	2.0 ± 0.0	2.7 ± 0.6	6.7 ± 0.6	14.0 ± 10.0	1.71 ± 0.20
BAF 1-1	*0.0*	*0.0*	*2.0*	*2.0*	*6.0*	*7.0*	*1.75*
BAF 1-2	*0.0*	*0.0*	*2.0*	*3.0*	*7.0*	*9.0*	*1.89*
BAF 1-3	*0.0*	*0.0*	*2.0*	*3.0*	*7.0*	*26.0*	*1.50*
BAF 2	0.7 ± 0.6	0.7 ± 0.6	3.0 ± 1.0	10.0 ± 3.6	9.7 ± 3.5	22.7 ± 1.2	1.81 ± 0.46
BAF 2-1	*0.0*	*0.0*	*2.0*	*13.0*	*6.0*	*24.0*	*1.28*
BAF 2-2	*1.0*	*1.0*	*4.0*	*11.0*	*10.0*	*22.0*	*2.03*
BAF 2-3	*1.0*	*1.0*	*3.0*	*6.0*	*13.0*	*22.0*	*2.13*
BAF 3	0.3 ± 0.6	0.3 ± 0.6	2.0 ± 0.0	4.7 ± 1.5	12.3 ± 5.5	50.0 ± 38.6	2.02 ± 0.44
BAF 3-1	*0.0*	*0.0*	*2.0*	*3.0*	*12.0*	*34.0*	*1.58*
BAF 3-2	*1.0*	*1.0*	*2.0*	*6.0*	*18.0*	*94.0*	*2.02*
BAF 3-3	*0.0*	*0.0*	*2.0*	*5.0*	*7.0*	*22.0*	*2.46*

Table 3.2 Coarse assessment of richness and total abundance (morphospecies pooled) determined for the dropstones and the sediment immediately surrounding them, using in-situ images taken with the remotely operated vehicle (ROV). More precise richness and abundance values are also provided for the dropstones that were analyzed post collection in the laboratory (Lab).

Level	Sediment (ROV)		Dropstone (ROV)		Dropstone (Lab)	
	Richness	*Abundance*	*Richness*	*Abundance*	*Richness*	*Abundance*
Global	***0.4 ± 0.2***	***0.4 ± 0.2***	***2.8 ± 0.6***	***6.4 ± 0.9***	***14.9 ± 7.6***	***87.3 ± 82.7***
LAB	**0.6 ± 0.2**	**0.6 ± 0.2**	**3.2 ± 1.0**	**7.0 ± 4.0**	**20.3 ± 5.1**	**145.9 ± 82.9**
LAB 1	0.7 ± 0.6	0.7 ± 0.6	4.3 ± 0.6	11.3 ± 0.6	16.0 ± 7.5	180.0 ± 129.1
LAB 1-1	*0.0*	*0.0*	*5.0*	*12.0*	*23.0*	*258.0*
LAB 1-2	*1.0*	*1.0*	*4.0*	*11.0*	*17.0*	*31.0*
LAB 1-3	*1.0*	*1.0*	*4.0*	*11.0*	*8.0*	*251.0*
LAB 2	0.3 ± 0.6	0.3 ± 0.6	2.7 ± 0.6	6.3 ± 3.1	26.0 ± 4.4	206.3 ± 64.0
LAB 2-1	*0.0*	*0.0*	*3.0*	*3.0*	*23.0*	*265.0*
LAB 2-2	*0.0*	*0.0*	*2.0*	*9.0*	*24.0*	*138.0*
LAB 2-3	*1.0*	*1.0*	*3.0*	*7.0*	*31.0*	*216.0*
LAB 3	0.7 ± 0.6	0.7 ± 0.6	2.7 ± 0.6	3.3 ± 0.6	19.0 ± 8.9	51.3 ± 50.1
LAB 3-1	*0.0*	*0.0*	*3.0*	*4.0*	*16.0*	*24.0*
LAB 3-2	*1.0*	*1.0*	*3.0*	*3.0*	*12.0*	*20.0*
LAB 3-3	*1.0*	*1.0*	*2.0*	*3.0*	*29.0*	*110.0*
BAF	**0.3 ± 0.3**	**0.3 ± 0.3**	**2.3 ± 0.6**	**5.8 ± 3.8**	**9.6 ± 2.8**	**28.9 ± 18.8**
BAF 1	0.0 ± 0.0	0.0 ± 0.0	2.0 ± 0.0	2.7 ± 0.6	6.7 ± 0.6	14.0 ± 10.0
BAF 1-1	*0.0*	*0.0*	*2.0*	*2.0*	*6.0*	*7.0*
BAF 1-2	*0.0*	*0.0*	*2.0*	*3.0*	*7.0*	*9.0*
BAF 1-3	*0.0*	*0.0*	*2.0*	*3.0*	*7.0*	*26.0*
BAF 2	0.7 ± 0.6	0.7 ± 0.6	3.0 ± 1.0	10.0 ± 3.6	9.7 ± 3.5	22.7 ± 1.2
BAF 2-1	*0.0*	*0.0*	*2.0*	*13.0*	*6.0*	*24.0*
BAF 2-2	*1.0*	*1.0*	*4.0*	*11.0*	*10.0*	*22.0*
BAF 2-3	*1.0*	*1.0*	*3.0*	*6.0*	*13.0*	*22.0*
BAF 3	0.3 ± 0.6	0.3 ± 0.6	2.0 ± 0.0	4.7 ± 1.5	12.3 ± 5.5	50.0 ± 38.6
BAF 3-1	*0.0*	*0.0*	*2.0*	*3.0*	*12.0*	*34.0*
BAF 3-2	*1.0*	*1.0*	*2.0*	*6.0*	*18.0*	*94.0*
BAF 3-3	*0.0*	*0.0*	*2.0*	*5.0*	*7.0*	*22.0*

Table 3.3 Coverage on the surface (%) of all morphospecies with global coverage above 1%. The surface was defined as any encrusting growth within 1 cm of the surface.

Morphospecies	**Global**	**LAB**	**BAF**	**LAB 1**	**LAB 2**	**LAB 3**	**BAF 1**	**BAF 2**	**BAF 3**
Electridae msp. 1	4.1 ± 5.8	-	8.2 ± 7.3	-	-	-	0.7 ± 1.2	15.3 ± 9.5	8.7 ± 10.7
Schizoporelloidea msp. 2	2.6 ± 1.3	3.6 ± 2.9	1.7 ± 2.9	3 ± 2.6	1 ± 1.7	6.7 ± 2.3	-	-	5 ± 7.8
Escharoides msp. 1	2.5 ± 3.5	-	5 ± 0.6	-	-	-	4.7 ± 8.1	4.7 ± 2.3	5.7 ± 3.5
Tubuliporidae msp. 1	2.2 ± 0.8	2.8 ± 1.4	1.7 ± 1.5	4.3 ± 0.6	1.7 ± 1.2	2.3 ± 2.1	2.3 ± 1.2	2.7 ± 0.6	-
Crisiidae msp. 1	1.8 ± 2.1	0.3 ± 0.6	3.3 ± 2.5	-	-	1 ± 1.7	5.7 ± 2.3	3.7 ± 1.2	0.7 ± 1.2
Porifera msp. 1	1.8 ± 2.6	-	3.7 ± 2.6	-	-	-	0.7 ± 1.2	5 ± 4.6	5.3 ± 3.5
Annelida msp. 1	1.8 ± 0.2	1.7 ± 1.5	1.9 ± 0.5	0.3 ± 0.6	3.3 ± 5.8	1.3 ± 1.5	1.3 ± 1.5	2.3 ± 1.2	2 ± 1
Aplousobranchia msp. 1	1.7 ± 2.4	-	3.4 ± 3.2	-	-	-	-	6.3 ± 6.7	4 ± 3.5
Haliclona xenomorpha	1.6 ± 2.2	3.1 ± 3.4	-	6.7 ± 11.5	2.7 ± 4.6	-	-	-	-
Serpulidae msp. 1	1.4 ± 0.2	1.3 ± 1.3	1.6 ± 1	1.3 ± 2.3	2.7 ± 1.5	-	2.7 ± 2.5	1 ± 1	1 ± 1
Porifera msp. 14	1.2 ± 1.6	2.3 ± 4	-	-	7 ± 12.1	-	-	-	-
Schizoporelloidea msp. 1	1.2 ± 0.2	1.3 ± 1.2	1 ± 1.2	1.7 ± 2.9	-	2.3 ± 2.1	2.3 ± 4	-	0.7 ± 1.2
Terebellidae msp. 1	1.2 ± 0.9	1.8 ± 2.8	0.6 ± 1	-	5 ± 3.5	0.3 ± 0.6	1.7 ± 1.5	-	-
Escharellidae msp. 2	1.1 ± 1.4	0.1 ± 0.2	2.1 ± 3.7	-	-	0.3 ± 0.6	6.3 ± 11	-	-

Table 3.4 Coverage in the canopy (%) of all morphospecies with global coverage above 0.5 %. The canopy was defined as any erect growth over 1 cm above the stone surface.

Morphopecies	**Global**	**LAB**	**BAF**	**LAB 1**	**LAB 2**	**LAB 3**	**BAF 1**	**BAF 2**	**BAF 3**
Heliometria glacialis	3.3 ± 4.4	6.4 ± 10	0.2 ± 0.4	1.3 ± 2.3	-	18 ± 31.2	-	-	0.7 ± 1.2
Haliclona xenomorpha	1.7 ± 2.4	3.3 ± 4.2	-	8.0 ± 13.9	2.0 ± 3.5	-	-	-	-
Crisiidae msp. 1	1.6 ± 1.6	0.4 ± 0.8	2.7 ± 2.1	-	-	1.3 ± 2.3	4.3 ± 2.5	3.3 ± 0.6	0.3 ± 0.6
Aglaopheniidae msp. 3	1.5 ± 2.1	-	3.0 ± 2.5	-	-	-	5.3 ± 4.9	3.3 ± 4.9	0.3 ± 0.6
Porifera msp. 14	0.9 ± 1.3	1.9 ± 3.3	-	-	5.7 ± 9.8	-	-	-	-
Philodoporidae msp. 1	0.9 ± 1.3	-	1.8 ± 1.2	-	-	-	0.7 ± 1.2	1.7 ± 1.5	3.0 ± 5.2
Sertulariidae msp. 1	0.9 ± 1.3	-	1.8 ± 1.7	-	-	-	3.3 ± 3.2	2.0 ± 3.5	-
Schizoporelloidea msp. 2	0.7 ± 1.0	1.4 ± 2.5	-	-	-	4.3 ± 7.5	-	-	-
Bryozoa msp. 1	0.7 ± 0.9	1.3 ± 1.8	-	3.3 ± 5.8	-	0.7 ± 0.6	-	-	-
Porifera msp. 2	0.7 ± 0.5	0.3 ± 0.6	1.0 ± 0.9	-	1.0 ± 1.7	-	-	1.3 ± 1.5	1.7 ± 1.5
Demospongiae msp. 1	0.6 ± 0.9	-	1.2 ± 1.2	-	-	-	-	2.3 ± 1.2	1.3 ± 1.5
Spinularia cf. *sarsii*	0.6 ± 0.9	-	1.2 ± 1.0	-	-	-	1.0 ± 1.7	2.3 ± 1.2	0.3 ± 0.6
Annelida msp. 1	0.6 ± 0.8	1.1 ± 1.9	-	-	3.3 ± 5.8	-	-	-	-
Porifera msp. 8	0.6 ± 0.8	-	1.1 ± 1.9	-	-	-	-	-	3.3 ± 4.9

3.10 Figures

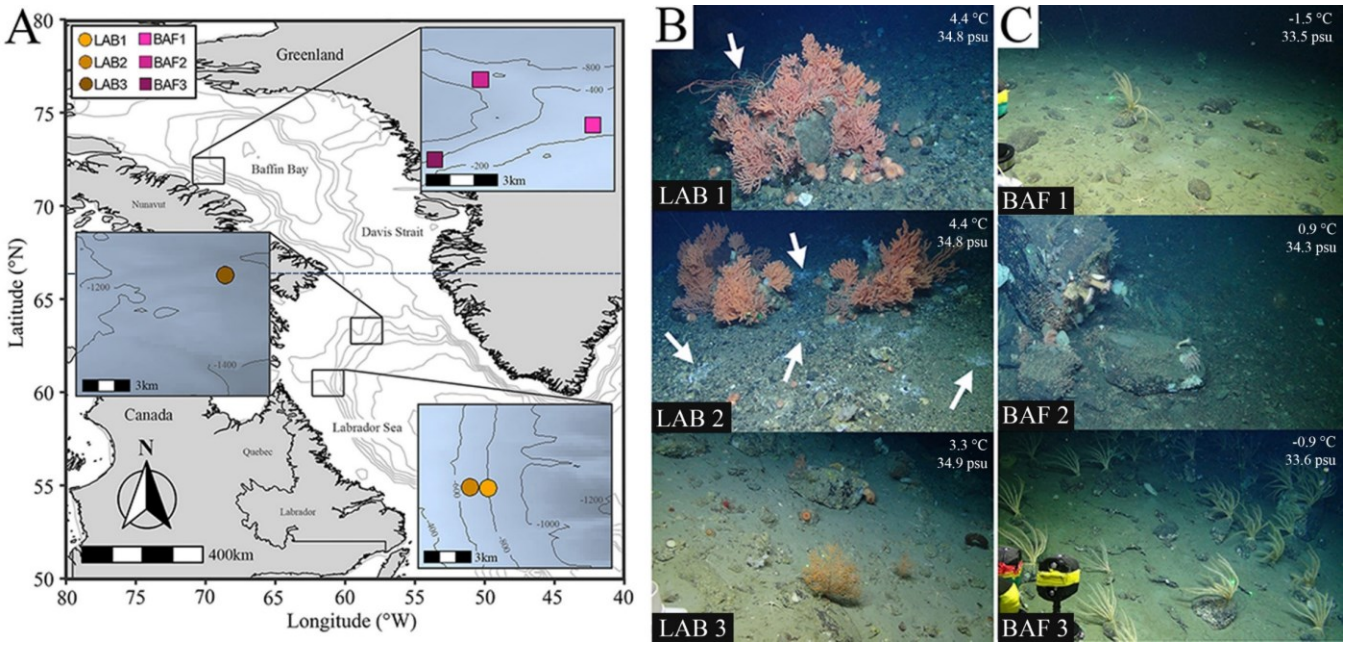

Figure 3.1 Locations of the six sites from which dropstones were collected. (A) General location of the sites, with insets showing bathymetry, and distance from the shore. (B) Examples of images taken with the remotely operated vehicle (ROV) at the three Labrador Sea (LAB) sites, top to bottom: LAB 1 showing colonies of *Primnoa resedaeformis* and other actiniarians on a large dropstone, with arrow indicating evidence of entanglement with fishing gear; LAB 2 with P. resedaeformis on dropstones surrounded by bacterial mats characteristic of hydrocarbon seeps; LAB 3 with dropstones on inclined slope harboring black coral, actiniarians, and sponges. (C) Examples of images from Baffin Bay (BAF) sites, top to bottom: BAF 1 with crinoids and serpulids on dropstones surrounded by silt; BAF 2 with actiniarians and sponges on dropstones; BAF 3 with crinoids and serpulids on dropstones lying on a steep slope.

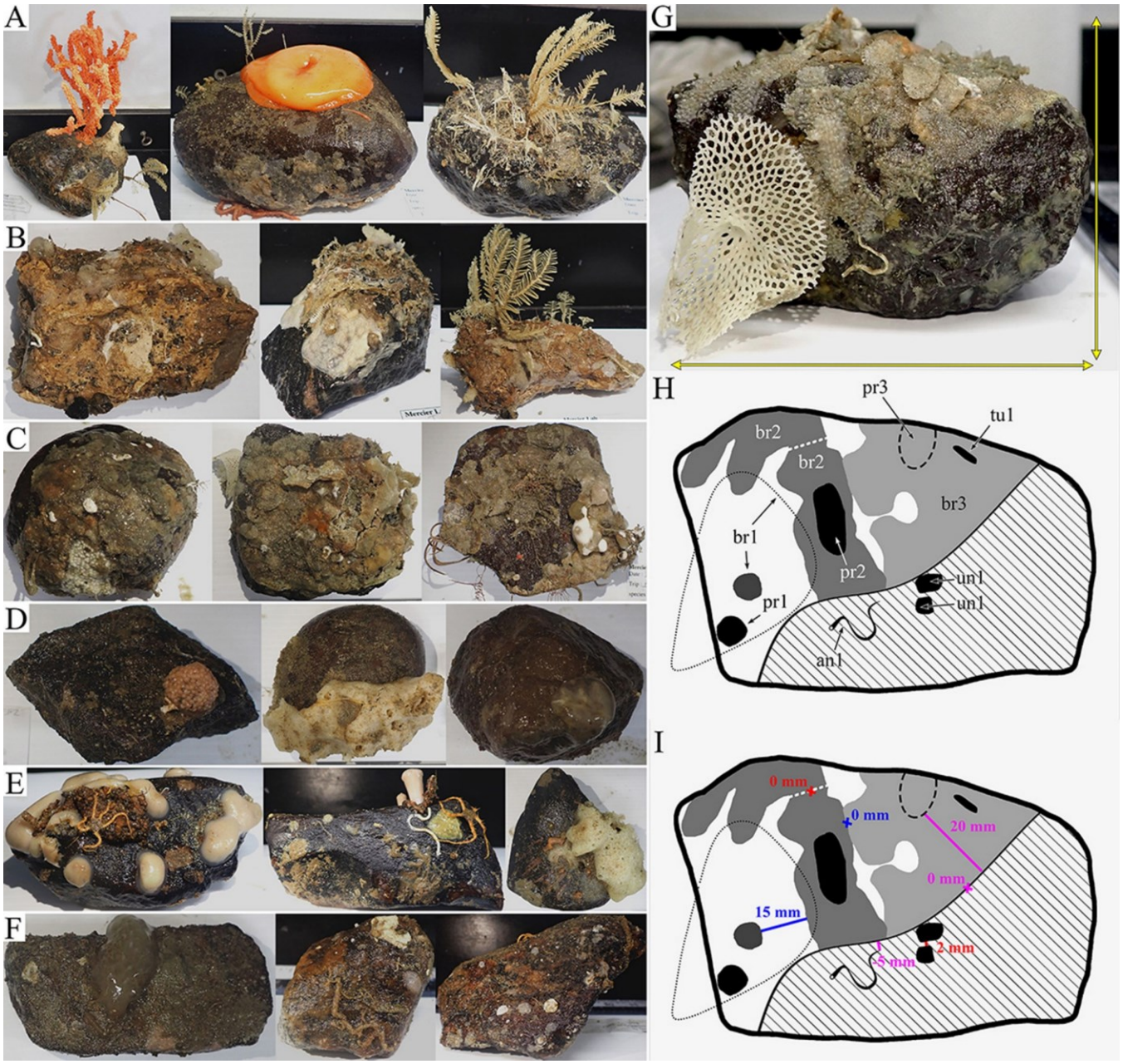
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Figure 3.2 (previous page) Dropstones collected at the different sites, drawn by hand and then traced digitally in Adobe Photoshop, including (A) LAB 1, (B) LAB 2, (C) LAB 3, (D) BAF 1, (E) BAF 2, and (F) BAF 3. See Supplementary Table 3.1 for all dropstone measurements. (G) One dropstone viewed from side, illustrating length and height measurements (yellow arrows), with width in addition being measured perpendicular to length. (H) A simplified example of a dropstone schematic drawing, traced digitally into Adobe Photoshop for clarity. Some morphospecies are not included as identified on the stone in order to show the different measurements taken. Representation of the dropstone face in G, with individuals and colonies outlined and sorted into phyla and numbered morphospecies (an = annelid, pr = porifera, br = bryozoan, tu = tunicate, un = unknown). Solid colours indicate visible morphospecies coverage. Dashed lines show coverage of primary colonizers that occurred under secondary colonizers. Dotted lines indicate morphospecies coverage in the canopy (which can extend beyond dropstone surface). Barred area represents the zone below the sediment line, marked by a solid black line. (I) Measurements of morphospecies positioning relative to the sediment line (pink), relative to conspecifics (intraspecific distance; red), and individuals of other morphospecies (interspecific distance; blue). An "X" is used where distance = 0 mm.

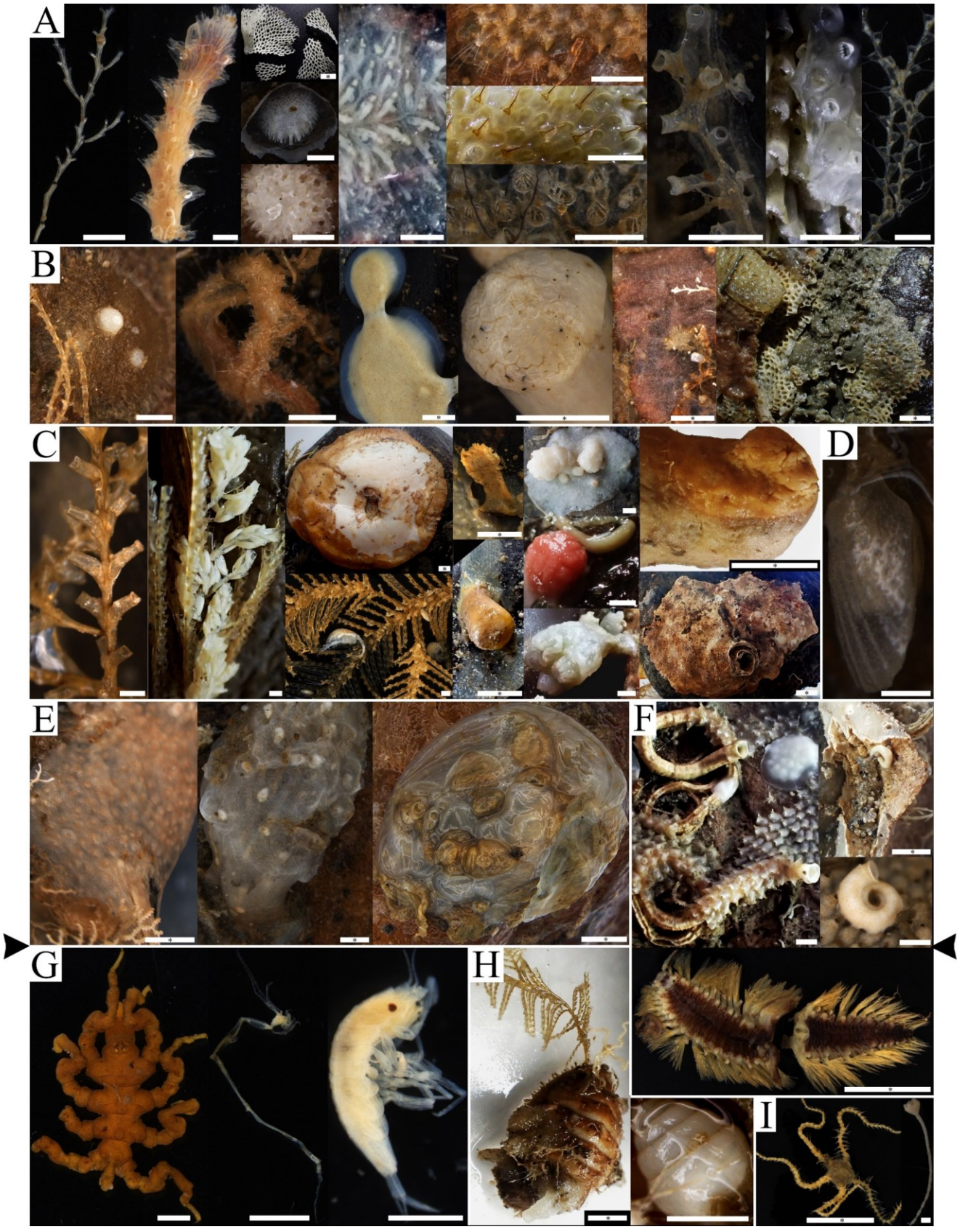
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Figure 3.3 (previous page) Illustrative examples of morphospecies recorded on dropstones (grouped by phylum). Triangles on the side show distinction between sessile morphospecies (panels A-E and top of panel F) and motile morphospecies (bottom portion of panel F, along with panels G-I). (A) Bryozoa, (B) Porifera, (C) Cnidaria, (D) Brachiopoda, (E) Chordata, (F) Annelida, (G) Arthropoda, (H) Mollusca, (I) Echinodermata. Scale bars are 1 mm; for larger taxa, an asterisk in the scale bar indicates it represents 1 cm.

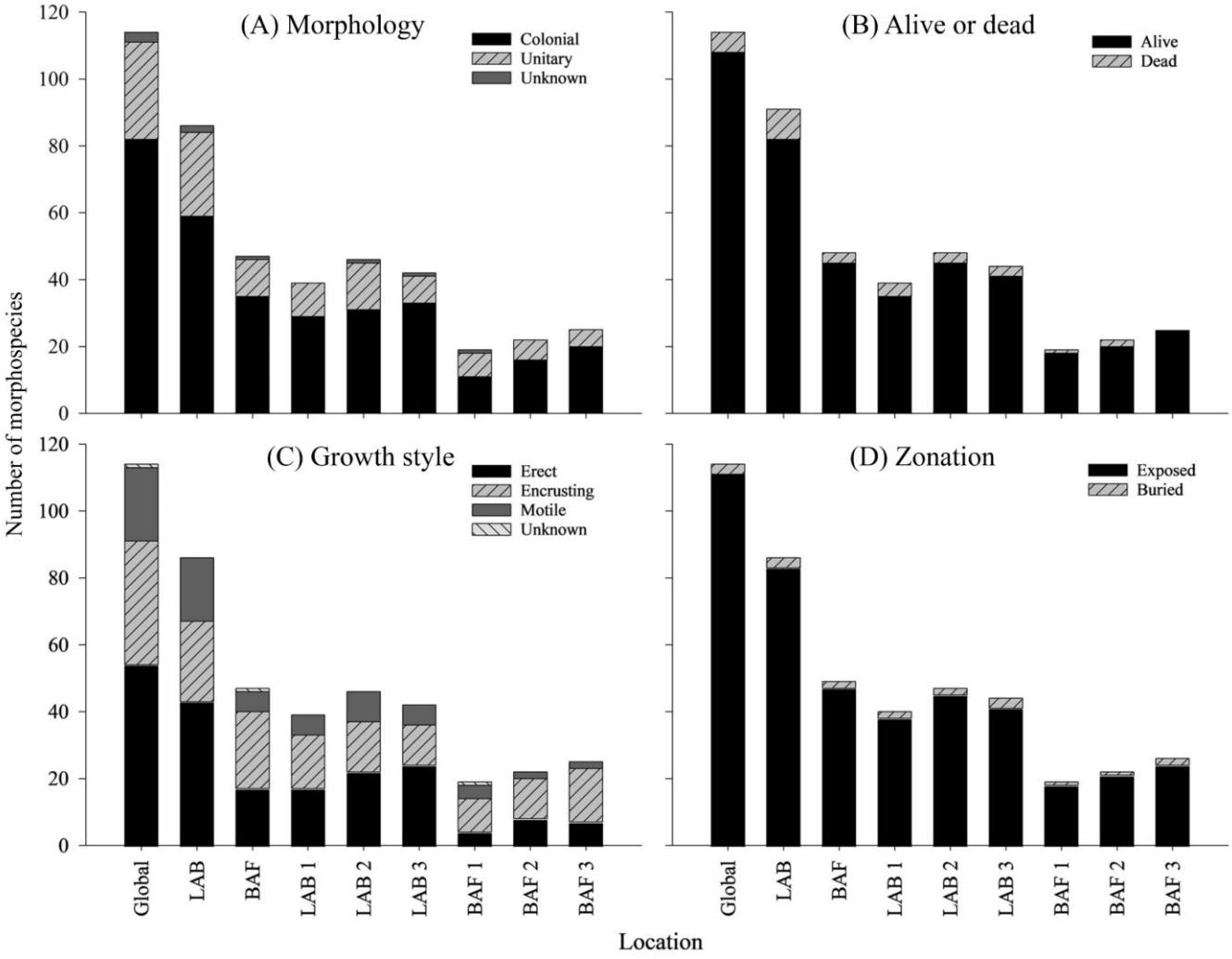

Figure 3.4 Qualitative categorizations of morphospecies as viewed by total number in each category overall, by region, and by site. (A) Morphology: colonial organisms, unitary (i.e., solitary) organisms, or unknown. (B) Alive or dead: morphospecies that were alive or dead at time of collection. (C) Growth style: growth pattern of morphospecies, whether sessile and erect, sessile and encrusting, motile, or unknown. (D) Zonation: morphospecies inhabiting the exposed surface above the sediment or the buried surface below the sediment.

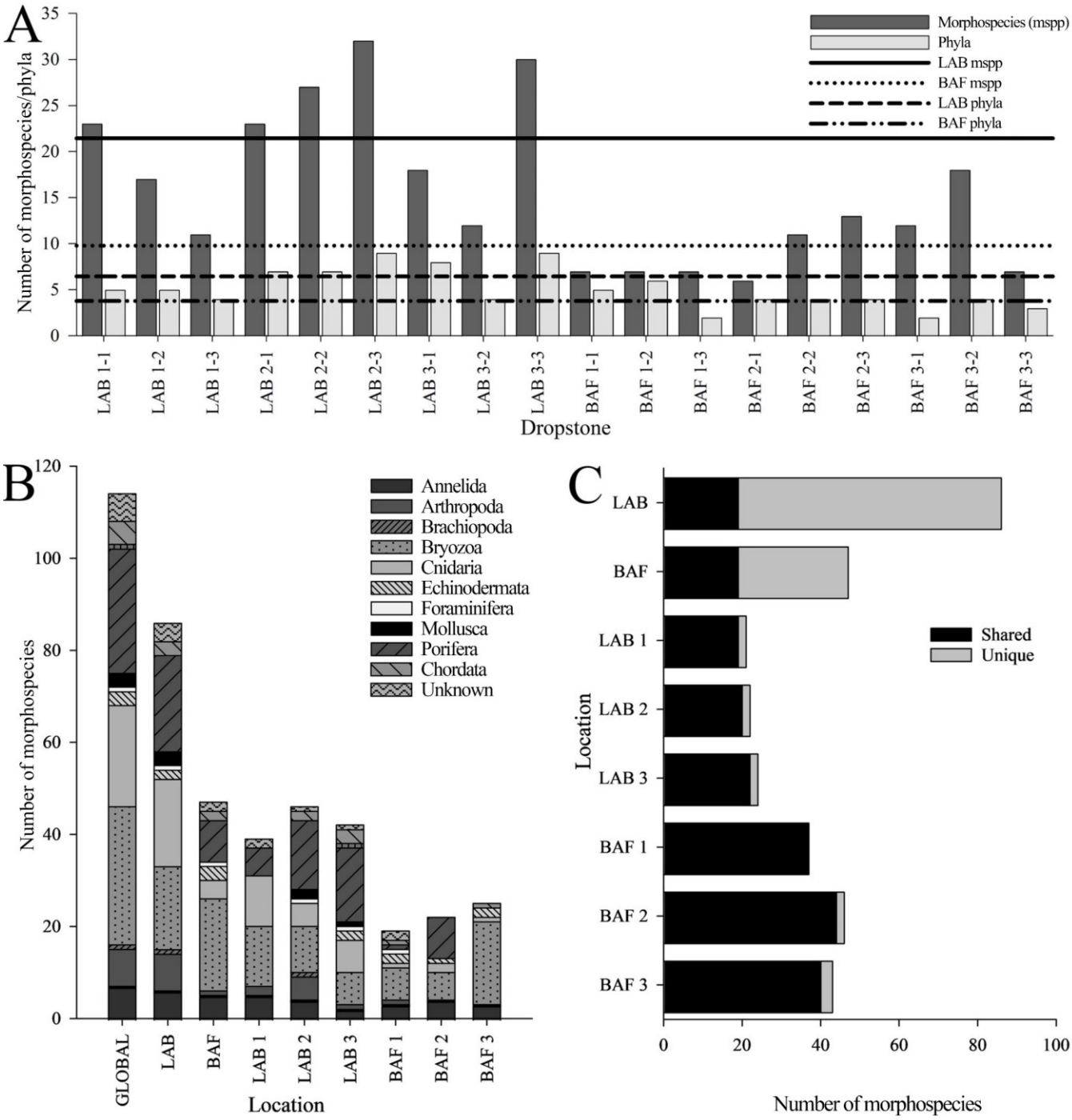

Figure 3.5 Distribution of morphospecies and phyla in three Labrador Sea (LAB) sites and three Baffin Bay (BAF) sites. (A) Number of morphospecies and phyla present on each dropstone at each site, and overall mean number of morphospecies and phyla for both regions (LAB and BAF). (B) Number of morphospecies by phyla globally, by region, and site. (C) Number of shared and unique morphospecies in each region and site.

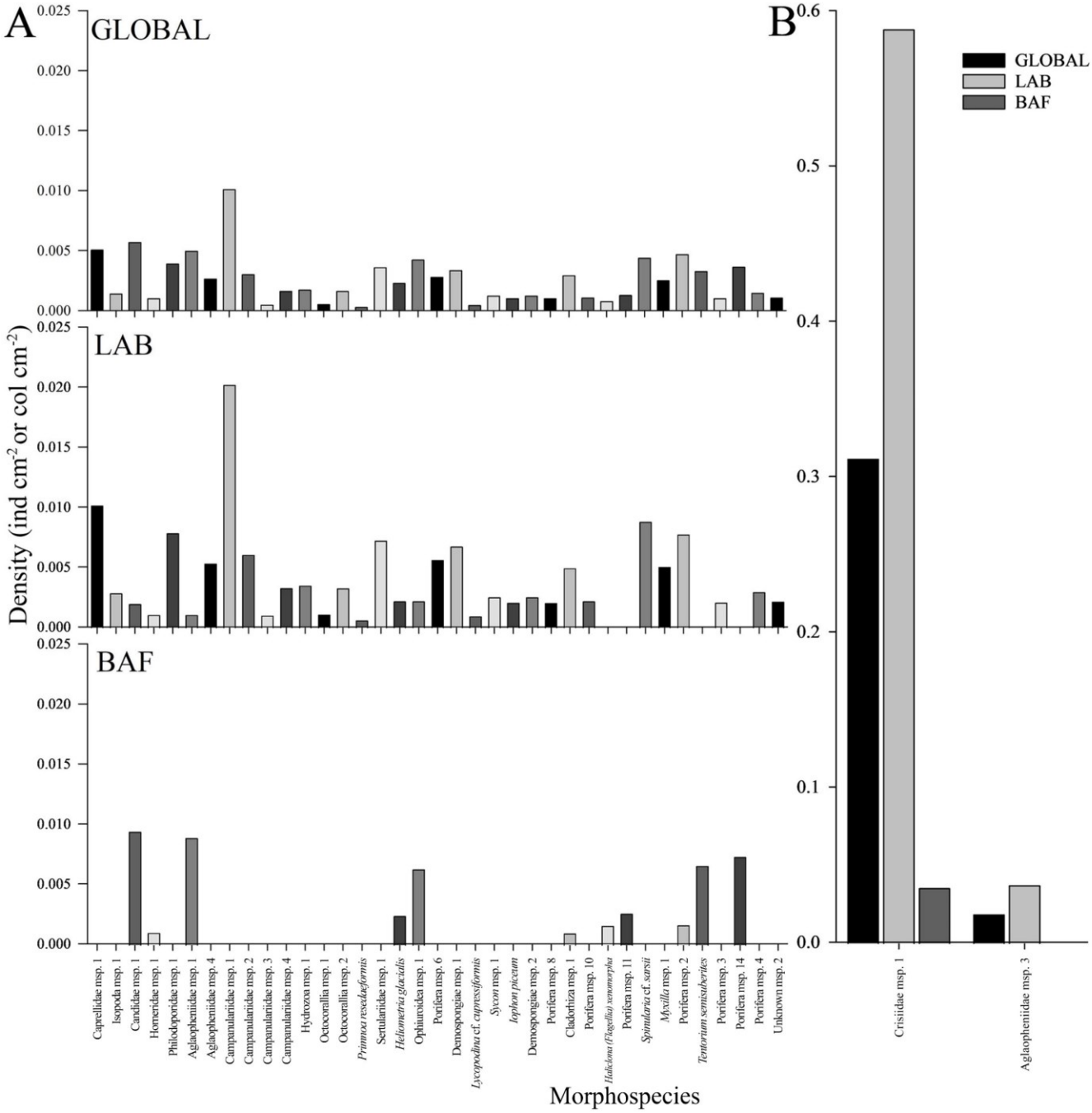

Figure 3.6 Density of all erect-sessile and motile morphospecies (msp) present as more than one individual or colony overall (n > 1) per cm2. (A) Density of morphospecies overall (top), and regionally i.e., Labrador Sea (LAB; middle) and Baffin Bay (BAF; bottom). (B) Density of two common erect-sessile morphospecies at the global and regional (LAB and BAF) level.

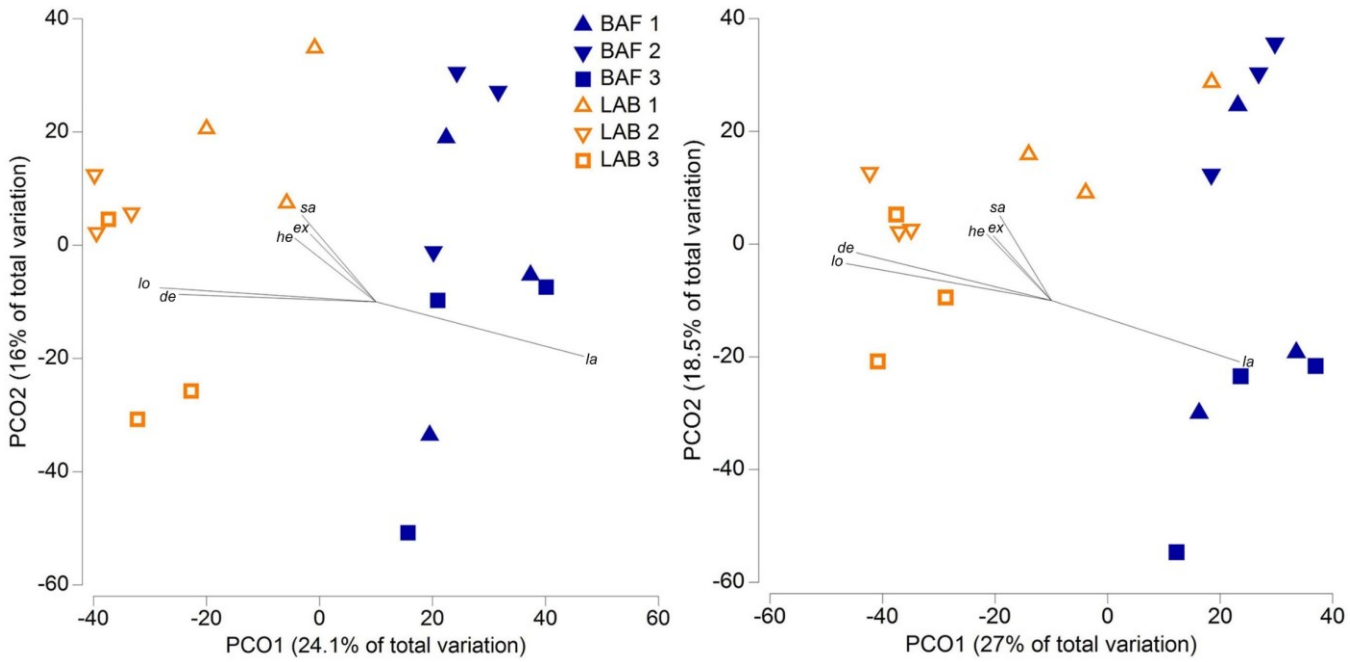

Figure 3.7 Principal coordinate analyses (PCO) plots based on Bray-Curtis resemblance matrices for regional and physical characteristics of dropstone collections in the Labrador Sea (LAB) and Baffin Bay (BAF). (A) Log-transformed morphospecies abundance data. (B) Presence/absence-transformed morphospecies abundance data. Characteristics vector overlay was based on Pearson correlations (> 0.5). Regional: la = latitude, lo = longitude, de = depth (m); physical: he = dropstone height (mm), sa = surface area (cm2), ex = exposed surface of dropstone (%).

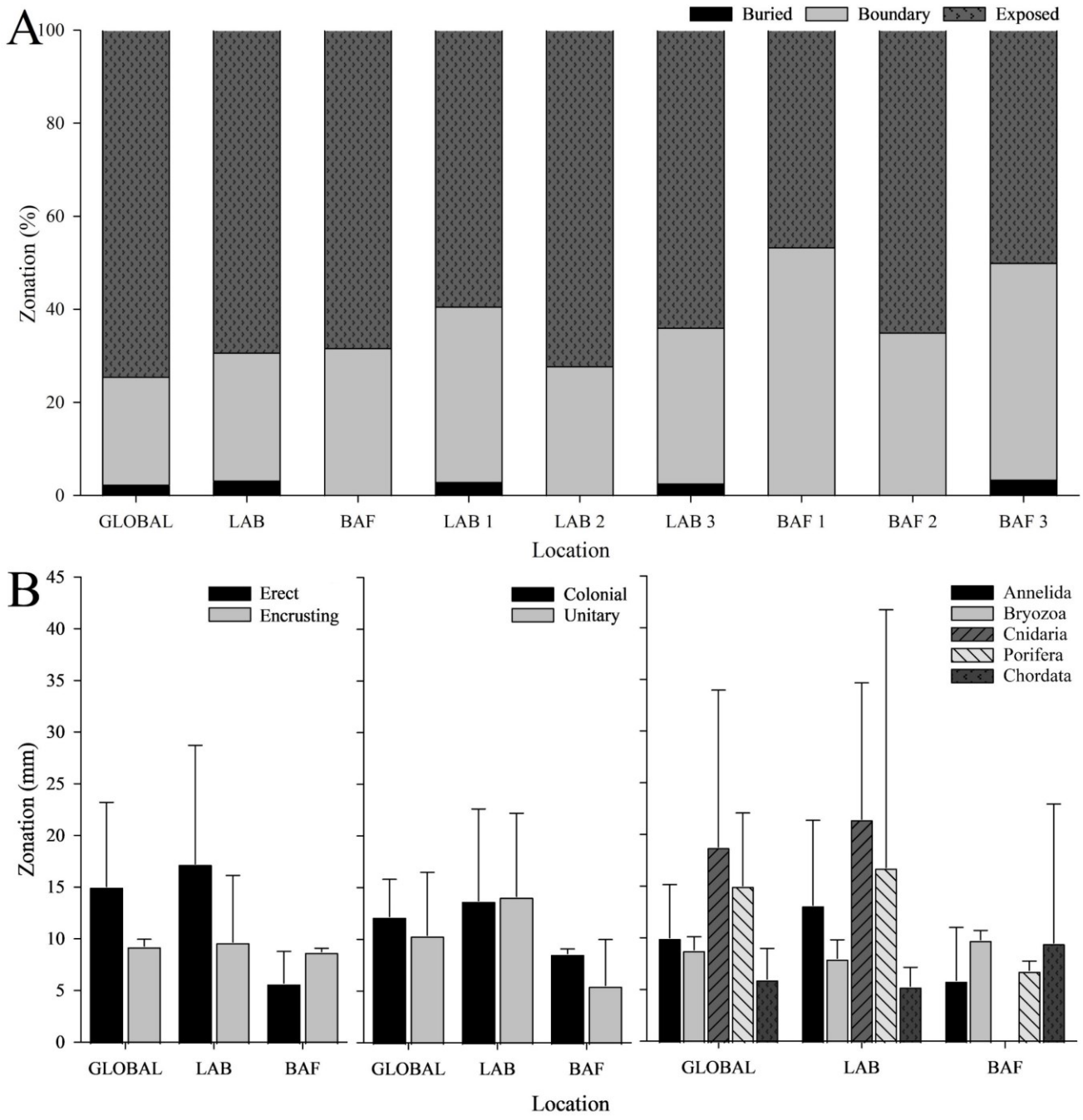

Figure 3.8 Zonation of morphospecies and phyla relative to the sediment line. (A) Proportional zonation examined as a percentage of morphospecies above the sediment line (Exposed), at the sediment line (Boundary), and below the sediment line (Buried). (B) Zonation of morphospecies based on growth pattern (left), morphology (middle), and phylum (right) at the global level and at the regional level across Labrador Sea (LAB) and Baffin Bay (BAF).

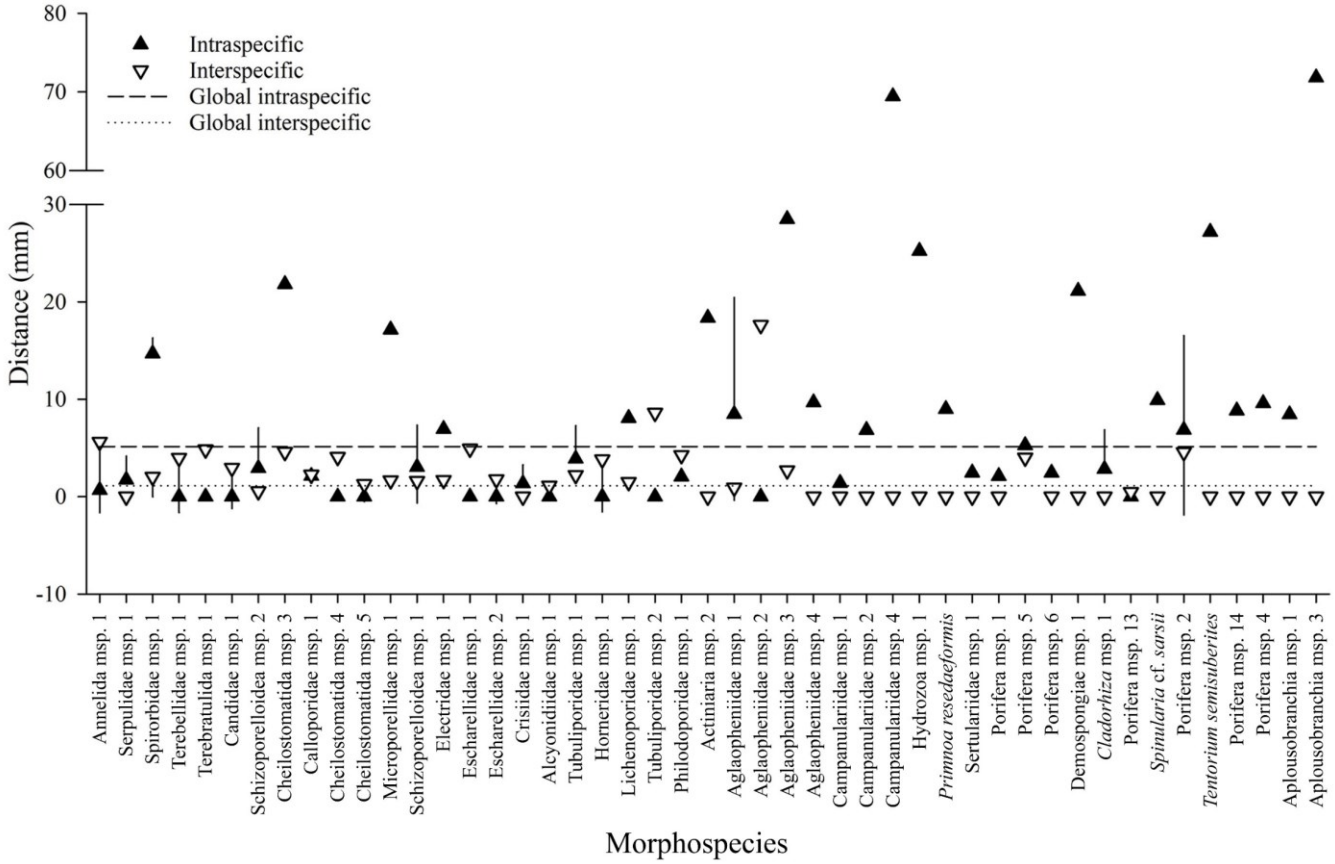

Figure 3.9 All morphospecies (msp/mspp) with measurable distances (mm) above zero between conspecifics (intraspecific distance) and allospecifics (interspecific distance). Error bars indicate standard deviation between dropstones with upward bars for intraspecific distances and downward for interspecific. No error bars indicate no deviation.

3.11 Appendix

3.11.1 Supplementary methods

3.11.1.1 Characterization of dropstone colonization from ROV footage

From the video footage, all epibenthic megafauna visible on dropstones and on the visually estimated comparable surface area of the immediately surrounding substratum (i.e., over a similar surface area to the dropstone surface area) were compared for richness (number of taxa present) and abundance (number of individuals/colonies of all taxa combined). Due to the opportunistic nature of the coarse comparison, photograph and video resolution were insufficient for fine-scale visualization (see below for fine analysis) and this dataset addressed only photographically visible epibenthic megafauna (>5 cm) or clear traces left by endobenthic megafauna (holes and mounds).

3.11.2 Supplementary results

3.11.2.1 Characterization of dropstone colonization from ROV images

Richness and abundance of visible epibenthic megafauna from ROV videos were consistently higher on dropstones (2.8 ± 0.6 mspp, 6.4 ± 0.9 ind) than the surrounding sediments (0.4 ± 0.2 mspp, 0.4 ± 0.2 ind) (Table 3.1). Examination of each dropstone independently revealed that richness and abundance varied from two to five morphospecies represented by two to 13 individuals. However, no epibenthic megafauna was visible in the sediment surrounding 10 dropstones (ind or col) and the remaining eight were surrounded by a single ophiuroid (Table 3.1). More broadly, LAB 1 dropstones had the highest richness and abundance (4.3 ± 0.6 mspp and 11.3 ± 0.6 ind); they were positioned on some of the most visually colonized sediment (0.7 ± 0.6 mspp and ind), similar to sediment surrounding dropstones at LAB 3 and BAF 2. Dropstones at BAF 1 had the lowest richness and abundance (2.0 ± 0.0 mspp and 2.7 ± 0.6 ind) with no visible colonization of the surrounding sediment. Overall, LAB had

higher richness and abundance, both on dropstones and sediment than BAF on the corresponding substrata (Table 3.1).

3.11.3 Supplementary tables

Supplementary table 3.1 Characterization of the six sites from which dropstones were collected in Labrador Sea (LAB; Figure 1B) and Baffin Bay (BAF; Figure 1C), including latitude, longitude, bottom depth, bottom temperature, bottom salinity, primary substratum present, and a description of each site (Desmarais et al. 2021). Bottom parameters were measured at each site using CTD-Rosette by Amundsen Science.

Site	Lat (°N)	Long (°W)	Depth (m)	Temp (°C)	Sal (psu)	Primary substratum	Description
LAB 1 (R18)	60.497	-61.210	766	4.4	34.8	Layered substratum, mud below coarse gravel. Cobble- and boulder-sized dropstones, as well as some authigenic carbonate crust.	Southernmost site, near a known coral hotspot in northeast Saglek Bank. Strong bottom currents (~20 cm s^{-1}) linked to macrotidal oscillation in Frobisher Bay.
LAB 2 (R19)	60.498	-61.232	822	4.4	34.8	Sand, coarse gravel, and cobble-sized dropstones.	West of LAB 1 (1.2 km), with similar bottom current conditions. Apparent trawl door scars and fishing line coral entanglements observed outside of the transect.
LAB 3 (R21)	63.347	-58.194	1308	3.3	34.9	Mud with cobble and boulder-sized dropstones, mud deposits visible on the top of all rocks.	Farther from the other two sites in the region (352.8 km northeast from LAB 2) and the deepest sampled, lying farther offshore and closer to Davis Strait. On a steep rocky ridge (~30°) between predominately flat muddy environments with extensive and unique soft-bottom *Keratoisis* coral colonies.
BAF 1 (R24)	71.38	-70.069	220	-1.5	33.5	Mud substratum with clusters of cobble- and boulder-sized dropstones, with mud deposits visible on top of many of the rocks.	Shallowest site, and close to a previously documented hydrocarbon seep.
BAF 2 (R26)	71.435	-70.205	497	0.9	34.3	Mud substratum with coarse gravel, cobble-, and boulder-sized dropstones, as well as exposed bedrock.	Northernmost site (7.8 km from BAF 1), at the top of a bedrock massif of a presumed fault in Scott Trough, and another potential hydrocarbon seep location.
BAF 3 (R27)	71.339	-70.26	239	-0.9	33.6	Mud and sand substratum with coarse gravel, cobble, and occasional boulder-sized dropstones and authigenic carbonate crust.	Above the scarp of the eroding southwest margin of Scott Trough in a turbidity current system located 10.9 km from BAF 2.

Supplementary table 3.2 Characterization of the dropstones collected (italic), with calculated averages by site, by region (bold), and overall (bold and italic). The error on the mean is the standard deviation. Associated dive numbers from Amundsen Science Expedition 2021 included in brackets after each site name.

Level	**Length**	**Width**	**Height**	**SA**	**Exposed**		**Base col.**		**Canopy col.**	
	(mm)	(mm)	(mm)	(cm2)	*SA (cm2)*	*Height (mm)*	*EX (%)*	*UN (%)*	*EX (%)*	*UN (%)*
Global	***114 ± 20***	***82 ± 19***	***61 ± 15***	***248 ± 111***	***154 ± 96***	***37 ± 15***	***42 ± 15***	***7 ± 6***	***18 ± 11***	***1 ± 2***
LAB	**129 ± 40**	**95 ± 26**	**72 ± 20**	**327 ± 198**	**221 ± 163**	**47 ± 20**	**51 ± 8**	**7 ± 6**	**22 ± 5**	**1 ± 1**
LAB 1 (R18)	175 ± 48	125 ± 23	95 ± 26	556 ± 244	408 ± 224	75 ± 24	52 ± 8	13 ± 8	27 ± 6	0 ± 0
LAB 1-1	*225*	*145*	*110*	*786*	*550*	*77*	*56*	*15*	*30*	*0*
LAB 1-2	*170*	*130*	*110*	*582*	*524*	*99*	*58*	*20*	*20*	*0*
LAB 1-3	*130*	*100*	*65*	*300*	*150*	*33*	*43*	*5*	*30*	*0*
LAB 2 (R19)	112 ± 21	82 ± 12	57 ± 13	218 ± 45	149 ± 73	36 ± 4	59 ± 18	2 ± 3	23 ± 14	0 ± 0
LAB 2-1	*95*	*72*	*55*	*170*	*102*	*33*	*48*	*5*	*15*	*0*
LAB 2-2	*105*	*80*	*70*	*225*	*113*	*35*	*50*	*0*	*15*	*0*
LAB 2-3	*135*	*95*	*45*	*259*	*233*	*41*	*80*	*0*	*40*	*0*
LAB 3 (R21)	100 ± 5	78 ± 31	65 ± 13	207 ± 41	107 ± 7	33 ± 10	43 ± 14	5 ± 5	17 ± 5	2 ± 3
LAB 3-1	*100*	*45*	*80*	*175*	*105*	*48*	*55*	*0*	*20*	*0*
LAB 3-2	*95*	*85*	*55*	*192*	*115*	*33*	*46*	*10*	*20*	*0*
LAB 3-3	*105*	*105*	*60*	*253*	*101*	*24*	*27*	*5*	*12*	*5*
BAF	**100 ± 17**	**68 ± 8**	**50 ± 6**	**169 ± 30**	**86 ± 11**	**26 ± 6**	**32 ± 3**	**7 ± 5**	**13 ± 8**	**1 ± 1**
BAF 1 (R24)	83 ± 20	67 ± 21	57 ± 9	153 ± 66	93 ± 71	34 ± 14	29 ± 15	3 ± 3	20 ± 17	0 ± 0
BAF 1-1	*95*	*60*	*58*	*156*	*62*	*23*	*15*	*0*	*10*	*0*
BAF 1-2	*95*	*90*	*65*	*217*	*174*	*52*	*44*	*5*	*40*	*0*
BAF 1-3	*60*	*50*	*47*	*86*	*43*	*24*	*28*	*5*	*10*	*0*
BAF 2 (R26)	117 ± 19	77 ± 26	49 ± 5	204 ± 76	92 ± 24	22 ± 3	34 ± 3	5 ± 0	15 ± 5	0 ± 0
BAF 2-1	*95*	*70*	*45*	*152*	*91*	*27*	*38*	*5*	*20*	*0*
BAF 2-2	*125*	*55*	*48*	*169*	*67*	*19*	*32*	*5*	*10*	*0*
BAF 2-3	*130*	*105*	*55*	*290*	*116*	*22*	*32*	*5*	*15*	*0*
BAF 3 (R27)	100 ± 38	60 ± 18	45 ± 25	152 ± 108	73 ± 34	23 ± 12	35 ± 12	13 ± 8	5 ± 7	2 ± 3
BAF 3-1	*105*	*45*	*20*	*90*	*45*	*10*	*23*	*15*	*13*	*5*
BAF 3-2	*60*	*55*	*45*	*89*	*62*	*32*	*34*	*20*	*1*	*0*
BAF 3-3	*135*	*80*	*70*	*276*	*110*	*28*	*47*	*5*	*1*	*0*

)

Supplementary table 3.3 Total abundance of all sessile-erect and motile morphospecies present as more than a single individual (n > 1) at the global, regional, and site level. Dash (-) indicates morphospecies not present. Asterisk (*) indicates phylum total abundance includes morphospecies present as one individual (see Supplementary Table 1).

Morphospecies	**GLOBAL**	**Region**		**Site**					
		LAB	*BAF*	*LAB 1*	*LAB 2*	*LAB 3*	*BAF 1*	*BAF 2*	*BAF 3*
Arthropoda*	**25**	**24**	**1**	**2**	**20**	**2**	**1**	**-**	**-**
Caprellidae msp. 1	13	13	-	-	11	2	-	-	-
Isopoda msp. 1	6	6	-	-	6	-	-	-	-
Bryozoa*	**797**	**770**	**27**	**304**	**414**	**52**	**2**	**-**	**25**
Bryozoa msp. 1	6	2	4	-	2	-	2	-	2
Crisiidae msp. 1	772	752	20	302	400	50	-	-	20
Horneridae msp. 1	2	1	1	-	-	1	-	-	1
Philodoporidae msp. 1	14	14	-	2	11	1	-	-	-
Cnidaria*	**243**	**236**	**7**	**186**	**36**	**14**	**1**	**1**	**5**
Aglaopheniidae msp. 1	6	1	5	-	-	1	-	-	5
Aglaopheniidae msp. 3	63	63	-	33	27	3	-	-	-
Aglaopheniidae msp. 4	5	5	-	-	-	5	-	-	-
Campanulariidae msp. 1	100	100	-	100	-	-	-	-	-
Campanulariidae msp. 2	30	30	-	30	-	-	-	-	-
Campanulariidae msp. 3	5	5	-	5	-	-	-	-	-
Campanulariidae msp. 4	3	3	-	-	-	3	-	-	-
Hydrozoa msp. 1	5	5	-	-	5	-	-	-	-
Octocorallia msp. 2	3	3	-	-	2	1	-	-	-
Primnoa resedaeformis	3	3	-	3	-	-	-	-	-
Sertulariidae msp. 1	13	13	-	12	1	-	-	-	-
Echinodermata*	**11**	**4**	**7**	**-**	**-**	**4**	**2**	**3**	**2**
Heliometria glacialis	4	2	2	-	-	2	1	-	1
Ophiuroidea msp. 1	6	2	4	-	-	2	-	3	1
Foraminifera	**4**	**3**	**1**	**-**	**2**	**1**	**1**	**-**	**-**
Porifera*	**89**	**73**	**16**	**7**	**47**	**19**	**1**	**15**	**-**
Porifera msp. 6	8	8	-	-	7	1	-	-	-
Demospongiae msp. 1	8	8	-	-	6	2	-	-	-
Lycopodina cf. cupressiformis	2	2	-	-	2	-	-	-	-
Sycon msp. 1	3	3	-	-	2	1	-	-	-
Porifera msp. 7	2	2	-	-	2	-	-	-	-
Iophon piceum	3	3	-	-	2	1	-	-	-
Demospongiae msp. 2	2	2	-	-	-	2	-	-	-
Cladorhiza msp. 1	9	8	1	-	7	1	-	1	-
Porifera msp. 10	2	2	-	-	-	2	-	-	-
Haliclona xenomorpha	2	-	2	-	-	-	1	1	-
Porifera msp. 11	2	-	2	-	-	-	-	2	-
Spinularia cf. sarsii	12	12	-	1	10	1	-	-	-
Myxilla msp. 1	6	6	-	1	3	2	-	-	-
Porifera msp. 2	10	9	1	-	5	4	-	1	-
Tentorium semisuberites	4	-	4	-	-	-	-	4	-
Porifera msp. 3	2	2	-	-	1	1	-	-	-
Porifera msp. 14	6	-	6	-	-	-	-	6	-
Porifera msp. 4	4	4	-	4	-	-	-	-	-
Unknown*	**6**	**5**	**1**	**2**	**2**	**1**	**1**	**-**	**-**
Unknown msp. 2	2	2	-	-	2	-	-	-	-

Supplementary table 3.4 Total abundance of all individuals or colonies of morphospecies present on dropstones collected across six sites in the Labrador Sea (LAB) and Baffin Bay (BAF).

Morphospecies	LAB 1-1	LAB 1-2	LAB 1-3	LAB 2-1	LAB 2-2	LAB 2-3	LAB 3-1	LAB 3-2	LAB 3-3	BAF 1-1	BAF 1-2	BAF 1-3	BAF 2-1	BAF 2-2	BAF 2-3	BAF 3-1	BAF 3-2	BAF 3-3
Annelida	**5**	**7**	**1**	**22**	**2**	**15**	**1**	**3**	**3**	**3**	**2**	**0**	**15**	**4**	**4**	**3**	**5**	**11**
Annelida msp. 1	1	2	0	3	1	4	1	2	1	1	0	0	0	0	2	0	2	9
Annelida msp. 2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Polynoidae msp. 1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Polynoidae msp. 2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Serpulidae msp. 1	2	2	0	15	0	11	0	1	2	0	2	0	13	2	1	0	0	0
Sipunculida msp. 1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Spirorbidae msp. 1	0	2	0	4	0	0	0	0	0	2	0	0	0	0	0	1	3	2
Terebellidae msp. 1	2	0	1	0	0	0	0	0	0	0	0	0	1	2	1	2	0	0
Arthropoda	**0**	**2**	**0**	**2**	**4**	**14**	**1**	**0**	**1**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
Amphipoda msp. 1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphipoda msp. 2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Arthropoda msp. 1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Caprellidae msp. 1	0	0	0	2	3	6	1	0	1	0	0	0	0	0	0	0	0	0
Gammaridea msp. 1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gammaridea msp. 2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Isopoda msp. 1	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0
Pycnogonum msp. 1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Brachiopoda	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
Terebratulida msp. 1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Bryozoa	**102**	**14**	**212**	**209**	**106**	**112**	**4**	**4**	**54**	**2**	**3**	**25**	**2**	**9**	**2**	**31**	**82**	**10**
Candidae msp. 1	0	0	0	0	2	0	0	0	0	0	0	2	0	0	0	1	1	0
Escharoides msp. 1	1	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
Schizoporelloidea msp. 2	0	0	0	0	0	0	0	1	2	1	0	1	0	0	1	2	8	6
Cheilostomatida msp. 3	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	3	0
Calloporidae msp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	1	0
Schizoporelloidea msp. 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Cheilostomatida msp. 4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Cheilostomatida msp. 5	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Microporellidae msp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	2
Smittinidae msp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Schizoporelloidea msp. 1	1	0	0	0	0	0	1	0	0	0	0	8	0	0	0	0	12	1
Electridae msp. 1	1	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
Cheilostomatida msp. 1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cheilostomatida msp. 2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Flustridae msp. 1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Electridae msp. 2	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	6	0
Escharellidae msp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
Escharellidae msp. 2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
Crisiidae msp. 1	96	6	200	200	100	100	0	0	50	0	0	0	0	0	0	0	20	0
Alcyonidiidae msp. 1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tubuliporidae msp. 1	1	1	10	2	1	1	0	0	0	1	1	11	2	7	1	10	14	0
Hippothoidae msp. 1	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Horneridae msp. 1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Lichenoporidae msp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	9	0
Tubuliporidae msp. 2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Tubuliporidae msp. 3	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Crisiidae msp. 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Philodoporidae msp. 1	0	2	0	2	0	9	0	1	0	0	0	0	0	0	0	0	0	0
Cnidaria	**146**	**6**	**34**	**3**	**3**	**30**	**5**	**0**	**9**	**1**	**0**	**0**	**0**	**0**	**10**	**0**	**5**	**0**
Actiniaria msp. 1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Actiniaria msp. 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0
Aglaopheniidae msp. 1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	5	0

(continued from previous page)

Morphospecies	LAB 1-1	LAB 1-2	LAB 1-3	LAB 2-1	LAB 2-2	LAB 2-3	LAB 3-1	LAB 3-2	LAB 3-3	BAF 1-1	BAF 1-2	BAF 1-3	BAF 2-1	BAF 2-2	BAF 2-3	BAF 3-1	BAF 3-2	BAF 3-3
Aglaopheniidae msp. 2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aglaopheniidae msp. 3	5	2	26	0	1	26	0	0	3	0	0	0	0	0	0	0	0	0
Aglaopheniidae msp. 4	0	0	0	0	0	0	4	0	1	0	0	0	0	0	0	0	0	0
Campanulariidae msp. 1	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Campanulariidae msp. 2	30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Campanulariidae msp. 3	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Campanulariidae msp. 4	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0
Campanulariidae msp. 5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Hydrozoa msp. 1	0	0	0	1	1	3	0	0	0	0	0	0	0	0	0	0	0	0
Octocorallia msp. 1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Octocorallia msp. 2	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Octocorallia msp. 3	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Octocorallia msp. 4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paragorgia cf. *arborea*	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Primnoa resedaeformis	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sertulariidae msp. 1	1	3	8	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Echinodermata	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**4**	**0**	**2**	**0**	**1**	**2**	**0**	**0**	**2**	**0**
Heliometra glacialis	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	1	0
Ophiuroidea msp. 1	0	0	0	0	0	0	0	0	2	0	0	0	1	2	0	0	1	0
Strongylocentrotus sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Crinoidea msp. 1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Mollusca	**0**	**0**	**0**	**0**	**0**	**2**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
Gastropoda msp. 1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Polyplacophora msp. 1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Porifera	**3**	**2**	**4**	**13**	**17**	**37**	**5**	**7**	**19**	**0**	**1**	**0**	**6**	**7**	**6**	**0**	**0**	**0**
Porifera msp. 1	1	0	0	0	1	7	1	3	1	0	0	0	0	0	0	0	0	0
Porifera msp. 5	0	1	0	3	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Porifera msp. 6	0	0	0	2	0	5	1	0	0	0	0	0	0	0	0	0	0	0
Demospongiae msp. 1	0	0	0	2	1	3	1	0	1	0	0	0	0	0	0	0	0	0
Lycopodina cf. cupressiformis	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Sycon msp. 1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Porifera msp. 7	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0
Iophon piceum	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Demospongiae msp. 2	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Porifera msp. 8	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Cladorhiza msp. 1	0	0	0	0	1	6	0	0	1	0	0	0	0	0	1	0	0	0
Porifera msp. 9	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Porifera msp. 10	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
Porifera msp. 22	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Haliclona xenomorpha	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0
Plocamionida ambigua	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Porifera msp. 11	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Porifera msp. 12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Porifera msp. 13	0	0	0	0	5	2	0	0	5	0	0	0	0	0	0	0	0	0
Spinularia cf. sarsii	1	0	0	2	3	5	0	0	1	0	0	0	0	0	0	0	0	0
Myxilla msp. 1	0	1	0	2	0	1	0	0	2	0	0	0	0	0	0	0	0	0
Porifera msp. 2	0	0	0	0	2	3	1	0	3	0	0	0	0	1	0	0	0	0
Tentorium semisuberites	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0
Porifera msp. 3	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
Porifera msp. 14	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0
Porifera msp. 4	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tunicata	**0**	**0**	**0**	**14**	**6**	**5**	**7**	**6**	**18**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**1**
Aplousobranchia msp. 1	0	0	0	10	6	2	6	6	15	0	0	0	0	0	0	0	0	0
Aplousobranchia msp. 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Aplousobranchia msp. 3	0	0	0	4	0	3	0	0	3	0	0	0	0	0	0	0	0	0
Ascidiacea msp. 4	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Tunicata msp. 1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Unknown	**2**	**0**	**0**	**2**	**0**	**0**	**1**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
Unknown msp. 1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Unknown msp. 2	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unknown msp. 3	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Unknown msp. 5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unknown msp. 6	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Supplementary table 3.5 Density of all erect-sessile and motile morphospecies present as one individual or colony overall (n = 1) per cm^2 on collected dropstones from Labrador Sea (LAB) and Baffin Bay (BAF).

Morphospecies	LAB 1-1	LAB 1-2	LAB 1-3	LAB 2-1	LAB 2-2	LAB 2-3	LAB 3-1	LAB 3-2	LAB 3-3	BAF 1-1	BAF 1-2	BAF 1-3	BAF 2-1	BAF 2-2	BAF 2-3	BAF 3-2	BAF 3-3	BAF 3-1
Candidae msp. 1	0	0	0	0	$8.9e^{3}$	0	0	0	0	0	0	$2.3e^{2}$	0	0	0	$1.1e^{2}$	$3.6e^{3}$	0
Cheilostomatida msp. 4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	$1.1e^{2}$	0	0
Crisiidae msp. 1	$1.2e^{1}$	$1.0e^{2}$	$6.7e^{1}$	$1.2e^{0}$	$4.4e^{1}$	$3.9e^{1}$	0	0	$2.0e^{1}$	0	0	0	0	0	0	0	$7.2e^{2}$	0
Horneridae msp. 1	0	0	0	0	0	0	$5.7e^{3}$	0	0	0	0	0	0	0	0	0	0	$1.1e^{2}$
Tubuliporidae msp. 2	0	0	0	0	$4.4e^{3}$	0	0	0	0	0	0	0	0	0	0	0	0	0
Crisiidae msp. 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	$1.1e^{2}$	0	0
Philodoporidae msp. 1	0	$3.4e^{3}$	0	$1.2e^{2}$	0	$3.5e^{2}$	0	$5.2e^{3}$	0	0	0	0	0	0	0	0	0	0
Aglaopheniidae msp. 1	0	0	0	0	0	0	$5.7e^{3}$	0	0	0	0	0	0	0	0	0	$1.8e^{2}$	0
Aglaopheniidae msp. 2	$1.3e^{3}$	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aglaopheniidae msp. 3	$6.4e^{3}$	$3.4e^{3}$	$8.7e^{2}$	0	$4.4e^{3}$	$1.0e^{1}$	0	0	$1.2e^{2}$	0	0	0	0	0	0	0	0	0
Aglaopheniidae msp. 4	0	0	0	0	0	0	$2.3e^{2}$	0	$3.9e^{3}$	0	0	0	0	0	0	0	0	0
Campanulariidae msp. 1	$1.3e^{1}$	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Campanulariidae msp. 2	$3.8e^{2}$	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Campanulariidae msp. 3	$6.4e^{3}$	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Campanulariidae msp. 4	0	0	0	0	0	0	0	0	$1.2e^{2}$	0	0	0	0	0	0	0	0	0
Campanulariidae msp. 5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	$3.4e^{3}$	0	0	0
Hydrozoa msp. 1	0	0	0	$5.9e^{3}$	$4.4e^{3}$	$1.2e^{2}$	0	0	0	0	0	0	0	0	0	0	0	0
Octocorallia msp. 1	0	0	0	0	0	0	0	0	$3.9e^{3}$	0	0	0	0	0	0	0	0	0
Octocorallia msp. 2	0	0	0	$1.2e^{2}$	0	0	0	0	$3.9e^{3}$	0	0	0	0	0	0	0	0	0
Octocorallia msp. 3	0	0	0	0	0	0	0	0	0	$6.4e^{3}$	0	0	0	0	0	0	0	0
Octocorallia msp. 4	$1.3e^{3}$	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paragorgia cf. arborea	$1.3e^{3}$	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Primnoa resedaeformis	$3.8e^{3}$	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sertulariidae msp. 1	$1.3e^{3}$	$5.2e^{3}$	$2.7e^{2}$	0	0	$3.9e^{3}$	0	0	0	0	0	0	0	0	0	0	0	0
Crinoidea msp. 1	0	0	0	0	$4.4e^{3}$	0	0	0	0	0	0	0	0	0	0	0	0	0
Porifera msp. 6	0	0	0	$1.2e^{2}$	0	$1.9e^{2}$	$5.7e^{3}$	0	0	0	0	0	0	0	0	0	0	0
Demospongiae msp. 1	0	0	0	$1.2e^{2}$	$4.4e^{3}$	$1.2e^{2}$	$5.7e^{3}$	0	$3.9e^{3}$	0	0	0	0	0	0	0	0	0
Lycopodina cf. cupressiformis	0	0	0	0	0	$7.7e^{3}$	0	0	0	0	0	0	0	0	0	0	0	0
Sycon msp. 1	0	0	0	0	$4.4e^{3}$	$3.9e^{3}$	$5.7e^{3}$	0	0	0	0	0	0	0	0	0	0	0
Iophon piceum	0	0	0	$5.9e^{3}$	$4.4e^{3}$	0	0	0	0	0	0	0	0	0	0	0	0	0
Demospongiae msp. 2	0	0	0	$5.9e^{3}$	0	$3.9e^{3}$	0	$5.2e^{3}$	0	0	0	0	0	0	0	0	0	0
Porifera msp. 8	0	0	0	0	0	0	0	$5.2e^{3}$	$3.9e^{3}$	0	0	0	0	0	0	0	0	0
Cladorhiza msp. 1	0	0	0	0	$4.4e^{3}$	$2.3e^{2}$	0	0	$3.9e^{3}$	0	0	0	0	0	$3.4e^{3}$	0	0	0
Porifera msp. 10	0	0	0	0	0	0	0	0	$7.9e^{3}$	0	0	0	0	0	0	0	0	0
Porifera msp. 15	0	0	0	0	0	0	0	0	$3.9e^{3}$	0	0	0	0	0	0	0	0	0
Haliclona xenomorpha	0	0	0	0	0	0	0	0	0	0	$4.6e^{3}$	0	0	0	$3.4e^{3}$	0	0	0
Porifera msp. 11	0	0	0	0	0	0	0	0	0	0	0	0	0	$5.9e^{3}$	$3.4e^{3}$	0	0	0
Spinularia cf. sarsii	$1.3e^{3}$	0	0	$1.2e^{2}$	$1.3e^{2}$	$1.9e^{2}$	0	0	$3.9e^{3}$	0	0	0	0	0	0	0	0	0
Myxilla msp. 1	0	$1.7e^{3}$	0	$1.2e^{2}$	0	$3.9e^{3}$	0	0	$7.9e^{3}$	0	0	0	0	0	0	0	0	0
Porifera msp. 2	0	0	0	0	$8.9e^{3}$	$1.2e^{2}$	$5.7e^{3}$	0	$1.2e^{2}$	0	0	0	0	$5.9e^{3}$	0	0	0	0
Tentorium semisuberites	0	0	0	0	0	0	0	0	0	0	0	0	0	$2.4e^{2}$	0	0	0	0
Porifera msp. 3	0	0	0	0	$4.4e^{3}$	0	0	0	$3.9e^{3}$	0	0	0	0	0	0	0	0	0
Porifera msp. 14	0	0	0	0	0	0	0	0	0	0	0	0	$4.0e^{2}$	0	0	0	0	0
Porifera msp. 4	0	0	$1.3e^{2}$	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aplousobranchia msp. 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	$1.1e^{2}$
Tunicata msp. 1	0	0	0	0	0	0	$5.7e^{3}$	0	0	0	0	0	0	0	0	0	0	0
Unknown msp. 1	0	0	0	0	0	0	0	0	0	$6.4e^{3}$	0	0	0	0	0	0	0	0
Unknown msp. 2	0	0	0	$1.2e^{2}$	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unknown msp. 3	0	0	0	0	0	0	$5.7e^{3}$	0	0	0	0	0	0	0	0	0	0	0

Supplementary table 3.6 Zonation of morphospecies on dropstones collected across the six sites, examined globally, by region (LAB and BAF), and by site (three per region). Data showing distance (mm) away from the sediment line that bisects the dropstone. Sediment line has set value of zero, so positive values are above the line and negative values below it. Error is standard deviation (absent for single individual or colony at the region or site level). Table excludes morphospecies occurring on a single stone (See Supplementary Table 3.3)

Morphospecies	Global	Region		Site					
		LAB	BAF	LAB 1	LAB 2	LAB 3	BAF 1	BAF 2	BAF 3
Annelida	11 ± 18.5	5.9 ± 9.9	15.4 ± 23	0 ± 0	10.2 ± 11.7	3.9 ± 8.9	24.9 ± 33.3	13 ± 11.3	5 ± 11.2
Annelida msp. 1	13.7 ± 22.6	0 ± 0	20.5 ± 25.3	0	0	0 ± 0	38 ± 53.8	21 ± 7	8.4 ± 14.5
Serpulidae msp. 1	8.3 ± 22	1.3 ± 3.5	13 ± 28.2	0	1.7 ± 4.2		39 ± 43.9	0 ± 0	0 ± 0
Spirorbidae msp. 1	9.4 ± 6.6	7.8 ± 7.6	12.5 ± 3.6	0		10.4 ± 6.9	10	15	
Terebellidae msp. 1	11.4 ± 13.3	14.5 ± 15.5	5 ± 7.1		22 ± 4.4	-8	5 ± 7.1		
Bryozoa	8.1 ± 15.1	9.4 ± 12.3	7 ± 17.2	10 ± 12.1	8 ± 7.4	9.4 ± 13.6	9.5 ± 25.8	5.3 ± 10.6	6.1 ± 9.7
Candidae msp. 1	5 ± 5.8	6.7 ± 5.8	0	0		10 ± 0		0	
Escharoides msp. 1	0 ± 0		0 ± 0				0	0 ± 0	0 ± 0
Schizporelloidea msp. 2	2.8 ± 8.4	4.2 ± 10.3	0 ± 0	12.5 ± 17.7	0	0 ± 0			0 ± 0
Cheilostomatida msp. 3	20.7 ± 3.6	20.7 ± 3.6		21	17	24			
Calloporidae msp. 1	29 ± 41.1	29 ± 41.1				29 ± 41.1			
Cheilostomatida msp. 5	8.5 ± 12.1	17	0	17			0		
Microporellidae msp. 1	5.7 ± 8.2	5.7 ± 8.2				5.7 ± 8.2			
Schizporelloidea msp. 1	0 ± 0	0 ± 0	0 ± 0	0		0 ± 0	0		0
Electridae msp. 1	4.8 ± 8.1		4.8 ± 8.1				0	6 ± 10.4	5 ± 8.7
Electridae msp. 2	7 ± 0	7 ± 0		7		7			
Escharellidae msp. 2	17.5 ± 24.8	35	0			35	0		
Crisiidae msp. 1	2.5 ± 7.1	0	2.9 ± 7.6			0	0 ± 0	0 ± 0	20
Alcyonidiidae msp. 1	0 ± 0		0 ± 0				0 ± 0		
Tubuliporidae msp. 1	15.7 ± 27.9	8.4 ± 11.4	25.4 ± 40.6	10 ± 17.4	5.7 ± 6.1	10 ± 14.2	50.7 ± 46.8	0 ± 0	
Hippothoidae msp. 1	0 ± 0		0 ± 0				0 ± 0		
Horneridae msp. 1	16 ± 11.4	8	24			8			24
Lichenoporidae msp. 1	0 ± 0	0 ± 0				0 ± 0			
Tubuliporidae msp. 3	7 ± 9.9	7 ± 9.9			14	0			
Philodoporidae msp. 1	12 ± 9.8		12 ± 9.8				8	10 ± 14.2	20
Cnidaria	21.2 ± 28.5	0 ± 0	24.5 ± 29.4	0	0 ± 0	0	37.4 ± 37.7	10.5 ± 11.8	18.3 ± 19
Aglaopheniidae msp. 1	0 ± 0	0	0			0			0
Aglaopheniidae msp. 3	22.4 ± 20.6		22.4 ± 20.6				29 ± 26.9	23.5 ± 5	0
Aglaopheniidae msp. 4	7.5 ± 10.7		7.5 ± 10.7						7.5 ± 10.7
Hydrozoa msp. 1	7 ± 12.2		7 ± 12.2					7 ± 12.2	
Octocorallia msp. 2	22.5 ± 24.8		22.5 ± 24.8					5	40
Sertulariidae msp. 1	19 ± 25.6		19 ± 25.6				25.4 ± 27.2	0	
Porifera	15.1 ± 19.2	6.9 ± 9.3	16.8 ± 20.3	8	6.8 ± 9.8		55 ± 27	13.8 ± 14.4	10.1 ± 12.8
Porifera msp. 1	13.5 ± 26.9		13.5 ± 26.9				67	0 ± 0	4.7 ± 8.1
Porifera msp. 5	24.7 ± 14.1		24.7 ± 14.1				26	38	10
Porifera msp. 6	17 ± 7.3		17 ± 7.3					18 ± 9.9	15
Demospongiae msp. 1	7.6 ± 17		7.6 ± 17					12.7 ± 22	0 ± 0
Sycon msp. 1	12 ± 17.5		12 ± 17.5					16 ± 22.7	4
Porifera msp. 7	2 ± 3.5	6	0 ± 0		6			0 ± 0	
Iophon piceum	21 ± 19.8		21 ± 19.8					21 ± 19.8	
Demospongiae msp. 2	6.4 ± 7.1		6.4 ± 7.1					7 ± 9.9	5
Porifera msp. 8	11.5 ± 16.3		11.5 ± 16.3						11.5 ± 16.3
Cladorhiza msp. 1	16.3 ± 22.7	0	21.7 ± 24.4		0			8.5 ± 12.1	48
Haliclona xenomorpha	4 ± 5.7	4 ± 5.7		8	0				
Plocamionida ambigua	9 ± 12.8	9 ± 12.8			9 ± 12.8				
Porifera msp. 11	8.5 ± 12.1	8.5 ± 12.1			8.5 ± 12.1				
Porifera msp. 13	23 ± 11.3		23 ± 11.3					19.5 ± 13.5	30
Spinularia cf. sarsii	27.2 ± 26.5		27.2 ± 26.5				74	13.4 ± 2.4	22
Myxilla msp. 1	15.8 ± 29.6		15.8 ± 29.6				60	1.5 ± 2.2	0
Porifera msp. 2	7 ± 14.1	3	8 ± 16		3			16 ± 22.7	0 ± 0
Porifera msp. 3	25.5 ± 14.9		25.5 ± 14.9					36	15
Tunicata	6 ± 7.5	9.5 ± 13.5	5.3 ± 6.7	19		0		4 ± 6.2	6.6 ± 7.7
Aplousobranchia msp. 1	7 ± 8.1		7 ± 8.1					4.7 ± 8.1	9.4 ± 9.1
Aplousobranchia msp. 3	3.7 ± 3.3		3.7 ± 3.3					3 ± 4.3	5

Supplementary table 3.7 Zonation of morphospecies on dropstones collected across six sites in Labrador Sea (LAB) and Baffin Bay (BAF). Data showing distance (mm) away from the sediment line that bisects the dropstone. Sediment line has set value of zero, so positive values are above the line and negative values below it.

Morphospecies	LAB 1-1	LAB 1-2	LAB 1-3	LAB 2-1	LAB 2-2	LAB 2-3	LAB 3-1	LAB 3-2	LAB 3-3	BAF 1-1	BAF 1-2	BAF 1-3	BAF 2-1	BAF 2-2	BAF 2-3	BAF 3-1	BAF 3-2	BAF 3-3
Annelida	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Annelida msp. 1	76.0	0.0	-	14.0	28.0	21.0	0.0	0.0	25.0	0.0	-	-	-	-	0.0	-	0.0	0.0
Annelida msp. 2	-	-	-	-	0.0	-	-	-	-	-	-	-	-	-	-	-	-	-
Polynoidae msp. 1	-	-	-	-	-	-	-	-	-	-	-	-	0.0	-	-	-	-	-
Polynoidae msp. 2	-	64.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Serpulidae msp. 1	70.0	8.0	-	0.0	-	0.0	-	0.0	0.0	-	0.0	-	-3.0	3.0	5.0	-	-	-
Sipunculida msp. 1	-	-	-	-	-	-	-	-	40.0	-	-	-	-	-	-	-	-	-
Spirorbidae msp. 1	-	10.0	-	15.0	-	-	-	-	-	0.0	-	-	-	-	-	18.0	5.0	8.0
Terebellidae msp. 1	0.0	-	10.0	-	-	-	-	-	-	-	-	-	17.0	24.0	25.0	-8.0	-	-
Arthropoda	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Amphipoda msp. 1	-	-	-	-	28.0	-	-	-	-	-	-	-	-	-	-	-	-	-
Amphipoda msp. 2	-	-	-	-	-	-	-	-	-	-	0.0	-	-	-	-	-	-	-
Arthropoda msp. 1	-	0.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Caprellidae msp. 1	-	-	-	0.0	32.0	40.0	0.0	-	0.0	-	-	-	-	-	-	-	-	-
Gammaridea msp. 1	-	57.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gammaridea msp. 2	-	-	-	-	-	17.0	-	-	-	-	-	-	-	-	-	-	-	-
Isopoda msp. 1	-	-	-	-	-	40.0	-	-	-	-	-	-	-	-	-	-	-	-
Pycnogonum msp. 1	-	-	-	-	-	30.0	-	-	-	-	-	-	-	-	-	-	-	-
Brachiopoda	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Terebratulida msp. 1	-	-	-	-	-	35.0	-	-	-	-	-	-	-	-	-	-	-	-
Bryozoa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Candidae msp. 1	-	-	-	-	0.0	-	-	-	-	-	-	0.0	-	-	-	10.0	10.0	-
Escharoides msp. 1	0.0	-	-	0.0	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-	-	-	-	-
Schizoporelloidae msp. 2	-	-	-	-	-	-	-	0.0	0.0	0.0	-	25.0	-	-	0.0	0.0	0.0	0.0
Cheilostomatida msp. 3	-	-	-	-	-	-	-	-	-	-	-	21.0	-	17.0	-	-	24.0	-
Calloporidae msp. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0	58.0	-
Schizoporelloidea msp. 3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	15.0	-	-
Cheilostomatida msp. 4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5.0	-	-
Cheilostomatida msp. 5	-	-	0.0	-	-	-	-	-	-	-	-	17.0	-	-	-	-	-	-
Microporellidae msp. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0	15.0	2.0
Smittinidae msp. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	15.0	-	-
Schizoporelloidea msp. 1	0.0	-	-	-	-	-	0.0	-	-	-	-	0.0	-	-	-	-	0.0	0.0
Electridae msp. 1	0.0	-	-	18.0	0.0	0.0	0.0	15.0	0.0	-	-	-	-	-	-	-	-	-
Cheilostomatida msp. 1	-	-	-	0.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cheilostomatida msp. 2	-	-	-	21.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Flustridae msp. 1	-	0.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Electridae msp. 2	-	-	-	-	-	-	-	-	-	-	7.0	-	-	-	-	-	7.0	-
Escharellidae msp. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	22.0	-
Escharellidae msp. 2	-	0.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	35.0	-
Crisiidae msp. 1	0.0	0.0	0.0	0.0	0.0	0.0	-	-	20.0	-	-	-	-	-	-	-	0.0	-
Ctenostomatida msp. 1	0.0	-	0.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tubuliporidae msp. 1	92.0	60.0	0.0	0.0	0.0	0.0	-	-	-	0.0	30.0	0.0	12.0	5.0	0.0	20.0	0.0	-
Hippothoidae msp. 1	0.0	0.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Horneridae msp. 1	-	-	-	-	-	-	24.0	-	-	-	-	-	-	-	-	-	-	8.0
Lichenoporidae msp. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0	0.0	-
Tubuliporidae msp. 2	-	-	-	-	35.0	-	-	-	-	-	-	-	-	-	-	-	-	-
Tubuliporidae msp. 3	-	-	-	-	-	-	-	-	-	-	-	-	-	14.0	-	-	0.0	-
Crisiidae msp. 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6.0	-	-
Philodoporidae msp. 1	-	8.0	-	20.0	-	0.0	-	20.0	-	-	-	-	-	-	-	-	-	-
Cnidaria	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Actiniaria msp. 1	-	63.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Actiniaria msp. 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0	-	-	-
Aglaopheniidae msp. 1	-	-	-	-	-	-	0.0	-	-	-	-	-	-	-	-	-	0.0	-
Aglaopheniidae msp. 2	52.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aglaopheniidae msp. 3	34.0	53.0	0.0	-	27.0	20.0	-	-	0.0	-	-	-	-	-	-	-	-	-
Aglaopheniidae msp. 4	-	-	-	-	-	-	15.0	-	0.0	-	-	-	-	-	-	-	-	-
Campanulariidae msp. 1	0.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Campanulariidae msp. 2	0.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Campanulariidae msp. 3	0.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Campanulariidae msp. 4	-	-	-	-	-	-	-	-	38.0	-	-	-	-	-	-	-	-	-
Campanulariidae msp. 5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0	-	-	-
Hydrozoa msp. 1	-	-	-	21.0	0.0	0.0	-	-	-	-	-	-	-	-	-	-	-	-
Octocorallia msp. 1	-	-	-	-	-	-	-	-	35.0	-	-	-	-	-	-	-	-	-
Octocorallia msp. 2	-	-	-	5.0	-	-	-	-	40.0	-	-	-	-	-	-	-	-	-

(Continued from previous page)

Morphospecies	LAB 1-1	LAB 1-2	LAB 1-3	LAB 2-1	LAB 2-2	LAB 2-3	LAB 3-1	LAB 3-2	LAB 3-3	BAF 1-1	BAF 1-2	BAF 1-3	BAF 2-1	BAF 2-2	BAF 2-3	BAF 3-1	BAF 3-2	BAF 3-3
Octocorallia msp. 3	-	-	-	-	-	-	-	-	-	0.0	-	-	-	-	-	-	-	-
Octocorallia msp. 4	110.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Paragorgia cf. arborea	85.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Primnoa resedaeformis	86.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sertulariidae msp. 1	0.0	54.0	22.0	-	-	0.0	-	-	-	-	-	-	-	-	-	-	-	-
Echinodermata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Heliometra glacialis	-	-	-	-	-	-	-	-	0.0	-	50.0	-	-	-	-	-	0.0	-
Ophiuroidea msp. 1	-	-	-	-	-	-	-	-	20.0	-	-	-	14.0	25.0	-	-	0.0	-
Strongylocentrotus sp.	-	-	-	-	-	-	-	-	-	-	0.0	-	-	-	-	-	-	-
Crinoidea msp. 1	-	-	-	-	0.0	-	-	-	-	-	-	-	-	-	-	-	-	-
Mollusca	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gastropoda msp. 1	-	-	-	-	-	18.0	-	-	-	-	-	-	-	-	-	-	-	-
Polyplacophora msp. 1	-	-	-	-	-	11.0	-	-	-	-	-	-	-	-	-	-	-	-
Porifera	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Porifera msp. 1	67.0	-	-	-	0.0	0.0	0.0	14.0	0.0	-	-	-	-	-	-	-	-	-
Porifera msp. 5	-	26.0	-	38.0	-	-	-	10.0	-	-	-	-	-	-	-	-	-	-
Porifera msp. 6	-	-	-	25.0	-	11.0	15.0	-	-	-	-	-	-	-	-	-	-	-
Demospongiae msp. 1	-	-	-	0.0	38.0	0.0	0.0	-	0.0	-	-	-	-	-	-	-	-	-
Lycopodina cf. cupressiformis	-	-	-	-	-	32.0	-	-	-	-	-	-	-	-	-	-	-	-
Sycon msp. 1	-	-	-	-	0.0	32.0	4.0	-	-	-	-	-	-	-	-	-	-	-
Porifera msp. 7	-	-	-	-	0.0	0.0	-	-	-	-	-	-	-	-	6.0	-	-	-
Iophon piceum	-	-	-	7.0	35.0	-	-	-	-	-	-	-	-	-	-	-	-	-
Demospongiae msp. 2	-	-	-	14.0	-	0.0	-	5.0	-	-	-	-	-	-	-	-	-	-
Porifera msp. 8	-	-	-	-	-	-	-	0.0	23.0	-	-	-	-	-	-	-	-	-
Cladorhiza msp. 1	-	-	-	-	0.0	17.0	-	-	48.0	-	-	-	-	-	0.0	-	-	-
Porifera msp. 9	-	-	-	-	-	-	-	0.0	-	-	-	-	-	-	-	-	-	-
Porifera msp. 10	-	-	-	-	-	-	-	-	18.0	-	-	-	-	-	-	-	-	-
Porifera msp. 15	-	-	-	-	-	-	-	-	7.0	-	-	-	-	-	-	-	-	-
Haliclona xenomorpha	-	-	-	-	-	-	-	-	-	-	8.0	-	-	-	0.0	-	-	-
Plocamionida ambigua	-	-	-	-	-	-	-	-	-	-	-	-	-	18.0	0.0	-	-	-
Porifera msp. 11	-	-	-	-	-	-	-	-	-	-	-	-	-	17.0	0.0	-	-	-
Porifera msp. 12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0	-	-	-
Porifera msp. 13	-	-	-	-	29.0	10.0	-	-	30.0	-	-	-	-	-	-	-	-	-
Spinularia cf. sarsii	74.0	-	-	12.0	16.0	12.0	-	-	22.0	-	-	-	-	-	-	-	-	-
Myxilla msp. 1	-	60.0	-	0.0	-	3.0	-	-	0.0	-	-	-	-	-	-	-	-	-
Porifera msp. 2	-	-	-	-	0.0	32.0	0.0	-	0.0	-	-	-	-	3.0	-	-	-	-
Tentorium semisuberites	-	-	-	-	-	-	-	-	-	-	-	-	-	28.0	-	-	-	-
Porifera msp. 3	-	-	-	-	36.0	-	-	-	15.0	-	-	-	-	-	-	-	-	-
Porifera msp. 14	-	-	-	-	-	-	-	-	-	-	-	-	2.0	-	-	-	-	-
Porifera msp. 4	-	-	18.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tunicata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aplousobranchia msp. 1	-	-	-	0.0	0.0	14.0	0.0	10.0	18.0	-	-	-	-	-	-	-	-	-
Aplousobranchia msp. 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0
Aplousobranchia msp. 3	-	-	-	0.0	-	6.0	-	-	5.0	-	-	-	-	-	-	-	-	-
Ascidiacea msp. 4	-	-	-	-	-	-	-	-	-	-	-	19.0	-	-	-	-	-	-
Tunicata msp. 1	-	-	-	-	-	-	0.0	-	-	-	-	-	-	-	-	-	-	-
Unknown	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unknown msp. 1	-	-	-	-	-	-	-	-	-	0.0	-	-	-	-	-	-	-	-
Unknown msp. 2	-	-	-	0.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unknown msp. 3	-	-	-	-	-	-	0.0	-	-	-	-	-	-	-	-	-	-	-
Unknown msp. 5	85.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unknown msp. 6	5.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Supplementary table 3.8 Intraspecific distances (mm) between neighbouring conspecifics for all morphospecies present on collected dropstones from six sites in the Labrador Sea (LAB) and Baffin Bay (BAF).

Morphospecies	LAB 1-1	LAB 1-2	LAB 1-3	LAB 2-1	LAB 2-2	LAB 2-3	LAB 3-1	LAB 3-2	LAB 3-3	BAF 1-1	BAF 1-2	BAF 1-3	BAF 2-1	BAF 2-2	BAF 2-3	BAF 3-1	BAF 3-2	BAF 3-3
Annelida	0	0	0	31.7	0	0	0	0	0	0	0	-	20.7	0	0	8.1	0	81.3
Annelida msp. 1	0	0	-	0	0	0	0	0	0	0	-	-	-	-	0	8.1	-	0
Serpulidae msp. 1	0	0	-	0	-	0	-	0	0	-	0	-	20.7	0	0	-	-	-
Spirorbidae msp. 1	-	0	-	31.7	-	-	-	-	-	0	-	-	-	-	-	0	0	81.3
Terebellidae msp. 1	0	-	0	-	-	-	-	-	-	-	-	-	0	0	0	-	0	-
Brachiopoda	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-	-	-	-
Terebratulida msp. 1	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-	-	-	-
Bryozoa	0	23.4	9.9	0	0	12.3	0	0	0	0	0	10.5	0	11.2	0	27.6	25.7	193.6
Bryozoa msp. 1	-	-	-	-	0	-	-	-	-	-	-	0	-	-	-	-	0	0
Escharoides msp. 1	0	-	-	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-
Schizoporelloidea msp. 2	-	-	-	-	-	-	-	0	0	0	-	0	-	-	0	27.6	0	25.1
Electridae msp. 1	-	-	-	-	-	-	-	-	-	-	-	0	-	0	-	-	-	65.5
Calloporidae msp. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4.2	0
Schizoporelloidea msp. 3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-
Cheilostomatida msp. 4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-
Cheilostomatida msp. 5	-	-	0	-	-	-	-	-	-	-	-	0	-	-	-	-	-	-
Microporellidae msp. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	51.5
Smittinidae msp. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-
Cheilostomatida msp. 2	0	-	-	-	-	-	0	-	-	-	-	3.5	-	-	-	0	-	17.3
Electridae msp. 3	0	-	-	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-
Cheilostomatida msp. 1	-	-	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cheilostomatida msp. 2	-	-	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Flustridae msp. 1	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Electridae msp. 2	-	-	-	-	-	-	-	-	-	-	0	-	-	-	-	-	-	13.9
Escharellidae msp. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Escharellidae msp. 2	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Crisiidae msp. 1	0	23.4	0.9	0	0	0	-	-	0	-	-	-	-	-	-	-	-	0
Alcyonidiidae msp. 1	0	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tubuliporidae msp. 1	0	0	9.0	0	0	0	-	-	-	0	0	7.0	0	11.2	0	-	11.3	14.4
Hippothoidae msp. 1	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Horneridae msp. 1	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	0	-	-
Lichenoporidae msp. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10.2	5.9
Tubuliporidae msp. 2	-	-	-	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-
Tubuliporidae msp. 3	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-	-	0
Crisiidae msp. 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-
Philodoporidae msp. 1	-	0	-	0	-	12.3	-	0	-	-	-	-	-	-	-	-	-	-
Cnidaria	86.4	6.4	19.2	0	0	80.2	19.3	-	126.1	0	-	-	-	-	18.4	-	-	16.9
Actiniaria msp. 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	18.4	-	-	-
Aglaopheniidae msp. 1	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-	-	16.9
Aglaopheniidae msp. 2	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aglaopheniidae msp. 3	69.2	0	10.9	-	0	4.5	-	-	56.6	-	-	-	-	-	-	-	-	-
Aglaopheniidae msp. 4	-	-	-	-	-	-	19.3	-	0	-	-	-	-	-	-	-	-	-
Campanulariidae msp. 1	1.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Campanulariidae msp. 2	6.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Campanulariidae msp. 3	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Campanulariidae msp. 4	-	-	-	-	-	-	-	-	69.5	-	-	-	-	-	-	-	-	-
Campanulariidae msp. 5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-	-
Hydrozoa msp. 1	-	-	-	0	0	75.7	-	-	-	-	-	-	-	-	-	-	-	-
Octocorallia msp. 1	-	-	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-
Octocorallia msp. 2	-	-	-	0	-	-	-	-	0	-	-	-	-	-	-	-	-	-
Octocorallia msp. 3	-	-	-	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-
Octocorallia msp. 4	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Paragorgia cf. arborea	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Primnoa resedaeformis	9.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sertulariidae msp. 1	0	6.4	8.3	-	-	0	-	-	-	-	-	-	-	-	-	-	-	-
Porifera	0	0	9.6	80.8	40.7	162.0	0	5.2	44.8	-	0	-	8.8	27.2	0	-	-	-
Porifera msp. 1	0	-	-	-	0	9.2	0	5.2	0	-	-	-	-	-	-	-	-	-
Porifera msp. 5	-	0	-	15.8	-	-	-	0	-	-	-	-	-	-	-	-	-	-
Porifera msp. 6	-	-	-	0	-	9.8	0	-	-	-	-	-	-	-	-	-	-	-
Demospongiae msp. 1	-	-	-	65.0	0	61.8	0	-	0	-	-	-	-	-	-	-	-	-
Lycopodina cf. cupressiformis	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-	-	-	-
Sycon msp. 1	-	-	-	-	0	0	0	-	-	-	-	-	-	-	-	-	-	-
Porifera msp. 7	-	-	-	-	0	0	-	-	-	-	-	-	-	-	0	-	-	-
Iophon piceum	-	-	-	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-
Demospongiae msp. 2	-	-	-	0	-	0	-	0	-	-	-	-	-	-	-	-	-	-
Porifera msp. 8	-	-	-	-	-	-	-	0	0	-	-	-	-	-	-	-	-	-
Cladorhiza msp. 1	-	-	-	-	0	22.7	-	-	0	-	-	-	-	-	0	-	-	-
Porifera msp. 9	-	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-	-
Porifera msp. 10	-	-	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-
Porifera msp. 15	-	-	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-
Haliclona xenomorpha	-	-	-	-	-	-	-	-	-	-	0	-	-	-	0	-	-	-
Plocamionida ambigua	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	-	-	-
Porifera msp. 11	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	-	-	-
Porifera msp. 12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-	-
Porifera msp. 13	-	-	-	-	0	0	-	-	0	-	-	-	-	-	-	-	-	-
Spinularia cf. sarsii	0	-	-	0	40.7	48.5	-	-	0	-	-	-	-	-	-	-	-	-
Myxilla msp. 1	-	0	-	0	-	0	-	-	0	-	-	-	-	-	-	-	-	-
Porifera msp. 2	-	-	-	-	0	10	0	-	44.8	-	-	-	-	0	-	-	-	-
Tentorium semisuberites	-	-	-	-	-	-	-	-	-	-	-	-	-	27.2	-	-	-	-

(Continued from previous page)

Morphospecies	LAB 1-1	LAB 1-2	LAB 1-3	LAB 2-1	LAB 2-2	LAB 2-3	LAB 3-1	LAB 3-2	LAB 3-3	BAF 1-1	BAF 1-2	BAF 1-3	BAF 2-1	BAF 2-2	BAF 2-3	BAF 3-1	BAF 3-2	BAF 3-3
Porifera msp. 3	-	-	-	-	0	-	-	-	0	-	-	-	-	-	-	-	-	-
Porifera msp. 14	-	-	-	-	-	-	-	-	-	-	-	-	8.8	-	-	-	-	-
Porifera msp. 4	-	-	9.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tunicata	-	-	-	81.5	2.7	10.7	13.0	9.9	115.3	-	-	0	-	-	-	0	-	-
Aplousobranchia msp. 1	-	-	-	14.8	2.7	0	13.0	9.9	10.3	-	-	-	-	-	-	-	-	-
Aplousobranchia msp. 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-
Aplousobranchia msp. 3	-	-	-	66.7	-	10.7	-	-	105.0	-	-	-	-	-	-	-	-	-
Ascidiacea msp. 4	-	-	-	-	-	-	-	-	-	-	-	0	-	-	-	-	-	-
Tunicata msp. 1	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-	-	-
Unknown	-	-	-	0	-	-	0	-	-	0	-	-	-	-	-	-	-	-
Unknown msp. 1	-	-	-	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-
Unknown msp. 2	-	-	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unknown msp. 3	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-	-	-

Supplementary table 3.9 Interspecific distances (mm) between neighbouring allospecifics for all morphospecies present on collected dropstones from six sites in the Labrador Sea (LAB) and Baffin Bay (BAF).

Morphospecies	LAB 1-1	LAB 1-2	LAB 1-3	LAB 2-1	LAB 2-2	LAB 2-3	LAB 3-1	LAB 3-2	LAB 3-3	BAF 1-1	BAF 1-2	BAF 1-3	BAF 2-1	BAF 2-2	BAF 2-3	BAF 3-1	BAF 3-2	BAF 3-3
Annelida	**0**	**3.2**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**3.1**	**0**	**-**	**0**	**0**	**6.3**	**5.2**	**7.9**	**3.6**
Annelida msp. 1	0	2.8	-	0	0	0	0	0	0	6.2	-	-	-	-	19.0	6.9	-	7.2
Serpulidae msp. 1	0	0	-	0	-	0	-	0	0	-	0	-	0	0	0	-	-	-
Spirorbidae msp. 1	-	6.9	-	0	-	-	-	-	-	0	-	-	-	-	-	3.4	0	0
Terebellidae msp. 1	0	-	0	-	-	-	-	-	-	-	-	-	0	0	0	-	15.9	-
Brachiopoda	-	-	-	-	-	4.8	-	-	-	-	-	-	-	-	-	-	-	-
Terebratulida msp. 1	-	-	-	-	-	4.8	-	-	-	-	-	-	-	-	-	-	-	-
Bryozoa	**1.8**	**2.1**	**0.6**	**0**	**0**	**0.6**	**0**	**0**	**0**	**0**	**0**	**1.8**	**3.6**	**4.0**	**5.0**	**6.8**	**0.8**	**4.4**
Bryozoa msp. 1	-	-	-	-	0	-	-	-	-	-	-	4.3	-	-	-	-	0	15.0
Escharoides msp. 1	0	-	-	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-
Schizoporelloidea msp. 2	-	-	-	-	-	-	-	0	0	0	-	0	-	-	0	5.8	1.7	2.2
Electridae msp. 1	-	-	-	-	-	-	-	-	-	-	-	3.8	-	6.0	-	-	-	3.9
Calloporidae msp. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.4	2.1
Schizoporelloidea msp. 3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-
Cheilostomatida msp. 4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4.1	-
Cheilostomatida msp. 5	-	-	0	-	-	-	-	-	-	-	-	2.5	-	-	-	-	-	-
Microporellidae msp. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5.0	0	0
Smittinidae msp. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-
Cheilostomatida msp. 2	0	-	-	-	-	-	0	-	-	-	-	0	-	-	-	8.8	-	3.9
Electridae msp. 3	0	-	-	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-
Cheilostomatida msp. 1	-	-	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cheilostomatida msp. 2	-	-	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Flustridae msp. 1	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Electridae msp. 2	-	-	-	-	-	-	-	-	-	-	0	-	-	-	-	-	-	3.4
Escharellidae msp. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4.9
Escharellidae msp. 2	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.5
Crisiidae msp. 1	0	0	0	0	0	0	-	-	0	-	-	-	-	-	-	-	-	0
Alcyonidiidae msp. 1	0	-	2.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tubuliporidae msp. 1	10.8	0	0	0	0	3.2	-	-	-	0	0	0	3.6	1.6	10	-	0	2.3
Hippothoidae msp. 1	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Horneridae msp. 1	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	7.6	-	-
Lichenoporidae msp. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	3.0
Tubuliporidae msp. 2	-	-	-	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-
Tubuliporidae msp. 3	-	-	-	-	-	-	-	-	-	-	-	-	-	4.4	-	-	-	12.8
Crisiidae msp. 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-
Philodoporidae msp. 1	-	12.7	-	0	-	0	-	0	-	-	-	-	-	-	-	-	-	-
Cnidaria	**3.9**	**6.3**	**0.8**	**0**	**0**	**0**	**0**	**-**	**0**	**0**	**-**	**-**	**-**	**-**	**0**	**-**	**-**	**1.8**
Actiniaria msp. 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-	-
Aglaopheniidae msp. 1	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-	-	1.8
Aglaopheniidae msp. 2	17.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aglaopheniidae msp. 3	9.9	12.6	1.6	-	0	0	-	-	0	-	-	-	-	-	-	-	-	-
Aglaopheniidae msp. 4	-	-	-	-	-	-	0	-	0	-	-	-	-	-	-	-	-	-
Campanulariidae msp. 1	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Campanulariidae msp. 2	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Campanulariidae msp. 3	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Campanulariidae msp. 4	-	-	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-
Campanulariidae msp. 5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-	-
Hydrozoa msp. 1	-	-	-	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-
Octocorallia msp. 1	-	-	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-
Octocorallia msp. 2	-	-	-	0	-	-	-	-	0	-	-	-	-	-	-	-	-	-
Octocorallia msp. 3	-	-	-	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-
Octocorallia msp. 4	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Paragorgia cf. arborea	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Primnoa resedaeformis	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sertulariidae msp. 1	0	0	0	-	-	0	-	-	-	-	-	-	-	-	-	-	-	-
Porifera	**0**	**6.0**	**0**	**0**	**0**	**0.2**	**0**	**0**	**0**	**-**	**0**	**-**	**0**	**3.0**	**0**	**-**	**-**	**-**
Porifera msp. 1	0	-	-	-	0	0	0	0	0	-	-	-	-	-	-	-	-	-
Porifera msp. 5	-	12.0	-	0	-	-	-	0	-	-	-	-	-	-	-	-	-	-
Porifera msp. 6	-	-	-	0	-	0	0	-	-	-	-	-	-	-	-	-	-	-
Demospongiae msp. 1	-	-	-	0	0	0	0	-	0	-	-	-	-	-	-	-	-	-
Lycopodina cf. cupressiformis	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-	-	-	-
Sycon msp. 1	-	-	-	-	0	0	0	-	-	-	-	-	-	-	-	-	-	-
Porifera msp. 7	-	-	-	-	0	0	-	-	-	-	-	-	-	-	0	-	-	-

(Continued from previous page)

Morphospecies	LAB 1-1	LAB 1-2	LAB 1-3	LAB 2-1	LAB 2-2	LAB 2-3	LAB 3-1	LAB 3-2	LAB 3-3	BAF 1-1	BAF 1-2	BAF 1-3	BAF 2-1	BAF 2-2	BAF 2-3	BAF 3-1	BAF 3-2	BAF 3-3
Iophon piceum	-	-	-	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-
Demospongiae msp. 2	-	-	-	0	-	0	-	0	-	-	-	-	-	-	-	-	-	-
Porifera msp. 8	-	-	-	-	-	-	-	0	0	-	-	-	-	-	-	-	-	-
Cladorhiza msp. 1	-	-	-	-	0	0	-	-	0	-	-	-	-	-	0	-	-	-
Porifera msp. 9	-	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-	-
Porifera msp. 10	-	-	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-
Porifera msp. 15	-	-	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-
Haliclona xenomorpha	-	-	-	-	-	-	-	-	-	-	0	-	-	-	0	-	-	-
Plocamionida ambigua	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	-	-	-
Porifera msp. 11	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	-	-	-
Porifera msp. 12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-	-
Porifera msp. 13	-	-	-	-	0	1.8	-	-	0	-	-	-	-	-	-	-	-	-
Spinularia cf. sarsii	0	-	-	0	0	0	-	-	0	-	-	-	-	-	-	-	-	-
Myxilla msp. 1	-	0	-	0	-	0	-	-	0	-	-	-	-	-	-	-	-	-
Porifera msp. 2	-	-	-	-	0	0	0	-	0	-	-	-	-	9.1	-	-	-	-
Tentorium semisuberites	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-	-	-
Porifera msp. 3	-	-	-	-	0	-	-	-	0	-	-	-	-	-	-	-	-	-
Porifera msp. 14	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-	-	-	-
Porifera msp. 4	-	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tunicata	**-**	**-**	**-**	**0**	**0**	**0**	**0**	**0**	**0**	**-**	**-**	**0**	**-**	**-**	**-**	**0**	**-**	**-**
Aplousobranchia msp. 1	-	-	-	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-
Aplousobranchia msp. 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-
Aplousobranchia msp. 3	-	-	-	0	-	0	-	-	0	-	-	-	-	-	-	-	-	-
Ascidiacea msp. 4	-	-	-	-	-	-	-	-	-	-	-	0	-	-	-	-	-	-
Tunicata msp. 1	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-	-	-
Unknown	**-**	**-**	**-**	**0**	**-**	**-**	**0**	**-**	**-**	**0**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**
Unknown msp. 1	-	-	-	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-
Unknown msp. 2	-	-	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unknown msp. 3	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-	-	-

Supplementary table 3.10 Occurrences of secondary colonization and epibiosis by allospecifics and conspecifics on each morphospecies present with documented colonizers and epibionts on dropstones collected from six sites in the Labrador Sea and Baffin Bay.

Morphospecies	Actinaria msp. 1	Actinaria msp. 2	Aglaopheniidae msp. 1	Aglaopheniidae msp. 2	Aglaopheniidae msp. 3	Aglaopheniidae msp. 4	Amphipoda msp. 1	Amphipoda msp. 2	Annelida msp. 1	Aplousobranchia msp. 1	Aplousobranchia msp. 2	Aplousobranchia msp. 3	Ascidiacea msp. 4	Campanulariidae msp. 1	Campanulariidae msp. 2	Campanulariidae msp. 3	Campanulariidae msp. 4	Campanulariidae msp. 5	Caprellidae msp. 1	Cheilostomatida msp. 1	Schizoporelloidea msp. 2	*Escharoides* msp. 1	Microporellidae msp. 1	Schizoporelloidea msp. 1	Electridae msp. 1	Escharellidae msp. 2	Crisiidae msp. 1	Tubuliporidae msp. 1	Hippothoidae msp. 1	Horneridae msp. 1	Lichenoporidae msp. 1	Gammaridea msp. 1	Gastropoda msp. 1	Heliometra glacialis	Hydrozoa msp. 1	Isopoda msp. 1	Octocorallia msp. 1	Octocorallia msp. 2	Octocorallia msp. 4	Ophiuroidea msp. 1	Philodoporidae msp. 1	Polynoidae msp. 1	Polynoidae msp. 2	Porifera msp. 1	Porifera msp. 5	Paragorgia cf. arborea	Porifera msp. 6	Demospongiae msp. 1	*Sycon msp. 1*	*Iophon piceum*	Demospongiae msp. 2	Porifera msp. 8	*Cladorhiza msp. 1*	Porifera msp. 10	Porifera msp. 15	*Haliclona xenomorpha*	Porifera msp. 12	Porifera msp. 13	*Spinularia cf. sarsii*	Porifera msp. 2	Porifera msp. 3	*Primnoa resedaeformis*	Serpulidae msp. 1	Sertulariidae msp. 1	Spirorbidae msp. 1	Terebellidae msp. 1	Crinoidea msp. 1	Unknown msp. 5	Unknown msp. 6
Annelida	0	1	0	0	0	0	0	0	1	2	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Annelida msp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Serpulidae msp. 1	0	0	0	0	0	0	0	0	1	2	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Terebellidae msp. 1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bryozoa	1	0	1	1	8	1	0	0	7	9	1	3	2	3	0	0	2	0	3	6	2	0	1	0	4	2	8	1	2	1	1	0	0	3	0	2	1	1	0	3	1	0	1	5	3	0	2	2	1	2	1	1	1	2	1	0	0	2	2	2	3	0	3	2	1	1	1	0	1
Escharoides msp. 1	0	0	0	0	1	0	0	0	2	4	0	2	0	1	0	0	1	0	0	1	1	0	0	0	3	0	2	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	2	0	0	1	1	0	2	1	0	1	1	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0
Schizoporelloidea msp. 2	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
Smittinidae msp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Schizoporelloidea msp. 1	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Electridae msp. 1	0	0	1	0	3	1	0	0	3	4	0	1	0	1	0	0	1	0	0	4	1	0	0	0	1	0	2	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	3	1	0	1	1	1	0	0	1	0	1	1	0	0	0	1	1	1	0	1	0	0	0	0	0	0
Flustridae msp. 1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Electridae msp. 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Crisiidae msp. 1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	0	1
Alcyonidiidae msp. 1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tubuliporidae msp. 1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Hippothoidae msp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Horneridae msp. 1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tubuliporidae msp. 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tubuliporidae msp. 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Philodoporidae msp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Cnidaria	1	0	0	0	1	0	1	0	1	3	0	0	0	1	1	1	0	0	4	2	0	1	0	1	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0	0	0
Actinaria msp. 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Aglaopheniidae msp. 1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aglaopheniidae msp. 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aglaopheniidae msp. 3	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aglaopheniidae msp. 4	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Campanulariidae msp. 4	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Cnidaria msp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paragorgia cf. arborea	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0
Primnoa resedaeformis	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
Sertulariidae msp. 1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mollusca	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Polyplacophora msp. 1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Porifera	0	0	0	0	1	0	0	1	3	6	0	0	0	1	1	0	0	1	0	2	2	0	0	0	2	0	2	0	0	0	0	0	1	1	1	0	0	0	1	3	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	4	0	1	0
Porifera msp. 1	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Porifera msp. 5	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Porifera msp. 7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Porifera msp. 8	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cladorhiza msp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Porifera msp. 9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Porifera msp. 10	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haliclona xenomorpha	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Plocamionida ambigua	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Porifera msp. 13	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Porifera msp. 2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tentorium semisuberites	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Porifera msp. 3	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Porifera msp. 14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0

Chapter 4: General Conclusion

4.1 Thesis summary

This thesis used a combination of artificial substratum deployments and dropstone collections to assess the recruitment and colonization preferences of epibenthic taxa to hard substrata in the deep sea of eastern Canada. It contributed to the current knowledge base by: (1) examining biodiversity of early recruits (≤1 y) for the first time on four common types of natural and artificial hard substrata to better understand the role substratum plays in larval recruitment; and (2) analyzing regional biodiversity, zonation, and ecological interactions among morphospecies forming well established communities on targeted dropstones.

In Chapter 2, the experimental results showed that the type of hard substratum influences the richness, abundance, diversity, and coverage of recruits, perhaps due to the different features associated with each substratum and how morphospecies utilize them. Settlement frames composed of four different types of substrata (three blocks each of mesh, plastic, stone; plus one panel of wood) had all individuals or colonies identified, counted, and their surficial position in relation to the substratum features defined. This study elaborates on the limited number of previous findings from fewer substratum types, such as Meyer-Kaiser et al. (2019) who found that deep-sea hard-bottom larvae in the Arctic exhibit preferences towards or against certain substrata like stone and plastic, as well as in relation to environmental cues such as altitude above the sea floor. In my study, each substratum type hosted unique morphospecies or dominated in different metrics, such as mesh dominating in richness and wood dominating in coverage, suggesting that offering fewer substratum types in experimental conditions may not result in a holistic view of the community present. Importantly, features of the substratum

beyond material appear to play a role as well. For example, flat plastic panels had lower species abundances than stones in Meyer-Kaiser et al. (2019), while more surficially complex plastic here had higher abundances than smoother stones in that study. The geographic site at which the settlement frames were deployed also had an effect on the recruitment patterns seen here, with variations in factors such as the altitude above the sea floor, depth, and whether the frame was partially obstructed by the deployment apparatus appearing to modulate morphospecies richness, abundance, and diversity.

Chapter 3 investigated the regional differences in morphospecies richness, abundance, coverage, and diversity on dropstones collected in the Labrador Sea and Baffin Bay, as well as the zonation patterns and preferences of the sessile hard-bottom taxa that made up these established communities. It also explored whether intra- and interspecific interactions affect regional patterns and zonation. The Labrador Sea dropstones dominated in all metrics over Baffin Bay, suggesting that latitudinal or depth gradients play a role in the regional dissimilarity; all stones also universally exhibited higher richness and abundance than the surrounding finer-grained substrata (i.e., mud, gravel). This aligns with and builds on previous work that found richness and abundance of species to be higher on isolated hard substrata than in finer-grained sediments (Amon et al. 2016; Meyer et al. 2016; Ziegler et al. 2017) and differences in hard-bottom species assemblages existing along latitudinal or depth gradients (reviewed by Canning-Clode 2009; Schulz et al. 2010; Vedenin et al. 2021). Encrusting bryozoans were found consistently positioned low in zonation, often near the stone-sediment boundary line, while coral colonies (*Primnoa resedaeformis*) occurred highest, corroborating previous findings that encrusting bryozoans position themselves on the sides of stones to avoid sedimentation (Barnes et al. 1996) and erect-growth suspension-feeders – such as corals – position themselves near the

tops of isolated hard substrata (Mullineaux 1988, 1989; Meyer-Kaiser et al. 2019). Morphospecies occurring either as singletons or in groups suggested that intraspecific interactions could affect the presence and positioning of conspecifics, while evidence of secondary colonization of primary colonizers, adjacent colonization, and overgrowth suggests the same could be true for allospecifics. Secondary colonization and epibiosis were common, perhaps indicating these processes are crucial to community building and succession; aligning with previous studies that suggest that certain epibionts required a specific host for recruitment (Meyer et al. 2016).

Together, the two chapters show that recruitment to and colonization of hard substrata in the deep sea result from complex processes influenced by many factors that are both organismal and environmental. The early-successional morphospecies present on the settlement frames in Chapter 2 differed both between the available substrata and from the morphospecies present in the well-established dropstone communities of Chapter 3, which also differed between regions. These differences indicate that deep-sea hard-bottom communities are slow-growing and undergo successional stages driven by environmental or substratum preferences, and by inter- and intraspecific interactions. In order to ensure a more holistic understanding of these communities, and how they might recover from disturbances, further experimental and observational studies must be adjusted to examine all stages and types of community.

4.2 Future directions

Deep-sea communities are not well understood, in particular in the ways that they can resist to and recover from disturbances. Examination of communities of different ages (i.e., primary recruits versus mature communities) allows us to better understand the stages of succession, and how increasing anthropogenic impacts in the deep sea might affect them.

Moving forward, and assuming that logistical challenges can be overcome, experimental studies of hard-bottom communities in the polar and subpolar deep seas would benefit from long-term and multi-stage study of community establishment (as opposed to the two "snapshots" of time used here), higher replication in deployments and collections to more thoroughly control for fine scale environmental factors (i.e., multiple recruitment panels deployed on the same mooring, or more dropstones collected more closely together), and further examination of the difference in community structuring between artificial and natural substrata (e.g., cleaned dropstones instead of commercial basalt blocks). Community resilience to disturbance is best understood through examinations of later-stage, established communities, while recovery is evidenced through early-successional species, and the characterization of different stages would not only provide novel information to the field but also offer insight into the time frames and structure of succession in the deep sea.

In Chapter 2, substratum type blocks were closely attached within a single frame, which is a common practice in the field. Colonization by hydrozoans along attachment bolts and the frame itself suggest that actual recruitment preferences may have been obscured by expansion of a colony across the connections through the frame. Future work could involve more distance between blocks or a barrier to slow horizontal colonization; as different species recruit and grow at different rates, this could increase the surety of locating specific recruitment points and associated preferences, as well as reduce any loss of recruits during the deployed time frame due to competition for space. Further, it is common in shallow-water studies to recover frames at the same site at different time points, such as every month, which deep-sea studies could benefit from doing as well in order to get a more complete view of recruitment. This could be difficult or impossible to do in the polar seas due to seasonal ice cover or regular frame recovery becoming

cost prohibitive. As Meyer-Kaiser et al. (2019) did with regular observations at a deployed settlement apparatus at the HAUSGARTEN observatory in the Fram Strait, it could be that these studies would need to be undertaken by more permanent facilities. Finally, further environmental monitoring in the immediate surroundings of the frame could explore other factors in the patterns seen between sites, e.g., implementing complimentary equipment such as a current meter or water sampling could shed insight on the fine-scale environment surrounding the frames.

The study in Chapter 3 also demonstrated that the colonizers visible on ROV camera or video footage were few compared to what was later observed post collections. Due to the opportunistic nature of the initial coarse comparison using video footage alone and the limitations in zooming capabilities by the ROV *ASTRID* used in this study, it is possible more morphospecies could have been observed in situ with a more powerful camera or purposeful video surveys, although many of the morphospecies observed in the laboratory analysis required microscopy to locate and to distinguish from other morphologically similar taxa. In particular, encrusting bryozoans – which were the richest phylum on the Baffin Bay dropstones, and second only to sponges in the Labrador Sea – were either not seen or had to be identified as one morphospecies by camera footage. Large, erect growth by sponges, corals, and tunicates also obscured the rock surface and associated colonizing morphospecies below. While video surveys already require investment of time, effort, and financial support, they could benefit from pairing with a small sampling of dropstones (as used here) to assist with comparisons between visible and actual colonization. This would be a valuable addition to the field, as without fine-scale examinations of collected substrata it is likely that smaller, more inconspicuous colonizers are missed, and thus important colonizing and biodiversity patterns can be overlooked.

Both studies could be built upon with similar studies being undertaken with complimentary larval collectors in order to compare the larval supply with the established community. This could increase our understanding of how community formation occurs, as few morphospecies repeated between the early communities detected on the settlement frames and the established communities present on dropstones. Pairing settlement frame and larval collector deployments and recovering replicates over shorter and longer time frames, as well as multiplying dropstone collections from the same site, could help clarify how some of these processes occur and over what temporal and geographic scales.

4.3 References

Amon DJ, Ziegler AF, Dahlgren TG, Glover AG, Goineau A, Gooday AJ, Wiklund H, Smith CR. 2016. Insights into the abundance and diversity of abyssal megafauna in a polymetallic-nodule region in the eastern Clarion-Clipperton Zone. Sci Rep. 6:30492. doi:10.1038/srep30492.

Barnes DKA, Rothery P, Clarke A. 1996. Colonisation and development in encrusting communities from the Antarctic intertidal and sublittoral. J Exp Mar Bio Ecol. 196(1):251–265. doi:10.1016/0022-0981(95)00132-8.

Canning-Clode J. 2009. Latitudinal patterns of species richness in hard-bottom communities. In: Wahl M, editor. Marine Hard Bottom Communities: Patterns, Dynamics, Diversity, and Change. Berlin, Heidelberg: Springer. (Ecological Studies). p. 81–87. https://doi.org/10.1007/b76710_5.

Meyer KS, Young CM, Sweetman AK, Taylor J, Soltwedel T, Bergmann M. 2016. Rocky islands in a sea of mud: biotic and abiotic factors structuring deep-sea dropstone communities. Mar Ecol Prog Ser. 556:45–57. doi:10.3354/meps11822.

Meyer-Kaiser K, Bergmann M, Soltwedel T, Klages M. 2019. Recruitment of Arctic deep-sea invertebrates: Results from a long-term hard-substrate colonization experiment at the Long-Term Ecological Research observatory HAUSGARTEN. Limnol Oceanogr. 64(5):1924–1938. doi:10.1002/lno.11160.

Mullineaux LS. 1988. The role of settlement in structuring a hard-substratum community in the deep sea. J Exp Mar Bio Ecol. 120(3):247–261. doi:10.1016/0022-0981(88)90005-6.

Mullineaux LS. 1989. Vertical distributions of the epifauna on manganese nodules: implications for settlement and feeding. Limnol Oceanogr. 34(7):1247–1262.

Schulz M, Bergmann M, von Juterzenka K, Soltwedel T. 2010. Colonisation of hard substrata along a channel system in the deep Greenland Sea. Polar Biol. 33(10):1359–1369. doi:10.1007/s00300-010-0825-9.

Vedenin A, Galkin S, Mironov AN, Gebruk A. 2021. Vertical zonation of the Siberian Arctic benthos: bathymetric boundaries from coastal shoals to deep-sea Central Arctic. PeerJ. 9:e11640–e11640. doi:10.7717/peerj.11640.

Ziegler AF, Smith CR, Edwards KF, Vernet M. 2017. Glacial dropstones: islands enhancing seafloor species richness of benthic megafauna in West Antarctic Peninsula fjords. Mar Ecol Prog Ser. 583:1–14. doi:10.3354/meps12363.