COMMUNITY ASSEMBLY OF BENTHIC INVERTEBRATES ON ISLAND-LIKE MARINE HARD SUBSTRATA

by

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DISSERTATION ABSTRACT

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Most of the seafloor is soft sediment, so hard substrata are isolated and island-like. In this dissertation, I explore how species distribution patterns on isolated marine hard substrata resemble terrestrial island communities, drawing on classical island biogeography theory and assembly rules, and describe how benthic invertebrate communities assemble in these island-like habitats.

Higher species richness occurred on larger substrata (dropstones and shipwrecks), paralleling terrestrial island communities. However, while larger islands have greater habitat diversity and primary productivity, marine hard substrata are simpler habitats. Greater elevation in the benthic boundary layer may expose fauna to faster current, higher food supply and larval flux. Substrata located closer together had more similar communities, another pattern that resembles terrestrial islands. Dropstone fauna had a clumped distribution, indicating that larvae may disperse among substrata located close together, resulting in similar communities.

In Svalbard fjords, benthic megafaunal communities were significantly different between Arctic- and Atlantic-influenced fjords. Depth and temperature had the greatest influence, with the highest diversity occurring in cold Rijpfjorden and on the north Svalbard shelf.

Recruitment in Svalbard fjords was spatially and temporally variable, with lower recruitment in Rijpfjorden than in Atlantic-influenced fjords and lower recruitment at greater depth. Most of the recruits in Svalbard fjords were fast-growing, poor-competitive opportunists. On shipwrecks, communities showed two mechanisms of colonization: mobile fauna with long-dispersing planktotrophic larvae, and encrusting fauna with lecithotrophic larvae. Encrusting species reproduce asexually to cover the wreck surface, and philopatry may build up dense populations, leading to uneven communities.

On terrestrial islands, non-random co-occurrence is attributed to interspecific competition, but for marine substrata, there may not be a relationship. Fauna were distributed randomly on settlement plates in Svalbard fjords, even when interspecific competition was observed. On dropstones, some morphotypes co-occurred non-randomly in the absence of overgrowth competition. Non-random co-occurrence on isolated marine hard substrata may be a result of restricted larval dispersal (for pairs co-occurring less than by chance) or epibiontism (for pairs co-occurring more often than by chance). While species distribution patterns on island-like marine hard substrata resemble terrestrial islands, the mechanisms are not necessarily the same.

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from Day One.

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CHAPTER I

GENERAL INTRODUCTION

The vast seafloor, accounting for some 71% of the surface of the planet, is mostly blanketed by soft sediments. This soft, muddy bottom is, however, dotted with various hard objects. Natural hard substrata are present along rocky shores, in subtidal rocky reefs and coral reefs, and in the form of random stones deposited on the seafloor. Other hard-substratum habitats occur at hydrothermal vents, cold seeps, whale falls, and seamounts in the deep sea (Young 2009). Anthropogenic hard substrata, the inevitable by-products of industry and commerce, are installed purposefully (i.e., oil platforms, wave-based energy generators) or inadvertently (i.e.,, shipwrecks, lost shipping containers, litter), on the seafloor (Taylor et al. 2014, Bergmann et al. 2015). Hard substrata on the seafloor are most often isolated, surrounded by sand or mud, and can be considered islands.

Throughout this dissertation, I define “islands” as habitats separated from similar habitats by a continuous, dissimilar habitat, i.e., stones surrounded by the soft, muddy seafloor. This definition is in line with the “individual-scale” definition of an island: a crucial phase of the life cycle of individual organisms takes place by necessity within the boundaries of the island, but the population on a single island is not necessarily isolated from the populations on other islands (Haila 1990). In this case, the life cycle phase taking place on marine hard-substratum islands is the benthic adult phase (for sessile benthic invertebrates).

There already exists an extensive literature dealing with the ecology of islands and island-like habitats, dating back to the 1960s and 1970s. In this dissertation, I consider two landmark publications, MacArthur and Wilson's (1967) island biogeography monograph and Diamond's (1975a) assembly rules. The basic tenets of these two theories have been applied to isolated populations and communities of organisms ranging from freshwater diatoms (Heino and Soininen 2005) to desert rodents (Brown et al. 2000). I begin by reviewing the elements of each theory that have survived in the literature and distilling the two works into a list of five species distribution patterns that can be applied to isolated marine hard substrata. I then review what is known about the ecology of these island-like marine habitats, to what extent they reflect the expected species distribution patterns and resemble terrestrial islands, and what mechanisms may be responsible. At the end of the Chapter II, I define critical gaps in research that may be filled by further investigations into the biology and ecology of species on marine island-like substrata.

Chapters III and IV of this dissertation concern species distribution patterns on isolated hard substrata on the seafloor, including shipwrecks in the northwestern Atlantic and dropstones in the Fram Strait. Using images and video recorded with underwater vehicles, I observe and document the species distribution patterns on these hard-substratum islands. I then apply the five species distribution patterns from Chapter II to the shipwreck and dropstone communities, in each case testing the hypothesis that marine island-like habitats have the same species distribution pattern observed on terrestrial islands. Potential mechanisms leading to the observed species distribution patterns are discussed in each case.

Chapter V serves as a preamble to Chapter VI by providing background on the environmental factors structuring benthic communities in Svalbard fjords. The comparison of Arctic- and Atlantic-influenced fjords may help predict future changes in the benthic communities as Atlantic water penetrates further into the Arctic. In Chapter VI, I delve more deeply into the process of community assembly on hard substrata at high latitude by observing recruitment in Svalbard fjords. I show how recruitment to hard substrata in fjords varies by season, by depth, and between Arctic- and Atlantic-influenced fjords. I also test for non-random co-occurrence, one of the patterns from Chapter II, for recruits on the settlement plates.

This dissertation bridges two traditions – terrestrial and marine ecology. The two disciplines have historically developed parallel to one another, but the application of hypotheses developed in one environment to a different environment can provide new insights.

CHAPTER II

ISLANDS IN A SEA OF MUD: INSIGHTS FROM TERRESTRIAL ISLAND THEORY FOR COMMUNITY ASSEMBLY ON INSULAR MARINE SUBSTRATA

ISLAND BIOGEOGRAPHY AS A FRAMEWORK

Ever since MacArthur and Wilson’s landmark monograph (1967), island biogeography has been one of the most studied topics in ecology. Most literature in this field has focused on terrestrial islands and habitat islands, but parasites have been studied using island theory (Kuris et al. 1980) and a number of island-like habitats in the sea have also been studied (Abele and Patton 1976, McClain et al. 2006, Schoener and Schoener 1981). Given that most of the seafloor is blanketed by soft sediments, any hard substratum is bound to be isolated and island-like. Habitats as diverse as stones, coral reefs, and hydrothermal vents can be considered “islands in a sea of mud” (Young 2009). For the purposes of this review, islands are defined as habitats separated from similar habitats by a continuous, dissimilar habitat, i.e., stones surrounded by the soft, muddy seafloor. “Terrestrial islands” refers to islands of land surrounded by ocean; “habitat islands” refers to other isolated terrestrial or freshwater habitats that can be considered ecological islands; all isolated marine habitats are termed “island-like.” How islands and island-like habitats come to be colonized and inhabited by a developed community of fauna is “community assembly,” here defined for marine habitats as a process including larval dispersal, recruitment, competition, predation, and succession. Several hypotheses concerning community assembly on islands have already been developed for terrestrial and freshwater habitats based on classical island theory (Brown et al. 2000, Fox and

Kirkland 1992, Heino and Soininen 2005, Holdaway and Sparrow 2006). Island hypotheses can potentially be used as a framework for understanding community assembly on isolated substrata in the sea.

"Classical island theory" is used in the context of this review to refer collectively to two previous works, those of MacArthur and Wilson (1967) and Diamond (1975a). Separately, the theories published in these works will be referred to as "island biogeography" (for MacArthur and Wilson 1967) and "assembly rules" (for Diamond 1975a). The publication of MacArthur and Wilson's monograph was a landmark in the history of ecology, representing a radical break from the previous focus on taxonomic descriptions in biogeography (Heaney 2000). The theory has since been tested empirically (Simberloff and Wilson 1970, 1969; Wilson and Simberloff 1969) but has also been criticized (Heaney 2000), modified extensively (Anderson and Wait 2001, Brown and Kodric-Brown 1977, Buckley 1982, Losos and Ricklefs 2010), and argued to be only applicable in a small number of cases (Haila 1990). Nevertheless, the MacArthur-Wilson equilibrium theory continues to influence modern ecological thought for islands and habitat islands (Whittaker and Fernandez-Palacios 2007). In fact, a new paradigm for island biogeography, the General Dynamic Model, still stands on a foundation of the classical MacArthur-Wilson theory while integrating time as a factor (Borregaard et al. 2015, Whittaker et al. 2008).

Diamond's assembly rules (1975a), a series of hypotheses based on the distribution of New Hebrides avifauna, were immediately controversial following publication in 1975 (e.g.,, Connor and Simberloff 1979, Diamond and Gilpin 1982). However, the ensuing debate in the literature led to the adoption of null models as a major tool for ecological analysis (Gotelli and Graves 1996) and, over the course of several decades, the development of several powerful statistical tools that are now in common practice (Gotelli 2000, Ulrich et al. 2009). “Assembly rules” has come to refer to any apparent biotic or abiotic force structuring guilds or communities (Belyea and Lancaster 1999) and has been used for a wide variety of fauna, including ants (Gotelli and Ellison 2002), rodents (Brown et al. 2000), birds (Blake 1991), and plants (Weiher et al. 1998).

Now being decades removed from the publication of the classical island theories, it is possible to view each theory through the lens of the debates and discussions they generated. For the purposes of this review, I will distill each classical island theory to its basic elements as they have survived in the literature, and then apply this framework to island-like habitats on the seafloor. Five patterns found on terrestrial islands and discussed in the classical island literature are as follows:

Species-area relationship and island size

MacArthur and Wilson (1967) noted a log-linear relationship between the size of an island and the richness of its fauna, of the form $S = cA^z$ (S is species richness; A is area; c and z are constants). When a log-transformation is used, the relationship becomes $\log(S) = z\log(A) + c$ (Fig. 1A). Similar patterns have been found for a variety of fauna and habitats (Connor and McCoy 1979), leading some to note that the species-area relationship is one of the few true laws in ecology (Lawton 1999).

Degree of isolation

The cornerstone of MacArthur and Wilson's equilibrium theory of island biogeography is the classic figure showing immigration and extinction curves on islands of varying size and level of isolation (MacArthur and Wilson 1967) (Fig. 1B). Islands closer to a mainland were theorized to have higher immigration, while larger islands were theorized to have more possible niches and lower extinction; where the immigration and extinction curves for a particular island crossed was the equilibrium number of species for that island (MacArthur and Wilson 1967). The basic assumption that island communities are in equilibrium is false in most cases (Heaney 2000); therefore, for the purposes of this review, the discussion will be restricted to species diversity on an ecological time scale. To put it concisely, higher diversity is expected on insular marine habitats in closer proximity to other similar habitats.

Incidence functions

Diamond (1975a) also observed a spectrum of life-history traits to exist on islands of different sizes. Small islands were inhabited only by fast-growing, generalist, "supertramp" species, while larger islands were also inhabited by long-lived, specialist, "high-S" species. The curve showing which sizes of islands a species is most likely to inhabit is called its incidence function (Fig. 1C).

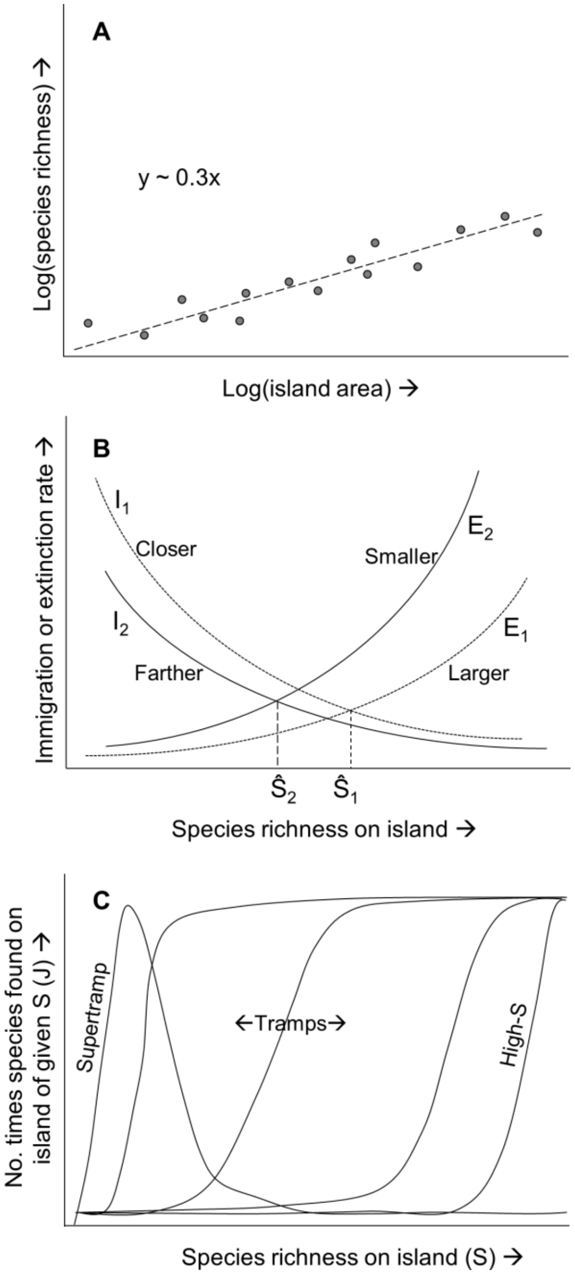

Fig. 1. Graphics associated with classical island theories. A, log-linear relationship between species richness on an island and the area of the island. Points are for illustration and do not depict actual data. After MacArthur and Wilson (1967). B, equilibrium theory of island biogeography. Immigration and extinction curves for two islands are shown; island 1 is closer to mainland and larger. Where the curves intersect is the equilibrium number of species (Ŝ) for that island. After MacArthur and Wilson (1967). C, incidence functions. "Supertramp" species are generalists that primarily inhabit islands with low species richness, "tramps" are intermediate, and "high-S" species inhabit islands with high species richness. After Diamond (1975a).

Nestedness

Nested patterns of fauna occur when smaller or more isolated islands are inhabited by smaller sub-sets of fauna, and species disappear in a consistent pattern such that each sub-set is “nested” within the next largest sub-set of fauna (Fig. 2A). There is some overlap in the concepts of incidence functions (above) and nestedness, because small sub-groups of fauna (found on smaller or more distant islands) generally contain only long-dispersing, fast-growing, opportunistic species, while larger sub-groups (found on larger or less isolated islands) also include long-lived, slow-growing specialists. There is also some interaction between the concepts of nestedness and succession, as young islands will be initially colonized by fast-growing opportunist species, while older islands will be inhabited by slower-growing superior competitors. However, on large islands, the fast-growing opportunist species may continue to inhabit sub-optimal niches alongside the slow-growing superior competitors as succession proceeds. Nested patterns were observed by MacArthur and Wilson (1967) and subsequent authors (Blake 1991, Kadmon 1995, Patterson and Atmar 1986) for birds and rodents on islands and island-like habitats, and the nestedness of fauna has implications for conservation (Cutler 1991).

Non-random co-occurrence

Non-random co-occurrence of species, by far the most controversial aspect of Diamond’s (1975a) theory, referred to pairs of species being found on the same island less often than expected by chance. Patterns of non-random co-occurrence were initially attributed to interspecific competition (Diamond 1975a). While non-random co-occurrence is relatively common in various faunas (Gotelli and McCabe 2002),

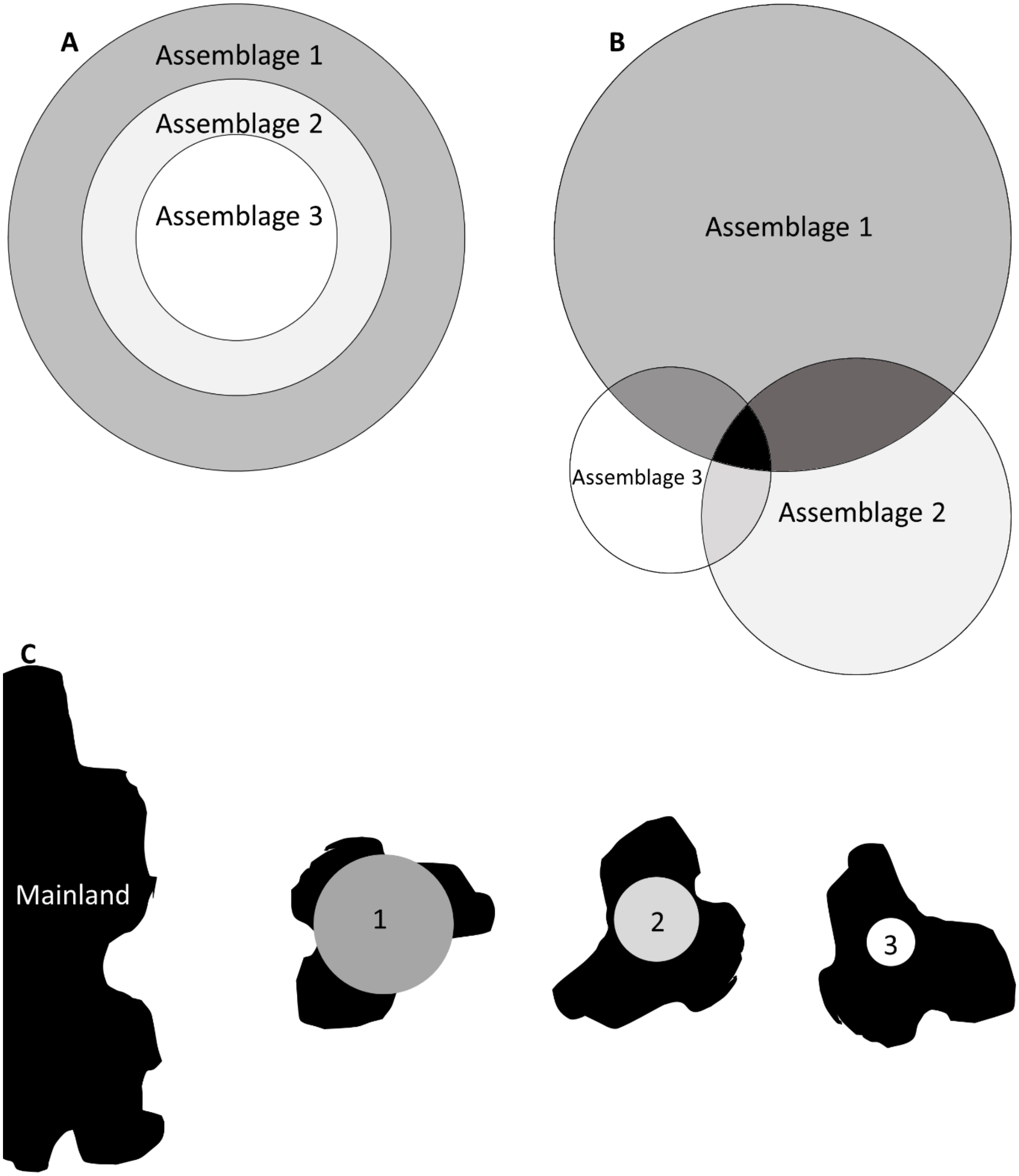

Fig. 2. A, Venn diagram depicting nested species assemblages. Assemblage 1 contains the largest number of species, and assemblages 2 and 3 are nested within it. B, Venn diagram depicting non-nested species assemblages. C, how nested species assemblages may occur on islands of different distances from a mainland source population.

the underlying mechanisms remain controversial and may include stochastic processes (Ulrich 2004). In this review, “negative non-random co-occurrence” will refer to species pairs co-occurring non-randomly less often than expected by chance, and “positive non-random co-occurrence” will refer to species pairs co-occurring non-randomly more often than expected by chance. Species distribution patterns that do not significantly differ from chance will be referred to as “random co-occurrence.”

Throughout the rest of this review, a modern understanding of these five basic patterns will be applied to island-like habitats in the marine environment, in order to show how island theory can increase our understanding of insular marine habitats. The mechanisms responsible will also be discussed.

SUBTIDAL AND DEEP-SEA HABITATS AS ISLANDS

Most marine hard substrata are isolated and island-like, ranging in size from landscape-scale features (seamounts, Clark et al. 2010; canyons, DeLeo et al. 2010; trenches, Jamieson et al. 2010) to medium-size structures (coral reefs, Jones et al. 2009; rocky reefs, Jones 1988; dropstones, Chapter IV) and small objects (manganese nodules, Mullineaux 1987; sea urchin tests, Gutt and Schickan 1998; hermit crab shells, Bałazy and Kukliński 2013; sponge stalks, Beaulieu 2001; and water-logged plant material, Wolff 1976, 1979). Chemosynthetic vents (Lutz and Kennish 1993), seeps (Sibuet and Olu 1998), and whale falls (Baco and Smith 2003) are isolated and island-like. Anthropogenic structures (shipwrecks, Perkol-Finkel et al. 2006; artificial reefs, Carr and Hixon 1997; shipping containers, Taylor et al. 2014; military discard, Kelley et al. 2015;

oil platforms, Gass and Roberts 2006; even litter, Bergmann et al. 2015) are also insular habitats.

Of the island-like marine habitats listed above and discussed in this review, seamounts are the most obvious analogue for terrestrial islands. For many years, seamounts were viewed as biodiversity hotspots with high endemicity and unique evolution (de Forges et al. 2000, Hubbs 1959, McClain et al. 2006, Rogers 1993). Mesoscale circulation above seamounts may retain larvae and lead to genetic differentiation between populations (Mullineaux and Mills 1997, Mullineaux 1994). It was originally hypothesized that larval retention could lead to speciation on seamounts, but this view has shifted in recent years. The apparent endemicity on seamounts may in fact be the result of undersampling (McClain 2007), and when samples from similar substrata, depths, and geomorphologies are compared, seamounts appear no more diverse than adjacent banks or continental slopes (Howell et al. 2010, O'Hara 2007). Ironically, seamounts, the closest geological analogue to terrestrial islands, may have very different ecology.

Coral reefs are well-known isolated habitats in tropical regions. Much research has been conducted to understand connectivity among coral reefs, both for corals themselves and for reef fish (Jones et al. 2009). The prevailing paradigm has shifted in the past decades from high connectivity to recruitment at natal reefs (Jones et al. 2005, Levin 2006), but the integration of oceanographic modeling and larval biology has increased our understanding of reef connectivity (Baums et al. 2006).

Submarine canyons present on continental margins the world over can also be considered island-like habitats. Because of their steep walls and narrow basins, canyons can focus bottom currents and internal waves, leading to turbulence and the resuspension of organic matter (Gardner 1989). Canyons can also serve as conduits to funnel terrestrial biomass into the deep sea (Vetter and Dayton 1999). These combined effects mean that submarine canyons have higher organic matter input and higher biomass of macro- and megafauna than the surrounding continental slope (De Leo et al. 2010, Vetter et al. 2010). Soft-bottom infaunal and epifaunal communities in canyons are significantly different from the adjacent continental slope, with different distribution patterns in each environment (Rowe 1971, Vetter and Dayton 1998). Canyons often feature boulders or rocky walls that are inhabited by cold-water corals not otherwise present on the continental slope (Roberts et al. 2009). Coral community composition varies among even adjacent canyons (Brooke and Ross 2014), and populations are genetically distinct among regions (Morrison et al. 2011).

Deep-sea trenches, located below 6,000 m, are unique habitats characterized by high bottom-water oxygen, high organic matter input, and extreme pressure (Jamieson et al. 2010). Though they feature primarily soft substrata, trenches could be considered island-like habitats; trench fauna show strong bathymetric zonation that at least partially isolates them from the surrounding abyssal plain (Jamieson et al. 2011). Some hadal species are found in multiple trenches (Jamieson et al. 2013), but the extent of population connectivity among trenches is still poorly understood.

Dropstones, another type of island-like hard substratum, are defined as stones of terrestrial origin that have become frozen in a glacier, carried out to sea by an iceberg, and are deposited on the seafloor when the iceberg melts (Kidd et al. 1981, Oschmann 1990). Dropstones are colonized by a variety of hard-bottom fauna (Oschmann 1990, Schulz et al. 2010) and increase habitat heterogeneity where they occur (Hasemann et al. 2013, MacDonald et al. 2010). Dropstones have faunal distributional patterns similar to terrestrial islands (Chapter IV).

Hydrothermal vents have been intensively investigated since their discovery in 1977, including landmark studies of larval dispersal (Kim et al. 1994, Marsh et al. 2001), recruitment (Mullineaux et al. 2000, Van Dover and Berg 1988), and succession (reviewed by Young 2009). Some researchers have interpreted a deterministic course of succession at vents (Hessler et al. 1988, Shank et al. 1998), while others have interpreted a more stochastic process dependent on larval availability in the water column (Mullineaux 1994, Tunnicliffe et al. 1997). Similarly, cold seeps are island-like chemosynthetic habitats, most common on continental margins (Sibuet and Olu 1998). They are colonized by some of the same genera and species as vents (Van Dover et al. 2002). Larvae of cold seep fauna may have long duration (Arellano and Young 2009), allowing for long-range dispersal among seeps (Olu et al. 2010, Young et al. 2012).

Whale falls are ephemeral habitats with a unique ecology (Glover et al. 2005, Rouse et al. 2009, Smith and Baco 2003). After the removal of flesh, whale bones support a community of sulphophilic fauna, including bathymodiolin mussels (Lorion et al. 2009, Lundsten et al. 2010). Other organic matter-falls, including wood- and plant-falls, also represent organic substrata in the deep sea, and they are colonized by numerous species of specialist xyolophagid and teredinid mollusks (Heß et al. 2008, McClain and Barry 2014). Wood-falls support anaerobic, sulfate-reducing microbes (Bienhold et al. 2013) and may even share fauna with whale falls (Lorion et al. 2009). The species that colonize and exploit chemosynthetic vents, seeps, whale falls, and other organic-matter falls in the deep sea are related on an evolutionary time-scale, though the exact relationships are still under debate (Distel et al. 2000).

Each of the insular hard substrata listed here will be considered in this review, and the processes of community assembly for each habitat type will be framed in the context of classical island theory as outlined above.

PATTERNS ON SUBTIDAL ISLANDS

Species-area relationship and island size

A log-linear relationship between species richness and island area is well-documented, even ubiquitous, for terrestrial habitats, and various mechanisms have been proposed as explanations. These include habitat diversity, primary productivity, resistance to disturbance, equilibrium achieved through a balance of immigration and extinction, clumped distributions of species, succession, and even sampling artifacts (Connor and McCoy 1979, Gotelli and Graves 1996, Hill et al. 1994, MacArthur and Wilson 1967).

Similar log-linear relationships of species (morphotype) richness to area have been found for marine substrata (Abele and Patton 1976, Huntington and Lirman 2012, Schoener and Schoener 1981, Chapters III, IV), but the explanations listed above are not satisfactory. For marine hard substrata, habitat diversity does not vary greatly with increasing size (Abele and Patton 1976), and extinction is rarely observed (Schoener and Schoener 1981). For substrata in the deep sea, primary production does not occur locally, and disturbance is relatively rare. The most parsimonious explanation for the species-area relationship on marine substrata is the “passive sampling hypothesis” (Connor and

McCoy 1979), which states that larger islands (substrata) are merely larger targets for dispersing propagules (Huntington and Lirman 2012, Chapters III, IV). Larger substrata have higher immigration rate and "fill up" more slowly, allowing more species to accumulate over time (Schoener and Schoener 1981).

Another reason for the species-area relationship in island-like marine habitats is that larger substrata extend further into the benthic boundary layer and are exposed to faster currents for suspension feeding (Vogel 1996). It is well-documented that dense populations of suspension-feeding organisms or planktivores inhabit topographic highs such as seamounts (Genin et al. 1986), rocky reefs (Meyer et al. 2014), pinnacles (Leichter and Witman 1997), and fjord sills (Mortensen et al. 2001), where there is greater turbulence and availability of particulate food. Even small structures, such as glass sponge stalks (Beaulieu 2001), manganese nodules (Mullineaux 1987), and sea urchin tests (Hétérier et al. 2008) are inhabited by suspension feeders seeking elevation out of the benthic boundary layer. The "passive sampling hypothesis" and its corollary of higher particulate food supply on larger substrata offer parsimonious explanations for species-area relationships on subtidal and deep-sea insular substrata (Chapter IV). The species-area relationship is ubiquitous (Lawton 1999), but the mechanisms causing this pattern in marine and terrestrial environments are not necessarily the same.

One exception should be noted for organic substrata such as wood-falls, where the higher species richness on larger substrata is more closely related to volume rather than surface area (McClain and Barry 2014). Thus, species richness is driven by energetic content of the wood rather than larval recruitment (McClain and Barry 2014, McClain et al. 2016). For seamounts, it should also be mentioned that the depth range, which is directly related to seamount size, is a prominent factor influencing faunal composition. Different communities are present at different depths along the seamount, and fauna are controlled by the characteristics of water masses at each given depth (Chivers et al. 2013, Clark et al. 2010, O'Hara and Tittensor 2010, Rogers 1993).

The application of a principle from terrestrial island theory can be applied to marine island-like substrata and provide insights for both systems. For example, if species-richness and island-area data are graphed in their raw form, without the traditional log transformation of each axis, the relationship is asymptotic (Chapter IV). The flattening curve may in fact indicate that only a certain number of species are capable of colonizing a given substratum, i.e., the species pool is finite (Chapters III, IV). Larger substrata are inhabited by a greater proportion of the available species, so the classical log-linear species-area relationship may in fact result from nothing more than a finite species pool.

Degree of isolation

MacArthur and Wilson discussed island size and the degree of isolation as two critical factors influencing the richness of fauna (MacArthur and Wilson 1967). The physical effects of substratum size – greater surface area and exposure to faster bottom current – have been discussed above. An empirical test of island biogeography theory showed lower immigration rate and lower species richness on islands further away from a source (Simberloff and Wilson 1970, 1969). For marine hard substrata, experimentally-cleared patches surrounded by benthic fauna were more readily colonized by asexual growth of encrusting individuals, whereas isolated patches had to be colonized by larval dispersal and showed size-dependent diversity (Keough 1984). Bryozoans recruited to patches of all size, whereas tunicates recruited to and dominated on large isolated patches (Keough 1984). The effects of isolation and the extent of connectivity among island-like marine habitats depend on the dispersal capabilities of the resident fauna and can be complex.

Descriptions of biogeography of marine benthos (Ekman 1953, Vermeij 1978), have led to the designation of biogeographic provinces for vents (Tunnicliffe et al. 1998, Van Dover et al. 2002) and seeps (Baco et al. 2010, Olu et al. 2010), as well as the bathyal, abyssal, and even hadal seafloor (Watling et al. 2013). Vicariance and allopatric speciation events have also been hypothesized for seamounts and hydrothermal vents (Shank 2010, Vrijenhoek 2010), but our understanding of these habitats is far from complete.

The most influential paradigms for the biogeography of isolated marine habitats are the so-called “island model” (Wright 1931) and “stepping-stone” or “isolation-by-distance model” (Wright 1943). The “island model” describes the colonization of isolated habitats from a single well-mixed larval pool, while the “stepping-stone model” points to short-range larval dispersal and a positive linear correlation between genetic and geographic distances for isolated populations (Vrijenhoek 1997). These models have been described for a variety of habitats, including coral reefs, hydrothermal vents, and cold seeps (Palumbi 2003, Tyler and Young 1999, Vrijenhoek 2010).

While the so-called “island model” draws on the terminology of classical island theory, there is an important distinction to be made. Neither MacArthur and Wilson (1967) nor Diamond (1975a) ever assumed the existence of a well-mixed pool of equallydispersing propagules; rather, they discussed the dispersal potential of individual species. Species with long-range dispersal capability and fast growth were theorized to be the first successful colonists of any island, while long-lived, short-dispersing species were said to arrive later or not at all (Diamond 1975a, MacArthur and Wilson 1967).

The concept of stepping stones appears in the deep-sea literature with reference to whale falls on both evolutionary and ecological time scales. In evolutionary time, it is hypothesized that sunken wood and whale carcasses served as “stepping stones” for the colonization of and adaptation to hydrothermal vents and cold seeps (Distel et al. 2000, Heß et al. 2008, Kiel and Goedert 2006). In ecological time, it has been hypothesized that whale falls serve as “stepping stones” to facilitate larval dispersal among vent and seep habitats (Smith and Baco 2003). However, both ideas remain controversial, and there is not sufficient evidence to support or refute either hypothesis (Amano and Little 2005, Smith and Baco 2003).

Incidence functions

Diamond (1975a) described “incidence functions” for the New Hebrides avifauna, using S-shaped curves to show the size of island each species was most likely to inhabit (Fig. 1C). Fast-growing opportunistic species (“supertramps”) were said to inhabit all but dominate smaller islands, whereas slow-growing specialists (“high-S species”) were found exclusively on larger islands. The end result was a nested pattern of fauna, with “supertramps” and “tramps” being ubiquitous and “high-S” species found only on larger islands.

Incidence functions have seldom been directly sought for isolated marine habitats, but re-examination of existing datasets show there are generally not different suites of species inhabiting differently-sized substrata. For example, Schoener and Schoener (1981) found that while different species dominated on settlement plates of different sizes, each species occurred on plates of all sizes. This result does not support the existence of incidence functions for marine fauna (Schoener and Schoener 1981). Decapod crustaceans inhabiting coral heads also occurred on various sizes of heads, without a split between species inhabiting small heads and species inhabiting large heads (Abele and Patton 1976). For dropstones on the west Svalbard continental slope, there was no correlation between the size of a stone and the species composition on the stone (Chapter IV). Higher species (=morphotype) richness was found on larger stones, but the morphotypes inhabiting each stone were randomly selected from the available species pool (Chapter IV).

Incidence functions, or the restriction of slow-growing, long-lived species to larger insular habitats may not be a common pattern for isolated marine habitats. Nevertheless, the potential for incidence functions and the resulting nested patterns of fauna are important to keep in mind because of the implications for conservation, discussed below.

Nestedness

Nestedness is a common pattern for a variety of terrestrial and aquatic fauna, in which ever-smaller or ever more-isolated habitats are inhabited by ever-smaller sub-groups of fauna that are nested within one another (Fig. 2A). Smaller islands have fewer resources and fewer niches, so only fast-growing opportunists can successfully establish populations. Distant islands can only be reached by long-dispersing, fast-growing opportunists, resulting in nested patterns.

For dropstones on the west Svalbard continental slope, it was hypothesized that a nearby “mainland” rocky reef served as a source of larvae to the stones, leading to a nested pattern of fauna further away from the reef (Chapter IV). However, no nested pattern was found; instead, dropstone fauna had a clumped distribution that most likely resulted from short-range larval dispersal among the stones, with only limited influence of the rocky reef (Chapter IV).

For deep-sea wood-falls, McClain et al. (2016) found that the sets of fauna on smaller falls were nested within fauna on larger wood-falls. However, in other cases, colonization of wood-falls has been variable and stochastic (McClain and Barry 2014, Pailleret et al. 2007).

Isolated marine habitats may experience a greater degree of connectivity driven by larval dispersal than is traditionally understood for terrestrial islands. There is also an element of stochasticity in the colonization of isolated marine habitats, because recruitment depends on larval availability, which may be temporally and spatially variable (Mullineaux et al. 2005, Siegel et al. 2008, Van Dover et al. 2001).

Save for the above examples, authors writing about isolated marine habitats usually do not test for nested patterns of fauna. However, there is a well-established methodology to detect nested faunal patterns, and a simple test could be easily incorporated into any routine data analysis (Ulrich and Gotelli 2007). It would be interesting to look for nested patterns of faunal distribution among seamounts, coral reefs, and hydrothermal vents – habitats that currently are or may in the future be designated as marine protected areas (MPAs). The biggest implication of nested faunal patterns in the literature in fact relates to the SLOSS (Single Large Or Several Small) debate about natural reserves and protected areas (Diamond 1975b, Tjørve 2010). If, according to their incidence functions, only fast-growing, opportunistic, generalist species are able to inhabit small islands or habitat islands, then small reserves would only conserve those opportunistic species, whereas a single large reserve would host niches for fast-growing generalists and long-lived specialists alike.

It is completely possible that isolated marine habitats will show different distribution and connectivity patterns than their terrestrial counterparts, and nested faunal patterns may never be found. If such patterns are found, they would inform the discussions about appropriate design of marine protected areas. Also, a better understanding of larval dispersal dynamics, connectivity, and gene flow among isolated marine habitats will improve MPA design (Levin 2006, Shanks et al. 2003).

Non-random co-occurrence

Negative non-random co-occurrence patterns of fauna were originally attributed to interspecific competition (Diamond 1975a). While non-random co-occurrence patterns have been found for a variety of fauna, the mechanisms responsible are various and can include stochastic processes (Ulrich 2004).

Negative non-random co-occurrence was observed for encrusting fauna on dropstones, but interspecific overgrowth competition was not observed (Chapter IV). Rather, epibiontism caused patterns of non-random co-occurrence for dropstone fauna, as many species pairs had positive non-random co-occurrence patterns (Chapter IV). Suspension-feeding species were observed on top of large hexactinellid sponges, presumably to gain an advantage in feeding. Commensalism has been observed for suspension feeders on biotic substrata at a variety of depths and latitudes (Beaulieu 2001, Gutt and Schickan 1998, Hétérier et al. 2008) and is well-documented for cold-water coral stands and sponge gardens (Cordes et al. 2008, Maldonado et al. 2015, Roberts et al. 2009). Epibionts may need their basibionts to different degrees – ranging from facultative to obligate relationships – and the associated species may have co-evolved in some cases (Shank 2010). How strongly commensal relationships affect faunal distribution remains uninvestigated for most habitats.

PROCESSES UNDERLYING THESE PATTERNS

Larval dispersal

For (non-chemosynthetic) marine insular habitats, empirical evidence suggests that larval dispersal patterns are taxon-specific and depend on life history (Grantham et al. 2003, Jones et al. 2009, Miller et al. 2010, Young et al. 2012). Short-duration lecithotrophic or brooded larvae are likely to recruit to their natal habitat (Bingham 1992, Jackson 1986, Marshall and Keough 2003, Shanks et al. 2003), while planktotrophic larvae disperse much farther. Short larval duration and self-recruitment may be an evolutionary stable state for fauna inhabiting isolated hard substrata, as there is no guarantee of finding a suitable substratum when dispersing far away (Cowen et al. 2000, Grantham et al. 2003, Shanks et al. 2003). Self-recruitment is common for shallow-water coral reefs (Jones et al. 2005, Swearer et al. 1999) and temperate rocky reefs (Altieri 2003, Grantham et al. 2003).

Cold-water corals, including *Paragorgia arborea* and the ubiquitous *Lophelia pertusa*, show evidence of genetic differentiation indicating restricted gene flow across ocean basins (Herrera et al. 2012) and among regions (Miller et al. 2010, Morrison et al. 2011). Coral stands close to one another spatially may be inbred or even clones, and reproduction by fragmentation has been hypothesized for numerous species (Brooke and Stone 2007, Le Goff-Vitry et al. 2004, Orejas et al. 2009). However, long-range dispersal has also been hypothesized for *L. pertusa*, given its propensity for colonizing oil and gas platforms (Gass and Roberts 2006). The larval biology and dispersal potential of cold-water corals are poorly known, with only a few studies on species of *Lophelia* and *Oculina* (Brooke and Järnegren 2013; Brooke and Young 2003, 2005). Coral-associated species in deep water also show various developmental modes with a tendency towards restricted dispersal (O'Hara et al. 2008, Rowden et al. 2010).

For deep-sea hydrothermal vents, larval dispersal appears to be more influenced by local circulation patterns than by larval duration (Marsh et al. 2001). It appears that hydrothermal vent invertebrates, including tubeworms and gastropods, do not disperse far away from their natal vent field, regardless of pelagic larval duration; across-ridge and reversing transport retains larvae near where they were spawned (Adams and Mullineaux 2008, Kim and Mullineaux 1998, Marsh et al. 2001). However, some species, including the vent crab *Bythograea thermydron*, have planktotrophic larvae that feed and disperse in surface waters (Dittel et al. 2005, Epifanio et al. 1999, Perovich et al. 2003). More isolated vents may have lower larval supply (Adams and Mullineaux 2008), but there is at least one documented example of a vent being colonized by larvae from 100s of km away (Mullineaux et al. 2010) and genetic patterns do not necessarily fit the predictions of short-range larval dispersal models (Chevaldonné et al. 1997). Clearly, more research is needed to understand colonization patterns at isolated hydrothermal vents, as even sequential studies at the same location provide conflicting results (Hunt et al. 2004, Mullineaux et al. 2000).

A better understanding of connectivity among insular marine habitats will be brought about by the integration of larval biology, physical oceanography, and population genetics. The biology of each species should be considered, especially considering that pelagic larval duration for marine species ranges from minutes (Altieri 2003) to a year or more (Arellano and Young 2009). It is also not accurate to assume a correlation between larval duration and dispersal range, as lecithotrophs may be capable of long-range dispersal (Tyler and Young 1999). Once larval, physical oceanographic, and genetic data can be integrated, the inaccurately-named "island model" for marine biogeography will become obsolete (Shank and Halanych 2007).

The concept of stepping stones may be helpful for future investigations of community dynamics in insular marine habitats. Anthropogenic hard substrata, including shipwrecks, shipping containers, fishing gear, and litter can be colonized by sessile fauna, thereby allowing these hard-bottom organisms to inhabit new areas of the seafloor (Bergmann and Klages 2012, Taylor et al. 2014). Benthic adults living on an anthropogenic substratum may release larvae, which could disperse to and settle on substrata outside their native ranges, leading to gene flow or species invasion among previously isolated habitats. The presence of anthropogenic hard substrata on the seafloor affects the communities of mobile predators in the surrounding area by attracting species typically associated with hard bottoms (Kilgour and Shirley 2008, Ross et al. 2016). If these mobile species also disperse via pelagic larvae and adults reproduce while near an anthropogenic hard substratum, outside of their previous range, these species could also disperse among previously isolated habitats.

Succession

A shift in the life-history traits of fauna over time was described for terrestrial islands under the terminology of r- and K-strategists by MacArthur and Wilson (1967) and under the terminology of supertramps, tramps, and high-S species by Diamond (1975a). In each case, the authors hypothesized that the first colonists on an island would be opportunistic, generalist species with high fecundity, long-range dispersal, and short life-span. As more colonists arrived, the initial colonists would be outcompeted and replaced by more specialist species with lower fecundity, short-range dispersal, and longer life-spans.

Succession is best understood for shallow hard substrata at temperate latitude. Previous studies on the east coast of the United States have shown that experimental substrata (settlement plates) are first colonized by acorn barnacles and spirorbid polychaetes, followed by a community of encrusting bryozoans, ascidians, and hydroids (Dean and Hurd 1980, Osman 1977). The third stage is dominated by blue mussels (Chalmer 1982, Dean and Hurd 1980) or one of the encrusting species from the second stage (Osman 1977). The course of succession can also depend on season and the order in which species arrive on a substratum (Pacheco et al. 2011, Sutherland 1974).

Acorn barnacles may enjoy early dominance on settlement plates because cyprid larvae do not require a thick biofilm for settlement (Keough and Raimondi 1996, Todd and Keough 1994). Barnacles have long-duration larvae capable of long-distance dispersal; they grow quickly and are poor competitors (Quinn 1982). Therefore, their position as the first colonists of an isolated hard substratum fits the expected life history scheme. For encrusting fauna, the first colonists are opportunists, characterized by fast growth and poor competitive ability, whereas species present later in succession are slower-growing superior competitors (Antoniadou et al. 2010, Edwards and Stachowicz 2010, Vance 1988). A similar shift in life-history traits has been observed on shallow (<30 m depth) shipwrecks and artificial reefs, with structures underwater for less than 20 years being dominated by opportunistic species (Carter et al. 1985, Pawlik et al. 2008, Perkol-Finkel and Benayahu 2005) and structures underwater for more than 100 years being inhabited by long-lived superior competitors, in a community not significantly different from nearby natural reefs (Perkol-Finkel et al. 2005, 2006).

While the process of succession is well-described for shallow marine hard substrata, the mechanisms responsible are less well-known. Connell and Slatyer (1977) described three models of succession: inhibition, in which early colonists inhibit settlement of later species and succession is driven by the removal of early colonists by predators; facilitation, in which early colonists modify the habitat to facilitate the settlement of later colonists that ultimately outcompete them; and tolerance, in which early colonists have short life-span and are replaced by slower-growing, longer-lived late succession species. Different authors have attributed succession in shallow marine hard substrata to each of the three mechanisms; facilitation (Osman and Whitlatch 1995a), tolerance (Edwards and Stachowicz 2010), and inhibition (Lubchenco 1983). Encrusting invertebrates recruit in higher abundance to fouling panels with already established fauna, indicating a possible facilitation mechanism (Keough 1998, Osman and Whitlatch 1995b, Walters et al. 1997). However, for tropical coral reefs, recruitment of fouling fauna was higher at an artificial reef, and these encrusting species may inhibit coral settlement (Perkol-Finkel and Benayahu 2007). Succession on marine hard substrata can involve regular species replacements to form a stable climax community (Vance 1988), but there is often an element of stochasticity not found in terrestrial systems. The first colonists to arrive and colonize a substratum impact the course of succession for the whole community (Sutherland 1974), and even the outcome of competition can depend on circumstance, including substratum texture, orientation, and latitude (Barnes and Kukliński 2003, Miller and Etter 2011, Walters and Wethey 1986).

Recruitment is lower and succession may occur more slowly on subtidal marine substrata at higher latitude (Barnes and Kukliński 2005, Beuchel and Gulliksen 2008, Kukliński and Barnes 2008, Kukliński et al. 2013, Stanwell-Smith and Barnes 1997, Stanwell-Smith et al. 1999, Svane and Lundälv 1981). Intertidal and shallow subtidal boulders in the Arctic and Antarctic are kept at an early stage of succession because of ice scour disturbance (Barnes et al. 1996, Kukliński and Barnes 2008, Kukliński 2009, Kukliński et al. 2006a). Eight years after a volcanic eruption in Jan Mayen, shallow subtidal communities (5 – 10 m) resembled old-ground (pre-eruption) shallow communities because both had low diversity and were dominated by opportunistic species, typical of early-succession, ice-scoured habitats (Gulliksen et al. 1980). Deeper (20 – 30 m) habitats were also at an early succession stage, dominated by the bivalve

Hiatella arctica, though these deeper communities were significantly different from more diverse, old-ground communities dominated by encrusting sponges (Gulliksen et al. 1980).

Very little is known about the process of succession on isolated marine hard substrata at greater depth. Shipwrecks found off the U.S. east coast (~100 m depth) were in a stage of mid-succession even after 91 years underwater (Chapter III). Similarly, long-lived climax species were conspicuously absent from a shipping container in Monterey Canyon at 1281 m depth (Taylor et al. 2014). Succession may proceed more slowly on deep insular hard substrata because their degree of isolation makes it improbable that they will be reached by the larvae of sessile, hard-bottom species, many of which are adapted for short-distance dispersal and self-recruitment (Chapter III, Grantham et al. 2003).

Long-lived cold-water corals often inhabit the steep rocky walls of submarine canyons (Tyler et al. 2009), mounds, and knolls (Roberts et al. 2009). Species of *Desmophyllum*, *Primnoa*, and *Lophelia* are incredibly slow-growing and long-lived, growing millimeters or less per year (Brooke and Young 2009, Risk et al. 2002), but the processes by which deep-water corals disperse, settle, and recruit on these substrata are largely uninvestigated. It would be interesting to know if these coral species are preceded on their substrata by any shorter-lived species that may potentially facilitate their recruitment.

For deep-sea habitats, succession is best understood at whale falls (Smith and Baco 2003). The first stage is the mobile-scavenger stage, in which large, mobile scavengers clean the flesh from the whale bones. Then, in the enrichment-opportunist stage, dense and species-rich macrofauna consume the organic material around the carcass (Baco and Smith 2003). Finally, in the sulphophilic stage, a chemoautotrophic community thrives on the lipids in the whale bones (Smith and Baco 2003, Treude et al. 2009). The stages often overlap (Goffredi et al. 2004), and the speed of succession depends on the presence of key mobile scavengers at the depth of the whale fall (Dahlgren et al. 2006, Fujiwara et al. 2007). Succession at whale falls is driven by a facilitation mechanism, as the consumers in each stage modify the carcass (i.e., removing flesh to expose the bones) to facilitate colonization by the next set of organisms. However, rather than being outcompeted by their successors, the organisms in each stage ensure their own demise by consuming the resources on which they thrive (Smith and Baco 2003). In this way, whale falls are different from other isolated marine habitats because the habitat is ephemeral and is consumed by its colonists.

The species that colonize whale falls are for the most part not whale-fall specialists (Smith and Baco 2003). Generalist mobile scavengers are drawn from the surrounding area, as are opportunistic macrofauna. Even the “bone worm” *Osedax* has also been documented to consume fish bones and cannot be considered a whale-fall specialist (Rouse et al. 2011). The life-history traits of most whale-fall species are unknown, especially the macrofauna, but species of *Osedax* have high fecundity, continuous reproduction, and are capable of long-range dispersal (Rouse et al. 2009). These characteristics can be considered adaptations to an ephemeral habitat (Rouse et al. 2009). Even though *Osedax* appears relatively late in whale-fall succession, it has the life-history characteristics of an opportunistic species. Whale-falls are ephemeral habitats that are consumed by their colonists; they are fundamentally different from other, longer-lasting isolated marine habitats.

Other ephemeral deep-sea habitats that are consumed by their colonists include wood- and plant matter-falls, and these too are inhabited by opportunistic species (Turner 1973, 1977). A number of mollusks, echinoderms, crustaceans, and polychaetes use wood- or plant matter-falls as substrate, shelter, or food (Wolff 1979). Invertebrates inhabiting wood- and plant matter-falls are opportunists (Samadi et al. 2010, Voight 2007, Young et al. 2013), and some mollusk species are able to live on both whale- and wood-falls (Lorion et al. 2009). The invertebrate communities on wood- or plant-falls are highly variable, even among substrata deployed at the same location for the same amount of time (Pailleret et al. 2007, Voight 2007). However, microbial communities are highly consistent, even among different ocean basins (Palacios et al. 2009). Microbial communities vary over time as the wood is consumed (Palacios et al. 2009), and there is also a predictable shift in the invertebrate community from inferior to superior competitors over time (Voight 2007). Succession of macrofauna on wood-falls may in fact resemble the process on whale-falls. The first colonists, xylophagid mollusks, create bore-holes that create habitat and facilitate colonization by other species (McClain and Barry 2014, Turner 1977) – similar to the removal of whale flesh by scavengers, which facilitates colonization of bone-exploiting species. Wood consumption by xylophagids creates a halo of wood chips and feces surrounding the wood-fall, where opportunistic infauna may take advantage of this organic enrichment (McClain and Barry 2014), similar to the enrichment-opportunist stage in whale fall succession. The process of succession on organic matter-falls differs from succession on permanent hard substrata, but evidence suggests there is a predictable succession, which is similar for wood- and whale-falls.

At hydrothermal vents in the tropical eastern Pacific, it has been hypothesized that the tubeworm *Tevnia jerichoana* provides a settlement cue to facilitate recruitment of *Riftia pachyptila* (Mullineaux et al. 2000). However, in a later experiment, *R. pachyptila* settled in the absence of *T. jerichoana*, providing contradictory results (Hunt et al. 2004). It has also been suggested that *T. jerichoana* is replaced by *R. pachyptila* because of abiotic factors, namely a decrease in hydrogen sulfide (Shank et al. 1998). Both *R. pachyptila* and *T. jerichoana* have similar egg size and developmental mode, though *T. jerichoana* has lower fecundity than *R. pachyptila* (Young 1999). Based on the life-history traits of both species, it would not be expected for *T. jerichoana* to be a pioneer species and *R. pachyptila* to be a climax species.

Alvinella pompejana has been described as a pioneer species on hydrothermal vents on the East Pacific Rise (Pradillon et al. 2005a). This species colonizes new or disturbed vent areas quickly; however, the majority of colonizing individuals likely migrated to the new area as juveniles, rather than recruiting from a larval stage (Pradillon et al. 2005a). In fact, *A. pompejana* embryos develop best at abyssal pressure, 10 – 15° C, and low sulfide flow – conditions found at the periphery of their natal vent fields – meaning the embryos or larvae may not disperse very far (Pradillon et al. 2005b). An alternative interpretation is that *A. pompejana* embryos remain in a state of arrested development until they reach surface waters (Pradillon et al. 2001). If the former interpretation proves true and *A. pompejana* develop near their natal vents and have restricted dispersal, then this species would not be expected to be a pioneer, early-succession species.

For hydrothermal vent sites at the Juan de Fuca Ridge, succession proceeds quickly, with newly-established communities resembling pre-eruption communities after only three years (Marcus et al. 2009). Much of this resemblance is due to the presence of *Ridgeia piscesae*, a habitat-forming tubeworm (Marcus et al. 2009, Tsurumi and Tunnicliffe 2003, Tunnicliffe et al. 1997). While post-eruption vent sites are quickly colonized by opportunistic species rare at other sites, recruitment of *R. piscesae* is far from deterministic: the species has settled at vents 7 months (Tunnicliffe et al. 1997) and 3 years post-eruption (Marcus et al. 2009). At some vent sites with low flow, *R. piscesae* dominance gave way to limpets (*Lepetodrilus fucensis*) 3 years post-eruption (Marcus et al. 2009). However, *L. fucensis* has also been observed to opportunistically and rapidly colonize disturbed vent areas (Sarrazin et al. 1997).

It has also been observed that tubeworms decrease in abundance as mussels (*Bathymodiolus thermophilus*) dominate later in the life of a vent (Hessler et al. 1988, Shank et al. 1998). However, *B. thermophilus* has small (50 μm) eggs, indicative of planktotrophic development and continuous reproduction (Young 1999) – characteristics of opportunistic, typically early-succession species.

It is possible that succession at hydrothermal vents does not fit the expected model of life-history traits described for terrestrial islands and observed in shallow marine habitats. Circulation patterns around vents retain larvae, so dispersal range is not necessarily related to larval duration (Marsh et al. 2001). However, more observations of hydrothermal vent communities are needed before definitive conclusions can be drawn.

Larval distribution around vents is spatially and temporally variable (Mullineaux et al. 2005), and recruits can settle outside the areas occupied by adults of the same species (Mullineaux et al. 1998). An alternative explanation for the *Tevnia-Riftia-Bathymodiolus* faunal transition is that vents are merely colonized by whatever larvae happen to be in the water column at the time (Mullineaux et al. 2010), and then self-recruitment leads to the development of dense populations. More research is needed to understand recruitment at hydrothermal vents, including repeated observations at the same sites.

Competition

The fauna of marine hard substrata mostly consist of sessile suspension feeders, and while non-random co-occurrence patterns have been found for these fauna (Chapter IV), it is an open question how and to what extent suspension feeders compete. Overgrowth competition occurs on shallow substrata (Sebens 1986), and the strength and hierarchical nature of overgrowth competition increases at higher latitude in both hemispheres (Barnes and Kukliński 2003, Barnes and Rothery 1996, Barnes 2002). However, it has been argued on theoretical grounds that suspension feeders do not compete for food (Levinton 1972, Lohse 2002). In contrast to benthic food sources, which exist on a 2-D surface and are likely to become depleted, particulate food sources are constantly renewed by bottom current (Levinton 1972, Lohse 2002). Field and laboratory experiments have shown contradictory results: that suspension-feeding bivalves are (Cote et al. 1994) or are not affected by intraspecific competition (Olafsson 1986). Suspension-feeding bryozoans, ascidians, and bivalves can alter flow or otherwise deplete particulate food resources, thereby affecting growth, body condition, or reproduction of individuals downstream (Dalby 1995, Myers 1990, Okamura 1984, Peterson and Black 1991, 1987). It could be expected that suspension feeders, especially erect forms, have a shading effect on downstream fauna, directing the current up and over them (Myers 1990, Vogel 1996). Communities of sessile suspension-feeders may also be food-limited in oligotrophic waters (Svensson and Marshall 2015).

Diamond (1975a) hypothesized that to reduce competition, species with similar niches (that consumed similar sizes of seeds) would not occur together. Interspecific competition for various sizes of seeds has also been shown to impact the distribution of desert rodents (Fox 1981). Deep-sea sponges are known to consume particulate size fractions ranging from microbes (Pile and Young 2006) to copepods (Vacelet and Boury-Esnault 1995), so it would be interesting to find out whether species that have negative non-random co-occurrence patterns consume similar size fractions and have the potential to compete interspecifically. Sponges and ascidians consume similar size fractions of ultraplankton at tropical latitude but not at temperate latitude, where food resources are more abundant (Pile 2005). It is possible that niche partitioning exists for paralvinellid polychaetes at hydrothermal vents, as *Paralvinella pandorae* is > 14x smaller where it co-occurs with *P. palmiformis*; the diets of the two species overlap (Levesque et al. 2003). Whether the species in the above examples negatively co-occur non-randomly on isolated substrata remains uninvestigated. The potential for and extent of competition for food resources among sessile suspension feeders may be important for understanding their distributions and non-random co-occurrence patterns.

GAPS IN KNOWLEDGE

Community assembly was defined at the beginning of this chapter to include all steps by which an uncolonized substratum comes to be occupied by a mature community of fauna – larval dispersal, recruitment, competition, predation, and succession. Each of these aspects of community assembly have been investigated in some insular marine habitats, but they are still incompletely understood, especially for habitats in deep water. Some similarities and differences between marine and terrestrial island-like habitats have been described above, along with how research in each environment can reciprocally inform the other and lead to a more complete understanding of the ecology of island-like habitats.

The ubiquitous log-linear relationship between species (morphotype) richness and area of a habitat may be due to nothing more than the finite nature of the species pool. Higher richness of fauna on topographic highs results from the abundant particulate food source available there. These relationships are well-understood and have clear corollaries between terrestrial and marine island-like habitats. However, gaps exist in other parts of our knowledge. The major gaps in knowledge of community assembly pertain to connectivity, larval dispersal, competition, facilitation, and succession on insular marine substrata.

Connectivity and larval dispersal

The extent of larval dispersal and connectivity among isolated marine habitats is a major research question that has only begun to be answered. Connectivity is best described for shallow-water habitats such as coral reefs (e.g., Jones et al. 2005). The prevailing paradigm for larval dispersal has made a pendulum-like swing in recent decades from high levels of connectivity among habitats to mostly self-recruitment (Levin 2006). However, genetic results do not necessarily reflect restricted dispersal and low connectivity among habitats (Adams and Mullineaux 2008). Investigations of connectivity are largely based on population genetics (Shank 2010), while larval biology is incompletely known or just inferred (e.g., Miller et al. 2010, Palumbi 2003). A wide variety of techniques are available for tagging and tracking adult organisms and larvae (Levin 1990, Levin et al. 1993, Thorrold et al. 2002), and these techniques are just beginning to be applied in deeper water (Génio et al. 2015). A better integration of population genetics, larval biology, and physical oceanography to build models of larval dispersal will increase our knowledge of connectivity for isolated marine habitats at all depths. Excellent examples of integrated studies include that of Baums et al. (2006) for coral reefs and Young et al. (2012) for cold seeps.

Competition and facilitation

One major point of discussion that has grown out of island theory, particularly Diamond’s assembly rules (1975a), is the strength and role of interspecific competition in community assembly. Very little is known about competition in the deep sea (McClain and Schlacher 2015). Even for shallow-water communities, the relative strength of competition for food resources among species is an interesting question. Experimental evidence suggests that suspension feeders compete for food in some cases (Dalby 1995, Myers 1990, Okamura 1984; Peterson and Black 1991, 1987). Thus, the possibility for niche partitioning is opened – different species may consume different size-fractions of particles where they co-occur in order to decrease interspecific competition. Niche partitioning has been demonstrated for terrestrial fauna and can be considered an example of an assembly rule (Belyea and Lancaster 1999).

The opposite of competition – facilitation, including commensalism, has also been shown to impact faunal distribution on island-like dropstones (Chapter IV). Given the ubiquity of commensal relationships in cold-water coral and sponge stands (Cordes et al. 2008, Maldonado et al. 2015, Shank 2010), positive non-random co-occurrence patterns are likely to be found in other habitats as well. Epibiotic relationships have also been documented for Antarctic sea urchins (Gutt and Schickan 1998), Arctic crabs (Dvoretsky 2012) and hermit crab shells (Bałazy and Kukliński 2013, Bałazy et al. 2016, Barnes et al. 2007). Epibiontism may be an important mechanism for suspension-feeding organisms to achieve greater elevation in the benthic boundary layer, exposing themselves to faster water flow and higher particulate food supply (Buhl-Mortensen et al. 2010).

Large, structural organisms can provide shelter and potential protection from predation for small, mobile organisms (Buhl-Mortensen et al. 2010, Stachowicz 2001), leading the species to have positive non-random co-occurrence (Bałazy et al. 2014). Facilitation can also impact the course of succession in marine insular communities (Osman and Whitlatch 1995b). Examples of positive biotic relationships, including facilitation, commensalism, and mutualism, abound for marine fauna (Buhl-Mortensen et al. 2010, Stachowicz 2001), and inclusion of these positive interactions will allow for more complete ecological theories (Bruno et al. 2003). For marine hard-bottom fauna, additional research into biotic interactions, both competitive and facilitative, would enlighten the process of community assembly.

Succession

While the process of succession is relatively well-described for shallow marine hard substrata, much remains to be discovered about the mechanisms responsible. Studies of succession should also be extended into deeper water, for both chemosynthetic and non-chemosynthetic habitats. Temporal change has been observed at deep-sea hydrothermal vents (Hessler et al. 1988), and hypotheses have been put forth to explain the observed changes (Mullineaux et al. 2000); however, our understanding is far from complete, as even sequential studies at the same sites provide contradictory results (Hunt et al. 2004). The mechanisms of succession may be different for sessile and mobile fauna (Mullineaux et al. 2003). Repeat observations at the same sites and further experimentation are required to understand the mechanisms of faunal change at vents.

For non-chemosynthetic habitats, very little is known about the process or mechanisms of succession in deep water. Single time-point observations have been made (Chapter III, Taylor et al. 2014), but a need exists for repeat observations at the same sites. The use of larval traps and settlement plates, which has already begun for chemosynthetic deep-sea habitats, should also be extended to non-chemosynthetic substrata. These data would show what larvae are available and recruit to a substratum; recruitment can be considered the first step in succession.

A DIRECTION FORWARD

The section above outlines three major veins for future research on community assembly of island-like marine habitats. The opportunity exists to use anthropogenic substrata deposited on the seafloor as “natural” experiments to observe community assembly on isolated marine substrata. Already the conspicuous absence of climax species from a nearby natural hard-bottom community has been noted for a shipping container underwater for 7 years, indicating the container community may be at an early stage of succession (Taylor et al. 2014). Anthropogenic substrata of different known ages at similar depth and latitude could be treated as snapshots of succession at different points in time. Larval traps or settlement plates could be outplanted at these locations to observe what species are available to recruit. Population genetics of the species present could reveal which natural-substratum source population the recruits originated from. Measurements of current speed and experiments in reproductive biology could be used to build models of larval dispersal. Shipwrecks, shipping containers, oil platforms and pipelines, military discard, even litter (Bergmann and Klages 2012, Gass and Roberts 2006, Kelley et al. 2015, Lira et al. 2010, Taylor et al. 2014) have all been colonized by sessile and mobile hard-bottom fauna (Kilgour and Shirley 2008, Ross et al. 2016), and these isolated substrata can be used as an opportunity for research into community assembly, especially if the sinking date is known.

This review has focused on two classical theories of island ecology, both decades old. However, a new model of island biogeography has been proposed by Whittaker et al. (2008), which incorporates time as a factor into the MacArthur-Wilson model to acknowledge the fact that few, if any, islands are actually in equilibrium. This General Dynamic Model has great potential to explain the species richness on terrestrial islands of varying size and age (Borregaard et al. 2015). Whether it can be applicable to other island-like habitats, including marine isolated substrata, remains unevaluated. The

General Dynamic Model may provide insights for the ecology and succession of seamounts and hydrothermal vents – direct island analogues with a finite life-span.

For the most part, marine ecology has developed independently of advances in terrestrial ecological thought. Ecological theories developed for terrestrial habitats may nonetheless be applicable to marine habitats and provide new insights.

BRIDGE I

Throughout the rest of this dissertation, I apply the principles of classical island theory discussed above to new datasets. I document the species distribution patterns on island-like marine hard substrata including shipwrecks, dropstones, and settlement plates, and discuss possible mechanisms of community assembly on each.

Chapter III concerns a series of eight shipwrecks located on the U.S. Atlantic margin. The ships were sunk in 1921-1924, so they were underwater for 88-91 years old at the time of sampling in 2012. Each wreck constitutes an island-like habitat, situated on the sandy seafloor isolated from other similar structures. The shipwrecks are large, complex habitats, including a variety of construction materials, intact and destroyed surfaces, and fishing gear that has become entangled on them. The invertebrate communities on the wrecks also have complex and variable distribution patterns within each wreck. There are significant differences among the wrecks, however, and I focus on these differences in Chapter III.

Each of the five species distribution patterns for island-like habitats can be applied to shipwrecks, to test the hypothesis that shipwreck fauna have the same distribution patterns as island fauna. I then discuss the possible mechanisms of community assembly on shipwrecks in Chapter III, looking into the life-history traits of each species present and comparing the communities on the shipwrecks to known stages of succession on shallow-water substrata.

In Chapter IV, I focus on a different kind of island-like marine habitat, dropstones in the Fram Strait. Dropstones were defined above as stones of terrestrial origin, which were deposited on the seafloor after being released from a melting iceberg. They are common in the HAUSGARTEN oceanographic observatory on the Arctic continental slope. Much like for shipwrecks, each of the five species distribution patterns from Chapter II can be applied. I test for higher species richness on larger stones, higher species richness on stones closer to a “mainland” rocky reef, “incidence functions” (correlation between biotic community composition and island size), nested assemblages of fauna at stations further away from the rocky reef, and non-random co-occurrence.

In chapters V and VI, I turn my attention to Svalbard fjords. I seek to understand how communities of hard-bottom invertebrates are assembled on island-like hard substrata. Chapter V serves as a preamble to chapter VI by outlining the megabenthic communities present in Atlantic- and Arctic-influenced fjords in north and east Svalbard and at stations on the north Svalbard shelf. In Chapter V, I show how the megabenthos in north Svalbard is affected by depth, temperature, and substratum heterogeneity.

Chapter VI features a recruitment experiment in Svalbard fjords. Recruitment can be considered the first stage in succession and an important early step in community assembly. I outplanted settlement plates in three different fjords at depths ranging 7 – 215 m, and at different times of year, to see how recruitment is influenced by temperature, depth, and season. Of the five species distribution patterns outlined for islands and island-like marine habitats, only non-random co-occurrence could be applied to the Svalbard settlement plate data. I tested for non-random co-occurrence on the settlement plates.

Throughout the remaining chapters of this dissertation, the ecology of island-like marine substrata in the North Atlantic and Arctic is described. Common species distribution patterns derived from classical island theory are sought in each case, and the possible mechanisms of community assembly are discussed.

CHAPTER III

THE BILLY MITCHELL FAUNA: INVERTEBRATE COMMUNITIES ON HISTORICAL SHIPWRECKS IN THE WESTERN ATLANTIC

Kirstin S. Meyer, Sandra D. Brooke, Andrew K. Sweetman, Maya Wolf, and Craig M. Young

INTRODUCTION

There are an estimated three million shipwrecks worldwide, only a fraction of which have been explored (UNESCO). A good understanding of the fouling fauna on shipwrecks may inform many important ecological questions, particularly in deep water. Shipwreck communities can inform our understanding of how habitat heterogeneity affects community assembly, as they constitute hard-substratum islands in a sea of mud. By knowing the sinking date of a shipwreck, one may describe the process of succession and estimate how long it takes for hard substrate communities to develop (Perkol-Finkel et al. 2005). Shipwrecks are isolated hard substrata, so they can be used as models for studies of connectivity, larval dispersal, and recruitment (Perkol-Finkel and Benayahu 2007, Amaral et al. 2010, Lira et al. 2010). By being composed of heavy metals and synthetic paints, they demonstrate the long-term effects of these materials on benthic communities (Walker et al. 2007, Work et al. 2008). Shipwrecks are essentially submerged islands of hard substratum, so they could show some of the same faunal distribution patterns and community assembly mechanisms as terrestrial islands. The analysis of such island-like marine habitats can provide new insights into terrestrial and marine ecology alike.

Shipwrecks are well-known as archaeological sites, but they can also serve as artificial reefs that provide habitat for algae (dos Santos et al. 2010), invertebrates (Pawlik et al. 2008, Lira et al. 2010), and fish (Mallefet et al. 2008). Even siboglinid tube worms, typically found in chemosynthetic habitats, have been discovered on degrading organic matter (paper, cotton, pineapple, twine) in Mediterranean and Atlantic shipwrecks (Dando et al. 1992, Hughes and Crawford 2008, Gambi et al. 2011). Shipwrecks increase local biodiversity by providing protection from predation, substrate for hard-bottom fauna, and by serving as concentration points for mobile species (Kilgour and Shirley 2008). Shipwrecks can have profound effects on the surrounding benthos, including the establishment of an entirely different community several meters beyond the physical structure of the wreck (Work et al. 2008).

Most historical and biological treatments of shipwrecks have taken place in shallow water and especially at depths accessible by SCUBA (Amaral et al. 2010, Lira et al. 2010, dos Santos et al. 2010); shipwrecks in deep water are less well-known (but see Hughes and Crawford 2008, Kilgour and Shirley 2008).

In this study, we focus on a series of eight shipwrecks at the edge of the continental shelf, located at ~100 m depth off the U.S. east coast. The present analysis concerns the invertebrate fauna on the shipwrecks only; fish communities present at each of the shipwrecks were analyzed by Ross et al. (2016). We examine the data for differences in the invertebrate communities on different sides of the wrecks and on different surfaces to understand how the structure of the wrecks affects the faunal distributions. We also apply several analyses to the shipwrecks derived from the classical literature for terrestrial island ecology (MacArthur and Wilson 1967, Diamond 1975a).

We focus on five elements of classical island theory, derived from MacArthur and Wilson's (1967) equilibrium theory of island biogeography and Diamond's (1975a) assembly rules. These elements were outlined in Chapter II, and in each case, we test the hypothesis that shipwreck fauna show the same distribution patterns as terrestrial island fauna. These five distributional patterns include: (1) a log-linear relationship between species richness and island (=shipwreck) area; (2) isolation-by-distance, that wrecks closer together have more similar communities; (3) "incidence functions," or the presence of different sets of species on shipwrecks of varying size; (4) nested distribution patterns of the fauna, in which ever-smaller sub-sets of fauna are found on ever-smaller wrecks; and (5) non-random co-occurrence, meaning some pairs of species are found together less often (negative non-random co-occurrence) or more often (positive non-random co-occurrence) than expected by random chance.

Item (2), the degree of isolation of the shipwrecks, deserves further clarification. MacArthur and Wilson (1967) discussed both the effect of isolation from a mainland and the role of islands as "stepping-stones," facilitating connectivity between other islands in the surrounding area. For marine hard-bottom habitats, these concepts have been reinterpreted in the "island model," which states that colonists on isolated substrata are selected from a well-mixed larval pool, and the "stepping-stone model," which states that larvae disperse among substrata, resulting in a positive correlation between genetic and geographic distances (Vrijenhoek 1997). These two models have been described for marine hard substrata as diverse as coral reefs (Palumbi 2003) and hydrothermal vents

(Vrijenhoek 2010). In the present analysis, we expect that shipwreck fauna produce larvae that disperse to the surrounding wrecks, so we test the hypothesis that wrecks closer to one another on the seafloor have more similar communities (the "stepping-stone" or "isolation-by-distance" model (Vrijenhoek 1997)). However, we also consider the life-history traits and dispersal capability of each individual species.

MacArthur and Wilson (1967) and Diamond (1975a) each described a shift in the life-history traits of island fauna in the course of succession, from long-dispersing, fast-growing generalist species to short-dispersing, slow-growing superior competitors. While we were unable to observe any shift in the life-history traits of shipwreck fauna over time (our data constitute a single time-point and all shipwrecks are approximately the same age), we nevertheless discuss what is known of the life histories of each of the present shipwreck species and propose hypotheses for future studies on isolated hard substrata in deep water.

METHODS

The shipwrecks in this study are located near the continental shelf break, east of Chesapeake Bay (Fig. 3). They include seven that were sunk in a series of bombing experiments in June-July 1921 and belong to the "Billy Mitchell fleet" (Wildenberg 2014). The eighth was sunk in artillery tests in 1924. The identity of each shipwreck is known, but in order to protect the historical integrity of the shipwrecks until they can be fully cataloged, neither the names nor the exact geographic coordinates of the shipwrecks will be published here. Instead, the shipwrecks will be referred to by numbers, following the nomenclature of Ross et al. (2016) (Table 1).

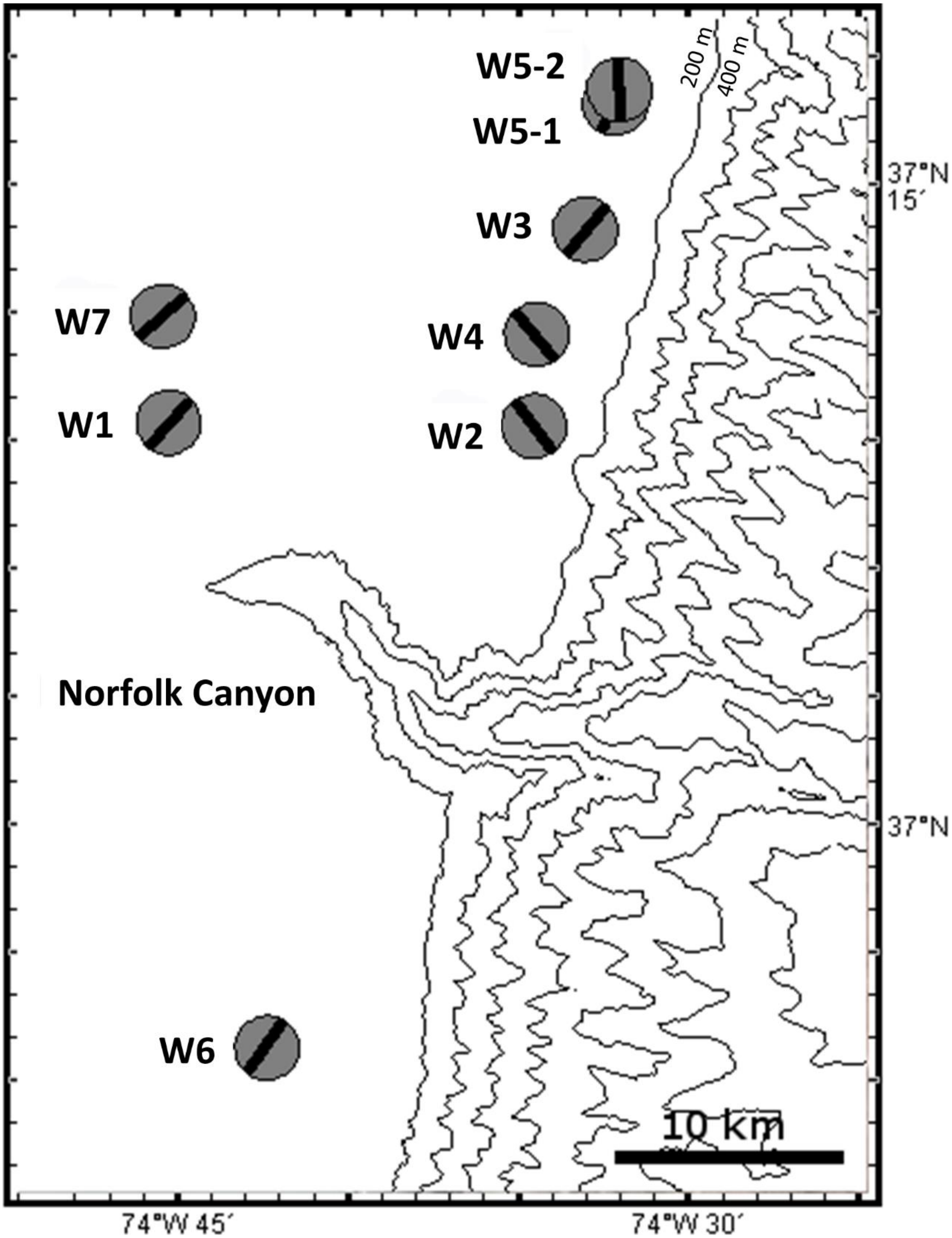

Fig 3. Map of shipwreck sites east of Chesapeake Bay. Black lines indicate orientation of the major axis of each shipwreck.

Table 1. Shipwrecks surveyed in 2012.

Shipwreck number	**Date**	**ROV dive number**	**Shipwreck type**	**Maximum altitude above seafloor (m)**	**Depth (m)**
W1	22-Sep-2012	ROV-2012-NF-22	Submarine	6	90
W2	23-Sep-2012	ROV-2012-NF-23	Battleship	18	113
W3	24-Sep-2012	ROV-2012-NF-24	Light cruiser	7	125
W4	26-Sep-2012	ROV-2012-NF-26	Destroyer	3	105
W5-1	26-Sep-2012	ROV-2012-NF-27	Destroyer	3	117
W5-2	26-Sep-2012	ROV-2012-NF-27	Destroyer	2	117
W6	27-Sep-2012	ROV-2012-NF-29	Battleship	14	118
W7	28-Sep-2012	ROV-2012-NF-30	Submarine	3	79

In 2012, the remotely operated vehicle (ROV) *Kraken II* (Univ. Connecticut), a 1000 m-rated science-class vehicle, was deployed from NOAA Ship *Nancy Foster*. A Kongsberg OE14-502 high-definition digital camera was mounted on the ROV during dives to collect video. The ROV's path of motion during the dives was driven by archaeological objectives rather than prescribed transects for the analysis of benthic fauna. Thus, videos were recorded with no consistent speed or distance from the wreck, and the ROV's lasers (used for distance calibration) remained off for the majority of each dive. In order to analyze the ROV videos, frame grabs were obtained from each video whenever the surface of the shipwreck was in clear view and a consistent distance from the surface of the wreck. Frame grabs that were anomalously close to or far away from the wreck, such that the invertebrate megafauna could not be clearly discerned, were excluded from analysis. The few frame grabs for which the lasers were switched on were used to calculate the average size of analyzable frame grabs of the shipwreck surface (mean = 1.45, SE = 0.13 m^2, n = 29). Thirty eligible frame grabs were then randomly sub-selected from each wreck and analyzed as described below. Voucher specimens of the most common species were collected using the ROV's manipulator arm.

In order to estimate the percent cover of sessile invertebrates, two hundred random points were overlain on each frame grab, and the number of points meeting each species or morphotype was counted. Mobile invertebrates were also recorded from each frame grab by simple count. The percentage of points belonging to the same plane was calculated and subtracted from 100 to estimate the shipwreck surface complexity. The number of points that intersected a net or other fishing gear were also counted, to determine the approximate percent cover of fishing gear on each wreck. Morphotypes (putative species based on morphology), were designated for those organisms of unknown identity for which no voucher specimen could be collected. Once the fauna had been quantified, we noted the dominant taxa for each wreck, defined as those species or morphotypes with a cumulative abundance at least one order of magnitude greater than other rarer taxa present on the wreck.

One morphotype, called the "brown tube complex" consisted of proteinaceous tubes with multiple species living on them. The tubes resemble similar structures made by chaetopterid polychaetes, though no living individuals were found in the "brown tube complex" voucher specimen collected from W1. Multiple species were epibionts on the tubes, including at least four species of hydroids (*Lafoea dumosa*, *Halecium* sp., *Modeeria rotunda*, *Nemertesia americana*), two species of bryozoans, a caprellid amphipod, a pycnogonid, the ophiuroid *Ophiocomina* sp., several errant polychaetes, a serpulid polychaete, and a chiton, all living on or around one another. Because each of the epibionts was too small to be seen without magnification, it was impossible to visually differentiate among the many species in ROV video. "Brown tube complex" was thus treated as one morphotype for the purposes of this analysis.

Frame grabs were categorized by the region of the ship where they were obtained. "Bottom" was defined as a frame grab in which the seafloor was visible or which was known to be directly adjacent to the seafloor based on video context. "Top" was defined similarly, for frame grabs in which the water column above the wreck was visible or which was known to be located at the top of the wreck based on video context; all other frame grabs were defined as "middle." More frame grabs were identified as "middle" (n = 182) or "bottom" (n = 144) than "top" (n = 71). In addition, frame grabs were categorized by their orientation – whether they featured a vertical, horizontal, slanted, or complex surface, the underside of the wreck, or a structure that protruded from the wreck (here termed a "pillar"). Frame grabs were also classified by compass bearing: north versus south side of the ship, and east versus west side.

Data were log(x+1)-transformed in order to reduce the effect of overly-dominant species, and multivariate statistics based on these transformed data in a Bray-Curtis similarity matrix were calculated using Primer v6 (Clarke and Gorley 2006). Analysis of similarity (ANOSIM) was used to test for differences in the biotic communities among wrecks, between different sides of the same wreck, and among different surfaces (vertical, horizontal, slanted, complex, underside, or pillar) within the same wreck.

In order to determine whether there was a log-linear relationship between species richness and area, such as that described by MacArthur and Wilson (1967), we graphed the total species richness on each wreck against the relative surface area of the wreck. It was impossible to find the absolute surface area of each wreck, given the complex nature of the wreck surfaces. Therefore, relative surface area was found by multiplying the total length of the wreck, its height (maximum altitude above the seafloor of the wreck's highest point), and its average surface complexity (surface complexity was calculated for each frame grab as described above).

To test whether wrecks in closer proximity to one another had more similar communities, we conducted a Mantel test using a Bray-Curtis similarity matrix based on the biotic data and a Euclidean distance matrix based on the latitude and longitude of each wreck. To test whether wrecks of similar size had more similar communities (and conversely, wrecks of different size had different communities), we conducted a Mantel test using a Bray-Curtis similarity matrix based on the biotic data and a Euclidean distance matrix based on the maximum height and length of each wreck. Mantel tests were conducted using the APE package in R (R Core Team 2013, Paradis et al. 2014).

We tested for nested patterns of the fauna in the program Nestedness (Ulrich 2006) using a fixed-fixed null model and the BR and N_1 indices according to the recommendations of Ulrich and Gotelli (2007). Finally, we tested for non-random co-occurrence patterns of the fauna in the program EcoSim (Entsminger 2014) using a fixed-fixed null model and the C-score index according to the recommendations of Gotelli (2000).

RESULTS

A total of 34 invertebrate morphotypes were observed on the eight shipwrecks. Of these morphotypes, 21 were identified at least to genus. The most common morphotypes are depicted in Fig. 4.

A list of the invertebrate fauna present at each shipwreck can be found in Table 2, including dominant taxa on each wreck. On four of the wrecks (W1, W5-1, W5-2, and W7), the most abundant taxon alone accounted for 60-80% of the fauna present on the wreck, and up to 85% of the fauna was accounted for by the two most common taxa (Fig. 5). The other four wrecks (W2, W3, W4, and W6) had more even communities, with only 20-40% of the fauna being accounted for by the most abundant taxon (Fig. 5).

Analysis of similarity (ANOSIM) revealed significant differences among the invertebrate communities on eight shipwrecks (Global $R = 0.612$, $p = 0.001$). An analysis of the sessile species also showed significant differences among wrecks (Global $R = 0.577$, $p = 0.001$); less extreme but still significant differences were found for the mobile species ($R = 0.275$, $p = 0.001$). These differences are shown graphically in an MDS plot (Fig. 6).

No consistent patterns in species richness or faunal abundance were found among different wreck surfaces (vertical, horizontal, slanted, complex, underside, or pillar). However, a multivariate analysis of similarity revealed significant differences among surfaces for five of the eight shipwrecks (W3, $R = 0.573$, $p = 0.001$; W4, $R = 0.258$, $p = 0.001$; W5-2, $R = 0.269$, $p = 0.024$; W6, $R = 0.336$, $p = 0.019$; W7, $R = 0.258$, $p = 0.021$). There were no consistent patterns in pairwise ANOSIM tests for different kinds of

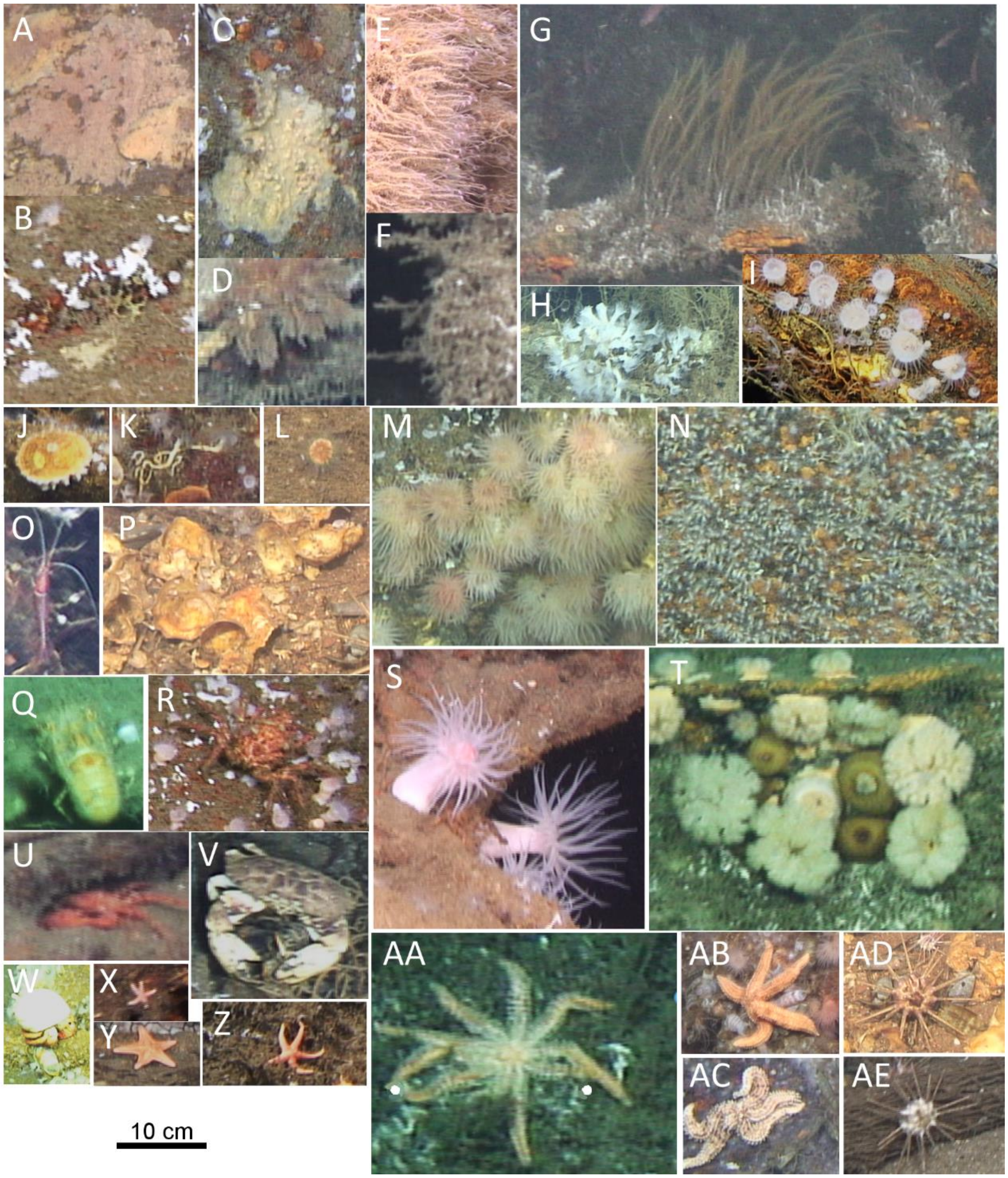

Fig. 4. Morphotypes observed in ROV video from shipwrecks. A, pink encrusting sponge; B, white didemnid ascidian; C, yellow encrusting sponge; D, pine hydroid; E, cf. Corynidae; F, brown tube complex; G, *Plumularia setacea*; H, white zoanthid; I, small white anemone; J, *Diodora tanneri*; K, cf. *Serpula* sp.; L, *Paracyathus pulchellus*; M, cf. Hormathiidae; N, *Corynactis delawrei*; O, red shrimp; P, *Crassostrea virginica*; Q, *Munida* sp.; R, *Rochinia crassa*; S, *Halcurias pilatus*; T, *Metridium senile*; U, *Euchirograpsus americanus*; V, *Cancer borealis*; W, *Paguristes lymani*; X, *Henricia* sp.; Y, *Odontaster hispidus*; Z, *Henricia oculata*; AA, *Coronaster briareus*; AB, *Sclerasterias tanneri*; AC, *Sclerasterias* sp.; AD, *Stylocidaris affinis*; AE, *Stylocidaris lineata*. Size scale is relative but not precise.

Table 2. Species and morphotypes present at each shipwreck. An x indicates presence; D indicates a dominant species on that particular wreck.

Species or morphotype	**W1**	**W2**	**W3**	**W4**	**W5-1**	**W5-2**	**W6**	**W7**
White didemnid ascidian	x	x	x	x	x	x	x	x
Yellow encrusting sponge	x	x	x	D	x	x	D	D
Pink encrusting sponge							x	
Metridium senile	D						x	
cf. Hormathiidae	x	D	x	x	x	x	x	
Halcurias pilatus			x		x	x		
Small white anemone		x	D		D	D	x	
Giant purple anemone				x				
White zoanthid	x	D	x	x	x	x	D	x
Corynactis delwarei		D					x	
Brown tube complex	D	x		D	x		x	D
Plumularia setacea	x			x			x	x
cf. Corynidae		D	x		x	x	x	
Pine hydroid			x	x		x		
Paracyathus pulchellus	x	x	x	x			x	
Crassostrea virginica		x	x					
Diodora tanneri		x	x	x	x			
Red shrimp						D		
Rochinia crassa		x	x	x	D	x	x	
Euchirograpsus americanus		x		x				
Cancer borealis				x				
Paguristes lymani		x			x	x		
Munida sp.		x		x				
cf. *Serpula*		x	x	x	x	x	x	
Henricia oculata	D						D	D

Table 2 cont.

Species or morphotype	**W1**	**W2**	**W3**	**W4**	**W5-1**	**W5-2**	**W6**	**W7**
Henricia sp.				x				
Sclerasterias tanneri		D	D	x	x	D	x	
Sclerasterias sp.				x			x	
Coronaster briareus	x			x	x			
Odontaster hispidus		x	x	x	x	x		
Ophiocomina sp.			x	x				
Stylocidaris lineata		x		D		x		
Stylocidaris affinis		x	x	D		x		
Coelopleurus floridanis		x						

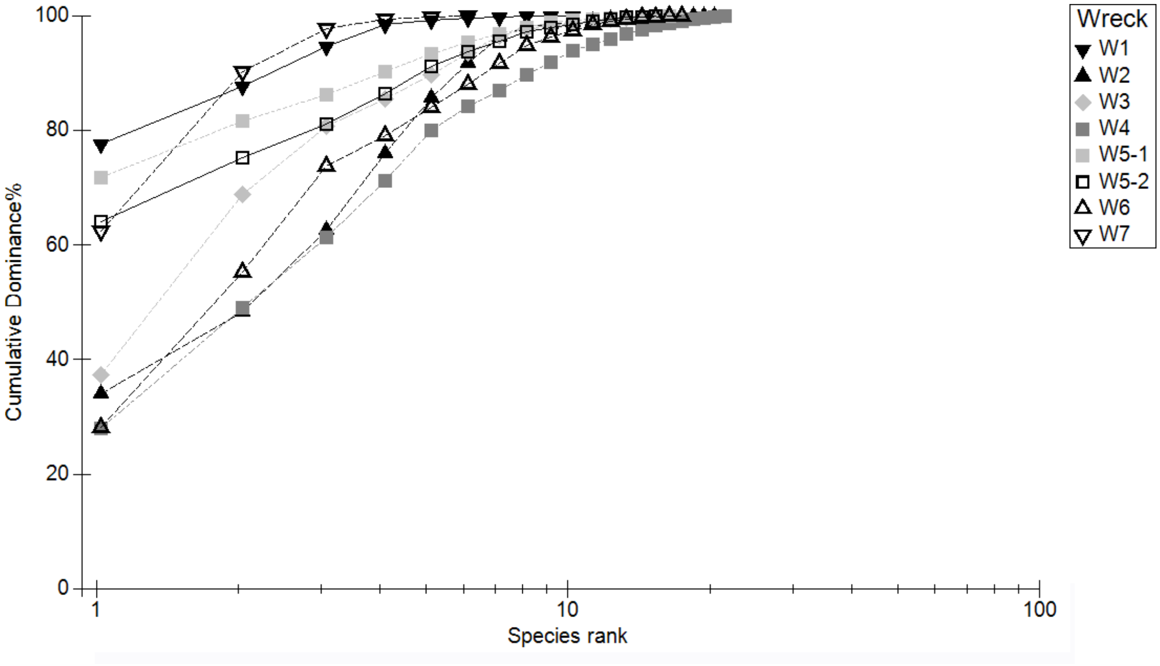

Fig. 5. Dominance plot showing cumulative percent community composition of fauna on shipwrecks on the U.S. Atlantic margin.

surfaces. In other words, those pairs of surfaces supporting the most different communities varied from wreck to wreck.

No significant relationships were found between invertebrate richness or abundance and the complexity of the shipwreck surface or the percent cover of fishing gear when analyzed within each wreck. Large nets were often observed entangled with structures on the shipwreck, and the nets were sometimes heavily colonized. For example, on W7, fishing nets and their attached floats formed semi-solid pillars extending above the wreck, which were covered in "brown tube complex" and the sea star *Henricia oculata* (Fig. 7). In other cases, fishing nets were heavily settled by encrusting sponges.

Multivariate differences between the north/south or east/west sides of a single wreck were only significant for W1 (Two-way crossed ANOSIM, N/S, R = 0.338, p = 0.044; E/W, R = 0.398, p = 0.020). The northwest side of W1 was almost completely covered in dense stands of "brown tube complex," while the southeast side of the wreck was densely populated by the anemone *Metridium senile*. The only wreck showing significant multivariate differences among the top, middle, and bottom of the wreck was W5-1 (ANOSIM, R = 0.414, p = 0.002).

Larger shipwrecks, with greater relative surface area, had higher taxon richness (Fig. 8). There was a logarithmic relationship between taxon richness and wreck relative surface area for the sessile fauna ($R^2 = 0.52$) and for all taxa together ($R^2 = 0.53$); mobile fauna showed a general increase in taxon richness with relative wreck area (Fig. 8).

Shipwrecks closer to each other geographically had more similar communities. This was true for all fauna together (Mantel test, $z = 8.07 \times 10^4$, $p < 0.001$) and for sessile

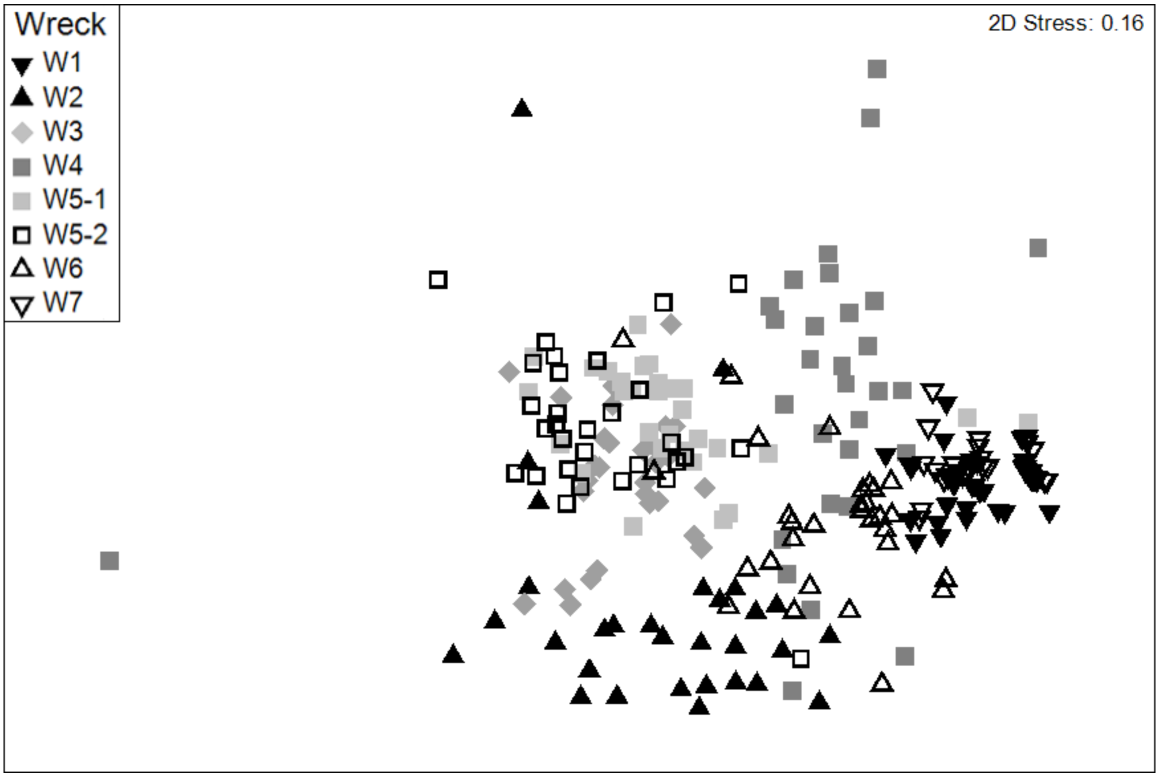

Fig. 6. Non-metric multi-dimensional scaling (nMDS) of the invertebrate communities observed at eight shipwrecks on the U.S. Atlantic margin. Each point represents one frame grab obtained from ROV video.

($z = 8.69 \times 10^4$, $p < 0.001$) and mobile fauna separately ($z = 1.80 \times 10^4$, $p < 0.001$). In addition, wrecks of the same size had more similar communities (or, conversely, wrecks of different size had different communities), for all fauna together (Mantel test, $z = 4.86 \times 10^7$, $p < 0.001$) and for sessile ($z = 5.43 \times 10^7$, $p < 0.001$) and mobile fauna separately ($z = 9.62 \times 10^6$, $p < 0.001$).

No evidence of nested faunal distribution patterns was found for the shipwreck fauna; the BR and N_1 indices (30 and 46, respectively) fell within the 95% confidence interval ranges generated by the null model (27 – 33 and 40 – 58, respectively). In

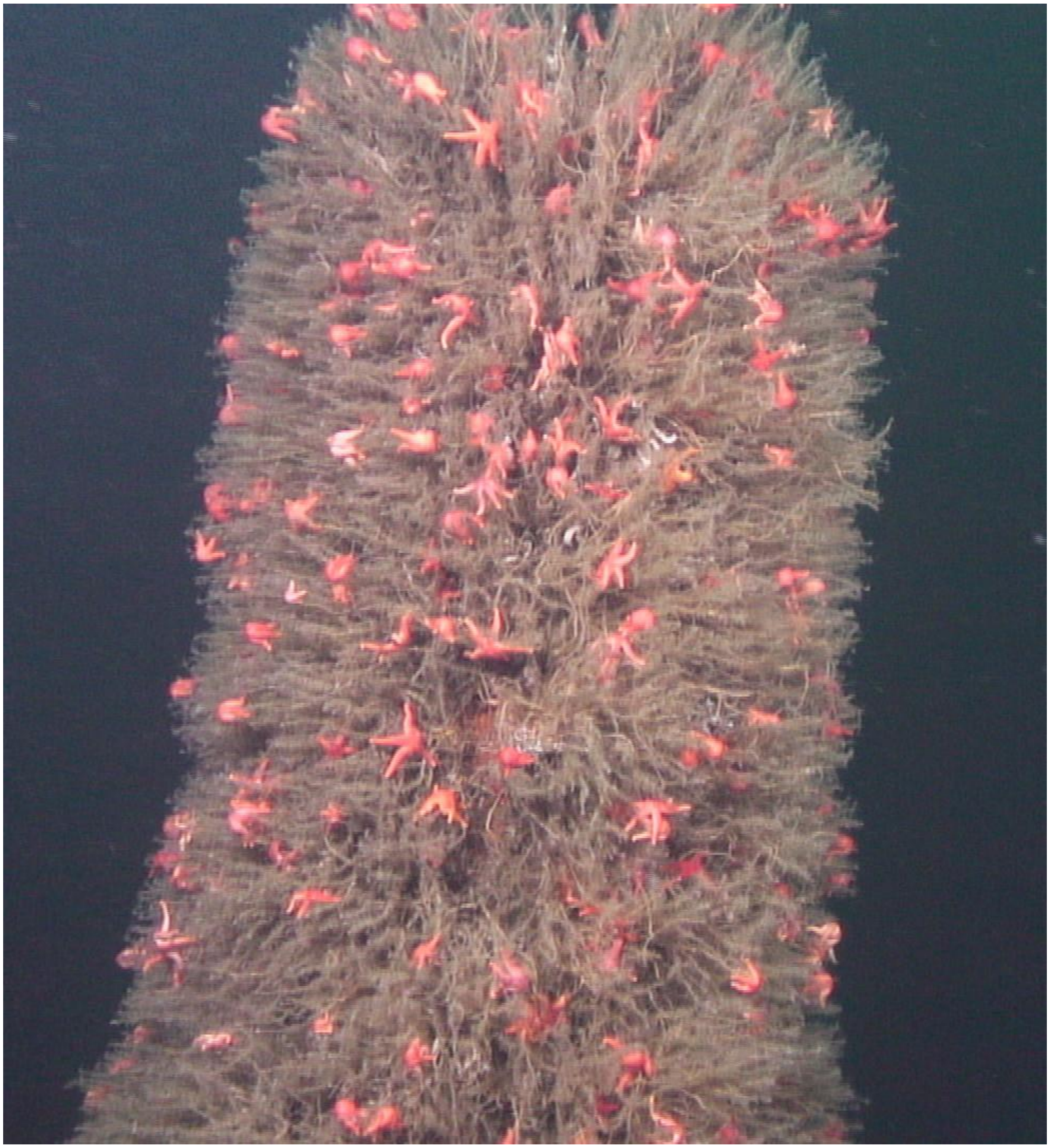

Fig. 7. Semi-solid fishing net “pillar” above wreck W7, densely inhabited by “brown tube complex” and *Henricia oculata*.

addition, the data showed no evidence of non-random co-occurrence patterns (p = 0.07), indicating that taxa were randomly distributed among the shipwrecks.

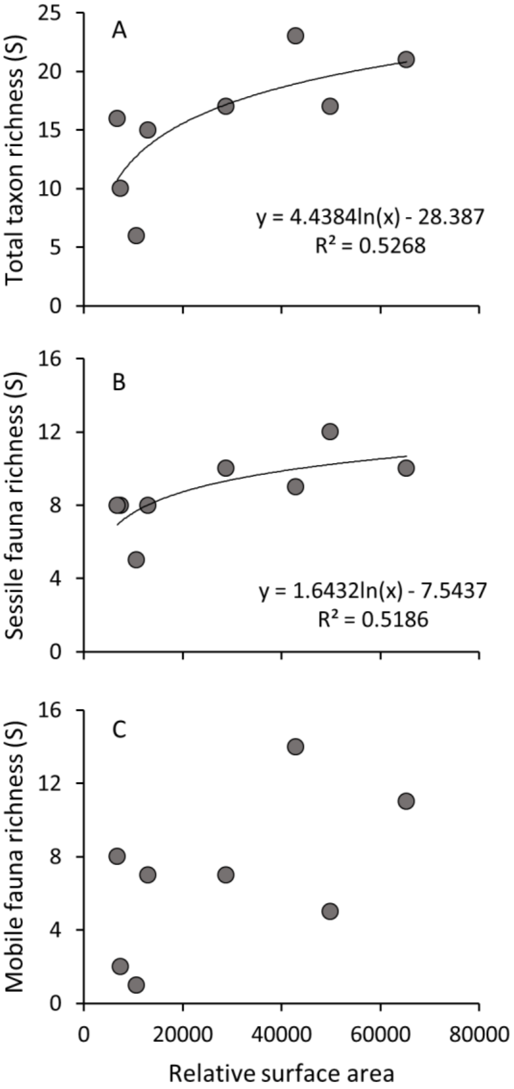

Fig. 8. Logarithmic relationships between relative surface area (height x length x surface complexity) of each shipwreck and A, richness of all fauna; B, sessile fauna; C, mobile fauna.

DISCUSSION

The results of this study show highly significant differences in the invertebrate communities among shipwrecks; however, patterns within each wreck were more complex. The wrecks themselves formed diverse and heterogeneous habitats, with different sizes, states of destruction, and coverages of fishing gear. Unfortunately, we cannot exclude the possibility that some differences in the communities within single wrecks were not detected as a result of the methodology (i.e., the lack of consistent video footage and limited taxonomic resolution); therefore we focus on differences among the wrecks for the remainder of this discussion.

Species-area relationship

Our results revealed some of the same faunal distribution patterns for shipwreck communities as for terrestrial islands. Higher taxonomic richness was found on larger wrecks, as predicted by MacArthur and Wilson (1967). The function $S = cA^z$ yields a linear relationship when both axes are log-transformed but a logarithmic relationship between taxonomic richness (S) and island area (A) when left untransformed. The logarithmic relationship may reflect the finite nature of the species pool, as even the largest substratum can only be colonized by a finite number of taxa, i.e., all those available. Each of the eight present shipwrecks were inhabited by sub-sets of the same 34 species or morphotypes.

On terrestrial islands, the species-area relationship has been explained by a variety of proposed factors. These include habitat diversity, primary productivity, resistance to disturbance, equilibrium achieved through a balance of immigration and extinction, clumped distributions of species, successional development, and sampling artifacts (MacArthur and Wilson 1967, Connor and McCoy 1979, Hill et al. 1994, Gotelli and Graves 1996). However, for island-like substrata in deep water, these explanations are not satisfactory (Chapter II). Terrestrial islands may have habitats as diverse as mountains, forests, and beaches, but the habitat diversity on marine substrata varies much less (Abele and Patton 1976). Primary productivity does not occur locally at the depths of the shipwrecks in this study, and successional development can be excluded because all wrecks are approximately the same age. The higher taxonomic richness on larger marine hard substrata can be best explained by the “passive sampling hypothesis” (Connor and McCoy 1979), which states that larger substrata are merely larger targets for dispersing larvae (Huntington and Lirman 2012, Chapter IV). Larger substrata have higher immigration rate and “fill up” more slowly, allowing more species to accumulate over time (Schoener and Schoener 1981). We find the “passive sampling hypothesis” the most parsimonious explanation for the higher taxonomic richness found on larger shipwrecks in this study.

Wrecks of similar size had more similar communities. This result could be interpreted as evidence for “incidence functions” – the presence of one suite of organisms on small wrecks and another suite of species on larger wrecks – but there is also another factor at play. Larger shipwrecks had higher taxon richness, meaning they were inhabited by larger sub-sets of the available taxon pool. Given large enough sub-sets of the available 34 species or morphotypes, the fauna present on the wrecks will begin to converge, as most of the available taxa will be present on the larger wrecks (Chapter IV). The four largest wrecks each hosted 17 – 23 of the 34 taxa, so it could be expected that their communities are more similar to one another than the communities on smaller wrecks.

Another possible explanation for the similarity among communities on the similar size wrecks is that the smaller wrecks happen to be geographically close to one another. Wrecks W5-1 and W5-2, both destroyers, are the smallest wrecks, at only 64 and 53 m long and 2 – 3 m off bottom at their highest points. These wrecks are also located only

500 m from one another on the seafloor. Wrecks W1 and W7, both submarines, are the next two smallest wrecks, and they are located only 16 km from one another but far away from all other wrecks. Wrecks located close together could seed each another with larvae. In fact, our data revealed that wrecks located closer to one another had more similar communities. Our data thus support the “stepping-stone” or “isolation-by-distance” model for shipwreck communities (but see below).

Faunal distribution patterns among wrecks

Our data showed no evidence of either nested faunal patterns or non-random co-occurrence of taxa. In other words, the set of taxa present on a given wreck did not appear to be selected from the available taxon pool according to any “assembly rule” (used here in the general sense following Belyea and Lancaster (1999)). Rather, the taxa inhabiting a particular wreck seemed to be selected randomly from the available taxon pool. Which species recruited to each wreck may merely be a matter of what larvae were present in the water column at the time the ships were sunk (Sutherland 1974). The above finding, that shipwreck fauna are randomly selected from the available species pool, is in line with the “island model” for larval dispersal among isolated marine habitats. It must therefore be considered that the “island” and “stepping-stone” or “isolation-by-distance” models are not mutually exclusive – larvae may settle randomly on shipwrecks initially, but then subsequent dispersal among close wrecks can cause their communities to become increasingly similar. The “island” and “stepping-stone” models are not actually the best way to conceptualize colonization of isolated marine habitats; a better understanding of larval dispersal and recruitment among these island-like habitats will be brought about by considering the life-history and dispersal capabilities of each individual species (Shank and Halanych 2007, Chapter II).

Meyer et al. (Chapter IV) conclude the taxa present on dropstones were randomly selected from the available pool, similar to the present shipwrecks. However, they found evidence of non-random co-occurrence among dropstones, whereas we found no evidence of this pattern for shipwrecks. It should be noted that individual dropstones were inhabited by a smaller fraction of the available taxon pool than the present shipwrecks – 26 of 56, or 46% of the available morphotypes (Chapter IV), whereas up to 67% of the available 34 taxa were found on a single shipwreck. Thus, the present shipwrecks may have only random co-occurrence because they are large enough to be inhabited by most of the available taxa. Non-random co-occurrence patterns may be less common on large, taxon-rich substrata.

Life-history traits and succession

Taxa observed on the present shipwrecks generally had two modes of larval dispersal: the motile fauna and solitary sessile species generally had long-duration planktotrophic larvae, while the encrusting or clonal fauna generally had short-duration lecithotrophic larvae. Species with planktotrophic larvae, long pelagic larval duration and/or high fecundity (or with congeners with these characteristics, if the reproductive mode for the shipwreck species is not known) include *Paracyathus, Crassostrea virginica, Rochinia, Cancer borealis, Euchirograpsus americanus, Paguristes lymani, Munida, Sclerasterias tanneri, Odontaster, Ophiocomina, Stylocidaris lineata*, and *Coelopleurus floridanis* (Buroker 1983, Chiantore et al. 2002, Fadlallah and Pearse 1982,

Table 3. Reproductive strategies of the shipwreck fauna. PLD, pelagic larval duration

Species or morphotype	**Reproductive strategy**	**Source**
White didemnid ascidian	Suspect lecithotrophic larva, asexual reproduction by budding as adult	
Yellow encrusting sponge	Suspect lecithotrophic larva, asexual reproduction by budding as adult	
Pink encrusting sponge	Suspect lecithotrophic larva, asexual reproduction by budding as adult	
Metridium senile	Planula larva, asexual reproduction by budding as adult	Bucklin 1987, Bucklin and Hedgecock 1982
cf. Hormathiidae	Larva unknown, suspect asexual reproduction by budding as adult	
Halcurias pilatus	Unknown	
Small white anemone	Larva unknown, suspect asexual reproduction by budding as adult	
Giant purple anemone	Unknown	
White zoanthid	Suspect lecithotrophic larva, asexual reproduction by budding as adult	
Corynactis delwarei	Congener *C. californica* has large planula larva, asexual reproduction by budding as adult	Holts and Beauchamp 1993, Chadwick and Adams 1991
Brown tube complex	Not applicable – species complex	
Plumularia setacea	Lecithotrophic planula, asexual reproduction by budding as adult	Carlton 2007
cf. Corynidae	Suspect medusa stage, asexual reproduction by budding as adult	
Pine hydroid	Suspect medusa stage, asexual reproduction by budding as adult	
Paracyathus pulchellus	Congener *P. stearnsii* has large feeding planula, PLD 4 weeks	Fadlallah and Pearse 1982
Crassostrea virginica	Broadcast spawner, high fecundity	Buroker 1983

Table 3 cont.

Species or morphotype	**Reproductive strategy**	**Source**
Diodora tanneri	*Diodora* spp. can broadcast spawn or lay eggs on substrata	Carlton 2007
Red shrimp	Suspect planktotrophic larva	
Rochinia crassa	Congener *R. vesicularis* has planktotrophic larva	Pohle & Marques 2003
Euchirograpsus americanus	Planktotrophic larva	Fransozo et al. 1998
Cancer borealis	Planktotrophic larva, PLD 4 months	Hines 1991
Paguristes lymani	Planktotrophic larva	Fransozo et al. 1998
Munida sp.	Planktotrophic larva, long PLD	Wenner 1983
cf. *Serpula* sp.	*S. vermicularis* has feeding trochophore, nectochaete larva, PLD 41-50 days	Young and Chia 1982
Henricia oculata	Congeners *H. sanguinolenta* and *H. pumila* brood young to crawl-away juvenile stage	Chia 1970, Eernisse et al. 2010
Henricia sp.	Congeners *H. sanguinolenta* and *H. pumila* brood young to crawl-away juvenile stage	Chia 1970, Eernisse et al. 2010
Sclerasterias tanneri	Bipinnaria, PLD > 2 years, juveniles capable of fission	Young et al. 2012, Fisher 1925
Sclerasterias sp.	Congener *S. tanneri* has bipinnaria, PLD > 2 years, juveniles capable of fission	Young et al. 2012, Fisher 1925
Coronaster briareus	Ecologically similar species in same family, *Labidiaster annulata*, has bipinnaria, brachiolaria	Janosik et al. 2008
Odontaster hispidus	Congener *O. validus* has planktotrophic, demersal, bipinnaria larva, PLD 7-9 months	Pearse 1965, Chiantore et al. 2002
Ophiocomina sp.	Congener *O. nigra* has ophiopluteus larva, PLD ~2 months	Lönning 1976

Table 3 cont.

Species or morphotype	**Reproductive strategy**	**Source**
Stylocidaris lineata	Echinopluteus larva, planktotrophic, PLD 3.5 months	Young et al. 1998, 2012
Stylocidaris affinis	Congener *S. lineata* has feeding echinopluteus	Young et al. 1998, 2012
Coelopleurus floridanis	Small eggs, planktotrophic larva	George et al. 1997

Fransozo et al. 1998, George et al. 1997, Hines 1991, Lönning 1976, Pearse 1965, Pohle and Marques 2003, Wenner 1983, Young et al. 1998, 2012) (Table 3). A planktotrophic larval stage would allow for colonization of shipwrecks by long-range dispersal from other hard-substratum habitats and dispersal of these species among the shipwrecks.

Besides just planktotrophic development, other shipwreck taxa have short-duration lecithotrophic larvae and reproduce by fission, budding, or fragmentation as adults. For example, W1 features abundant *Metridium senile*, which have a large planula larva and reproduce by budding or fragmentation when well-fed as adults (Bucklin and Hedgecock 1982, Bucklin 1987). The “white zoanthid” morphotype and *Corynactis delwarei* most likely reproduce asexually by budding as adults, in addition to reproducing sexually via a lecithotrophic larval stage (Chadwick and Adams 1991, Holts and Beauchamp 1993) (Table 3). The anemone morphotypes “cf. Hormathiidae” and “small white anemone” are distributed in dense clumps that suggest asexual reproduction by budding as adults (Chia 1976). Even the motile species *Sclerasterias tanneri* can reproduce by fission as a juvenile (Fisher 1925) (Table 3).

Of the taxa observed on the wrecks, those with lecithotrophic larvae and asexual reproduction by budding as adults tended to be dominant species on the wrecks (Table 2). “Yellow encrusting sponge” was dominant on W4, W6, and W7; *Metridium senile* dominated W1. “Small white anemone” dominated W3, W5-1, and W5-2, while “cf. Hormathiidae” dominated W2. Short larval duration and restricted dispersal range make it less likely that a species with a lecithotrophic larva would reach an isolated shipwreck. However, a small number of successfully-recruiting individuals of a species with a lecithotrophic larva could generate a dense population on the wreck. Many hard-bottom species are adapted for philopatry, recruiting back to their natal substratum (Grantham et al. 2003). Larvae produced by shipwreck colonists are likely to recruit to the same wreck in the second generation, so philopatry may be an important mechanism generating dense populations of sessile invertebrates on the wrecks.

In contrast, solitary or motile organisms with planktotrophic larvae would require many recruitment events and/or migration of adults from the surrounding area to generate a large population on a wreck. Eight of the 13 suspected or known taxa with lecithotrophic larvae and asexual reproduction as adults were dominant on at least one wreck, while only three of the 19 solitary or motile species species with planktotrophic larvae were dominant on any wreck (*Rochinia crassa*, *Stylocidaris lineata*, and *Henricia oculata*) (Table 2, Table 3).

Given the tendency for encrusting fauna with lecithotrophic larvae to dominate the shipwrecks, we hypothesize that the wrecks were each initially colonized by a small number of individuals that built up dense populations through philopatry and asexual budding as adults. In fact, four of the wrecks in fact showed a high degree of dominance, with 60-80% of the fauna belonging to the most common taxon alone. These four wrecks were all the smallest wrecks, which have the least surface area and can therefore be most easily covered by encrusting species. The remaining four wrecks, the largest ships, also had 20-40% of the fauna accounted for by the most common species, but this lesser degree of dominance may be merely a result of the greater surface area on these wrecks and the finite growth rates of encrusting organisms.

Interestingly, only one of the species found on the shipwrecks, *Henricia oculata*, is likely to brood its young to a crawl-away stage. Two congeners of *Henricia, H. sanguinolenta* and *H. pumila,* are known to brood their young (Chia 1970, Eernisse et al. 2010). *Henricia oculata* was a dominant species on W1, W6, and W7, where it occurred in high density. It is possible that brooding may have contributed to these high densities by allowing the young of only a few mating pairs to dominate the wreck after dispersing only a short distance from their parents.

The above survey of reproductive strategies shows two common themes in the life histories of shipwreck fauna: long-range dispersal via planktotrophic larvae, and short-range dispersal via lecithotrophic larvae accompanied by asexual reproduction as adults. The one possible exception is *Henricia oculata* (Table 3). Long-range dispersal is a life-history characteristic typical of early-succession species in a variety of environments (Connell and Slatyer 1977). MacArthur and Wilson (1967) and Diamond (1975a) both discussed a shift from long-dispersing, fast-growing generalist species to slow-growing superior competitors with restricted dispersal in the course of succession on islands. To explore the idea of succession, the invertebrate community composition on the shipwrecks would need to be compared to that of a natural (older) hard-bottom habitat with similar depth and similarly high relief. Unfortunately, the area surrounding the shipwrecks features mostly sand or gravel habitats, with some low-relief boulders (Steimle and Zetlin 2000, S. Brooke, unpublished data). A direct comparison is therefore impossible.

Shipwreck communities in shallow water have been shown to undergo a shift in life history characteristics of the fauna with time. In the Red Sea, a series of shallow shipwrecks (4-25 m) were inhabited by opportunistic species with far-dispersing larvae when young (<20 years underwater), but older artificial reefs (>100 years) were characterized by long-lived species with restricted dispersal and superior competitive ability (Perkol-Finkel and Benayahu 2005, Perkol-Finkel et al. 2005). Artificial reefs offshore of California (13 m) were inhabited by opportunistic species after 3 years underwater (Carter et al. 1985). A 4-year-old wreck off the coast of Florida (27 m) was also characterized by fast-growing species (Pawlik et al. 2008), while a 119-year-old wreck in the Red Sea (15-19 m) was found to have no significant differences from the adjacent natural reef when similar (horizontal) surfaces were considered (Perkol-Finkel et al. 2006).

For shallow hard substrata at temperate latitude, succession usually proceeds in three stages: acorn barnacles and serpulid polychaetes are the first to colonize, followed by a community of encrusting ascidians, bryozoans, ascidians, and hydroids; the third stage is characterized by dominance of blue mussels or one of the species from the second stage (Osman 1977, Dean and Hurd 1980, Chalmer 1982). The order of succession can depend on seasonal recruitment (Pacheco et al. 2011). Acorn barnacles may enjoy early dominance on settlement plates because cyprid larvae do not require a thick biofilm for settlement, in contrast to other sessile species (Todd and Keough 1994, Keough and Raimondi 1996). The presence of calcareous organisms (*Balanus* and *Crassostrea*) on a substratum has been shown to facilitate recruitment of mid-succession colonial species (*Botyrllus, Botrylloides, Diplosoma*) (Osman and Whitlatch 1995a).

Our data constitute a single time-point, so we were not able to observe the process of succession on the shipwrecks. However, we can hypothesize based on fauna present that the present shipwrecks are in the second successional stage described above, because they are dominated by a variety of encrusting species and morphotypes – ascidians, sponges, and hydroids. *Crassostrea virginica* and a serpulid polychaete were present on 2 and 6 wrecks, respectively but were never dominant; these fauna may be the last remnants of the early-succession (typically calcareous) fauna. Three soft coral colonies were also observed on W2, in frame grabs not randomly sub-selected for analysis; this slow-growing taxon could be the first of the late-succession colonists.

A shipwreck discovered in 2015 near Norfolk Canyon (dive 4800, 2163 m, DSV *Alvin*) was sparsely inhabited by crinoids, sea pens, hexactinellid sponges, and brisingid sea stars (Fig. 9). A single zoarcid fish and a galatheid were also present. Based on historical artifacts found at the shipwreck site, the best estimate is that this shipwreck sank prior to 1820, making it >100 years older than the Billy Mitchell shipwrecks discussed in this study (D. McVeigh, North Carolina State Univ., unpublished data). This shipwreck consisted of low-relief structures (bricks, debris, and a length of chain on the deep seafloor) and is at greater depth, making a direct comparison to the Billy Mitchell shipwrecks impossible. Nevertheless, the suspension feeders inhabiting the 1820 wreck

Fig. 9. A brisingid sea star living on chain from a pre-1820 shipwreck at Blake Ridge, near Norfolk Canyon. External still obtained from DSV *Alvin*.

were all long-lived fauna with slow growth, long generation time, and restricted dispersal. The differences in life-history characteristics between the Billy Mitchell fauna and the inhabitants of the 1820 wreck provides anecdotal evidence that shipwreck communities may undergo succession accompanied by a shift in reproductive and life-history strategies similar to that observed in shallow-water environments (Perkol-Finkel et al. 2005, Edwards and Stachowicz 2010).

To our knowledge, no study has yet described the processes of succession and community development in artificial reefs at any depth > 30 m. Succession in deep-water communities is poorly understood. The shipwrecks included in this study had been underwater for 88-91 years at the time of sampling, but the communities still appear to be in a stage of mid-succession. Shipwrecks at shallower depth (4-25 m) were inhabited by late-succession species and showed no differences from nearby natural reefs after 100-119 years underwater (Perkol-Finkel et al. 2005, 2006). It is possible that the shipwrecks' isolated location makes it more difficult for the short-duration larvae of "late-succession" species to reach the wrecks, thereby causing succession to proceed slowly (Chapter II). Studies on deep-water isolated hard substrata are typically limited to single time-point observations (Taylor et al. 2014), but this study can serve as an effective base-line for characterizing succession in the Billy Mitchell shipwreck communities in the future.

This study had some logistical limitations, all stemming from the fact that no intentional transects along the shipwrecks were recorded for the biotic analysis. Nevertheless, our results show important differences in the biotic communities among the wrecks and provide insights for the ecology of island-like habitats on the seafloor.

BRIDGE II

Shipwrecks are large, complex, anthropogenic habitats with variable species distribution patterns within a single wreck. However, other, simpler island-like systems are formed by natural hard substrata, such as dropstones on the deep seafloor. There are some similarities in the species distribution patterns between dropstones and shipwrecks. Both systems have higher species richness on larger substrata and more similar communities on substrata located close together. However, there are also some differences related to the relative sizes of shipwrecks and dropstones. While shipwrecks are large, complex, and may be inhabited by the majority of the available species pool, dropstones are much smaller and have fewer species. Species on dropstones are also not distributed randomly. In the next chapter, I present the ecology of dropstone communities and apply the five distribution patterns from Chapter II to the dropstone fauna, in each case testing the hypothesis that species distribution patterns on dropstones are the same as on terrestrial islands. I then discuss the possible mechanisms leading to the observed species distribution patterns on dropstones.

CHAPTER IV

ROCKY ISLANDS IN A SEA OF MUD: BIOTIC AND ABIOTIC FACTORS STRUCTURING DEEP-SEA DROPSTONE COMMUNITIES

Kirstin S. Meyer, Craig M. Young, Andrew K. Sweetman, James Taylor, Thomas Soltwedel, and Melanie Bergmann

INTRODUCTION

Island fauna have been of interest to ecologists for many years because of the unique characteristics they possess: the contradictory phenomena of nanism and gigantism, and low species richness countered by high endemicity (Whittaker and Fernandez-Palacios 2007). The fauna and flora in island-like habitats have filled a substantial body of ecological literature, as an understanding of isolated habitats informs such wide-ranging problems as dispersal, succession and the design of natural reserves (Tjørve 2010).

Even though much of the island ecology literature centers on terrestrial habitats, the deep sea contains numerous isolated hard-bottom habitats (Young 2009) with high biodiversity that may function like islands. Island-like habitats at the deep sea floor range in size from landscape-scale features such as seamounts (Clark et al. 2010) and canyons (De Leo et al. 2010) to isolated chemosynthetic communities at hydrothermal vents (Lutz and Kennish 1993), cold seeps (Sibuet and Olu 1998), sunken wood (Bienhold et al.

2013) and whale falls (Smith and Baco 2003), to small-scale structures such as manganese nodules (Mullineaux 1987), sea urchin tests (Hétérier et al. 2008) and sponge stalks (Beaulieu 2001).

In this study, we focus on the isolated hard-bottom communities on dropstones in the Fram Strait, between Greenland and Svalbard. Dropstones are stones, here defined as anything larger than a pebble (> 6.4 cm, Wentworth 1922), that become frozen in glaciers, are carried out to sea and released by melting icebergs. They constitute the most common hard substrata north of 45° N in the North Atlantic (Kidd et al. 1981). They are inhabited primarily by sessile, suspension-feeding invertebrates (Oschmann 1990, Schulz et al. 2010) and can serve as a "resting place" for motile fauna such as shrimps and amphipods. Dropstones increase habitat heterogeneity and megafaunal diversity where they occur (MacDonald et al. 2010). The presence of a dropstone can also lead to higher functional diversity of the surrounding meiofauna (Hasemann et al. 2013). Dropstones, like most other hard substrata in the deep sea (Young 2009) are essentially hard-substratum islands surrounded by a sea of mud.

Using image analysis, we quantify the biotic and abiotic factors structuring dropstone communities. Classical island theory (including MacArthur and Wilson's (1967) equilibrium theory of island biogeography and Diamond's (1975a) assembly rules) have pointed to the influence of island size (Connor and McCoy 1979), proximity to a mainland (MacArthur and Wilson 1967), and interspecific competition (Diamond 1975a) on insular fauna. Each of these classical theories has been criticized and modified since first publication (Connor and Simberloff 1979, Anderson and Wait 2001), filling a large body of literature even in recent years (Lomolino 2000, Gotelli 2001, Whittaker et al. 2008, Borregaard et al. 2015). In this analysis, we examine the effects of these classical factors on dropstone communities – size, proximity to a potential source population, and biotic interactions among the fauna. Biotic interactions indicated by the position of organisms (overgrowth competition, epibiontism) can be directly observed using image analysis.

Five species distribution patterns are commonly found on terrestrial islands (Chapter II): (1) a log-linear relationship between species richness and island size, (2) "incidence functions," or different community composition on islands of different size, (3) higher species richness on islands located closer to a mainland source population, (4) nestedness, or ever-smaller or ever-more-isolated habitats being inhabited by ever-smaller sub-sets of species, such that each sub-set is nested within the next-largest faunal sub-set, and (5) non-random co-occurrence, or pairs of species being found together less (negative non-random co-occurrence) or more (positive non-random co-occurrence) than expected by chance.

In this study, we apply these five species distribution analyses to dropstone communities, in each case testing the hypothesis that dropstone communities have the same species distribution patterns as terrestrial islands. We compare our results to patterns found in terrestrial island communities and discuss how our findings may enlighten current thought on other island-like habitats.

METHODS

Image collection

Images of the seafloor were recorded in July 2012, during expedition ARK XXVII/2 of German research icebreaker RV *Polarstern*, from five stations in the LTER (Long-Term Ecological Research) observatory HAUSGARTEN, in the eastern Fram Strait (Soltwedel et al. 2005). Bottom temperature in the study area is ~ -0.8° C, and bottom current speed is ~5 cm s^{-1} to the northwest (Soltwedel et al. 2016, Meyer et al. 2014). Four of the five stations (S3, HG IV, N3, N5) analysed represent soft-sediment sites and constitute a latitudinal transect along the 2500 m isobath, while the remaining station, here referred to as "Senke," includes a steep deep-water rocky reef (Table 4, Fig. 10). However, at the Senke site, photographs included in the present image analysis were all recorded from the soft-sediment seafloor at the foot of the reef (Meyer et al. 2014). The Senke rocky reef is the only rocky reef known in the HAUSGARTEN area, as most of the seafloor is composed of soft sediments (Soltwedel et al. 2005). Dropstone densities along the latitudinal transect (S3, HG IV, N3) are not significantly different, but there are more pebbles at the northerly stations, corresponding to increased ice cover (Taylor et al. 2016).

Table 4. Summary of Ocean Floor Observation System (OFOS) deployments to photographically sample dropstones during ARK XXVII/2

Photographic transect no.	**Station**	**Date (2012)**	**Start latitude (N)**	**Start longitude (E)**	**Start depth (m)**	**End latitude (N)**	**End longitude (E)**	**End depth (m)**
PS80/176-1	S3	19-Jul	78° 37.04′	5° 00.07′	2360	78° 37.00′	5° 8.56′	2352
PS80/179-3	HG IV	21-Jul	79° 01.98′	4° 09.75′	2630	79° 03.88′	4° 17.18′	2409
PS80/186-5	N5	24-Jul	79° 56.07′	3° 07.98′	2534	79° 55.63′	3° 05.69′	2554
PS80/193-1	N3	26-Jul	79° 36.04′	5° 09.88′	2748	79° 33.53′	5° 16.99′	2608
PS80/196-1	Senke	27-Jul	79° 05.98′	4° 23.01′	2296	79° 06.02′	4° 33.92′	2041

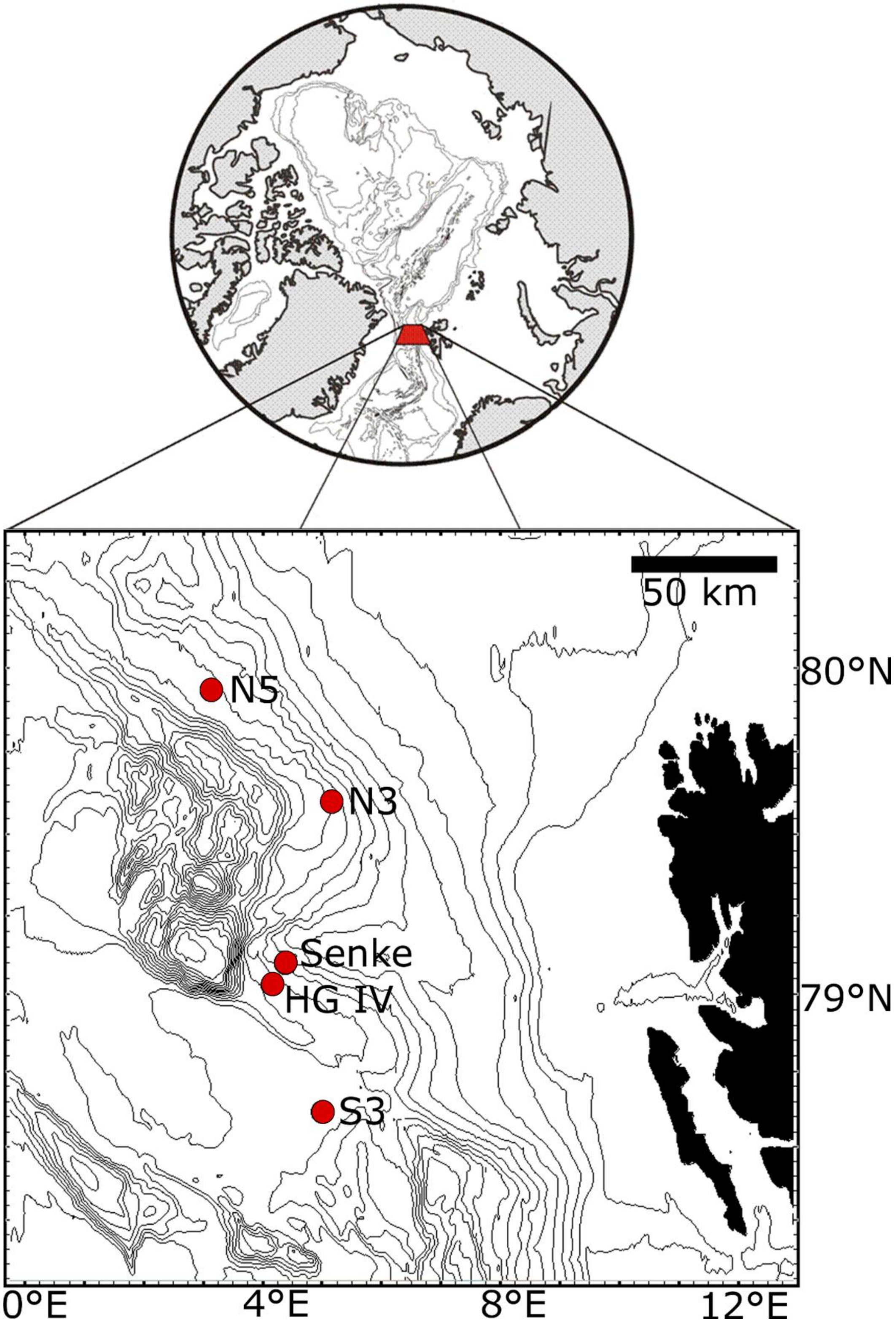

Fig. 10. Map of stations in the HAUSGARTEN observatory where dropstone images were recorded. Depth contours are shown every 250 m.

Images were recorded using a downward-facing towed camera system, the Ocean Floor Observation System (OFOS), and specifics are reported by Meyer et al. (2013) for 2012 sampling. The target altitude was 1.5 m, and each image shows approximately 3-4 m^2 of the sea floor. Three lasers were each mounted 52 cm apart on the camera frame to produce points in the photos that were used for size reference. Images were recorded automatically every 30 s (7 – 8 m apart), and additional manually-triggered images were recorded when objects of interest were observed. Each image was geo-referenced with a unique latitude and longitude.

Image analysis

Images that were unusually bright, unusually dark, or outside the most common range of altitudes (1.3 – 1.6 m) were considered ineligible for analysis. In order to calculate the density of stones at each station in 2012, 40 automatically-recorded images (which did not necessarily contain dropstones) were randomly sub-selected from the eligible images at each station, and the number of stones in each image was counted and divided by the image area to give stones m^{-2}. In order to assess the change in dropstones and pebble densities over time, 80 images per year were randomly selected from eligible OFOS images at stations N3 and S3 in 2011 – 2015 (Taylor et al. 2016).

For the analysis of dropstone fauna, 40 automatically-recorded eligible images showing stones of any size were randomly sub-selected for each station. These stones observed in the automatic images were primarily of small size (cobbles, 6.4–25.6 cm, Wentworth 1922) for every station except Senke; therefore, an additional 40 manually-triggered images containing boulders (> 25.6 cm, large enough to be seen without zooming in on the image) were also randomly sub-selected from the eligible images for stations S3, HG IV, N3 and N5. This procedure was used so that the full size range of dropstones would be represented in the dataset. Images containing large stones also featured many small stones, and every stone in the images was counted. Altogether, 541 images and 1677 individual stones were analyzed.

The plan area of each stone was traced using the freehand selection tool and measured in ImageJ (NIH, USA). Megafauna present on each stone were counted and sorted into morphotypes. Some morphotypes could be identified by comparison of the images to Bergmann et al. (2011). For those morphotypes also observed on the rocky reef at station Senke, morphotype names in this study match the names used by Meyer et al. (2014).

Data analysis

In order to determine whether dropstones were randomly distributed on the seafloor, we tested if the frequency distribution of stone densities differed significantly from a Poisson distribution using a G-test in Biomstat v4 (Exeter Software, USA). A G-test was also used to determine if dropstone fauna were randomly distributed by comparing to a Poisson distribution. Changes in dropstone density over time were tested with ANOVA, using a Levene’s test to establish homoscedasticity. Logarithmic best-fit curves of the abundance, richness, evenness, and diversity of fauna against stone size and non-parametric correlations of these biotic indices against distance to the Senke rocky reef were constructed using Biomstat. The variables “morphotype richness” and “stone area” were each log-transformed to see whether dropstone communities showed the classical log-linear relationship between these variables (Connor and McCoy 1979). Correlations between the biotic community composition and other dropstone parameters (stone size, location, distance to the Senke rocky reef) were sought using Mantel tests in R (R Core Team 2013, Paradis et al. 2014).

In order to test for significant nested patterns of the megafauna, we used the N_1 and BR indices in the software Nestedness (Ulrich 2006) according to the recommendation of Ulrich and Gotelli (2007) and a fixed-fixed null model to generate 95% confidence intervals of each index. Non-random patterns of species co-occurrence were sought for each station using the software EcoSim (Entsminger 2014). According to the recommendation of Gotelli (2000) for archipelago-like datasets, we used a fixed-fixed null model and the C-score index. To detect pairwise non-random co-occurrence patterns in the megafauna, we used the software Pairs (Ulrich 2008), once again applying the C-score index of co-occurrence and a fixed-fixed null model. Bayes M criterion was used to assess significance of pairwise comparisons, following Gotelli and Ulrich (2010).

RESULTS

Dropstones as habitats

Dropstones had a clumped distribution on the seafloor. The frequency distribution of stone densities was skewed right and differed significantly from a Poisson distribution (G-test, $G = 326$, $p < 0.001$; Fig. 11) with a variance-to-mean ratio of 8.3. However, a test for spatial auto-correlation of stone density against distance to the Senke rocky reef indicated a significant negative correlation (Mantel test based on Euclidean distance matrices, $z = 2.6 \times 10^8$, $p = 0.001$), meaning that images the same distance from the

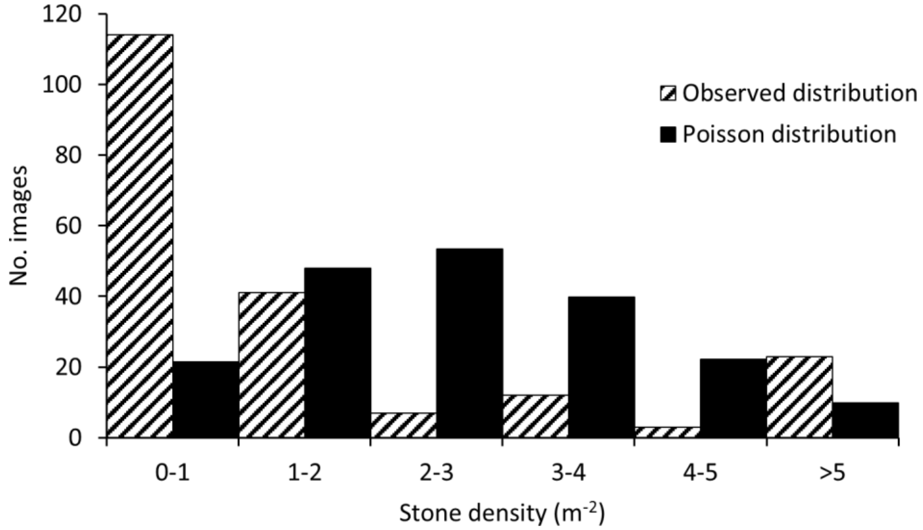

Fig. 11. Frequency distribution of stone densities in 40 randomly sub-selected images from each station, and a Poisson distribution with the same mean. A significant difference between the two distributions (see text) indicates a clumped distribution of dropstones in the study area.

Senke rocky reef had significantly *dissimilar* stone densities. In other words, clusters of stones were distributed on the seafloor without regard for distance from the rocky reef. Distance to the reef could thus be considered as an independent variable potentially influencing dropstone communities.

Dropstones and pebbles each had significantly higher density at station S3 in 2015 than in 2011 – 2013 (dropstones, ANOVA, $F = 3.39$, $p = 0.018$; pebbles, ANOVA, $F = 202.65$, $p < 0.001$; Fig. 12). At station N3, the density of dropstones was not significantly different among years (ANOVA, $p > 0.05$), but pebbles had higher density in later years (2013-2015) than in 2011-2012 (ANOVA, $F = 42.77$, $p < 0.001$; Fig. 12).

Dropstone size was not significantly spatially auto-correlated (Mantel test using Euclidean distance matrices based on stone size and latitude/longitude, $z = 7.6 \times 10^7$, $p = 0.243$) and is also not significantly correlated to distance from the Senke rocky reef (Mantel text using Euclidean distance matrices, $z = 3.8 \times 10^9$, $p = 0.963$). Therefore, the

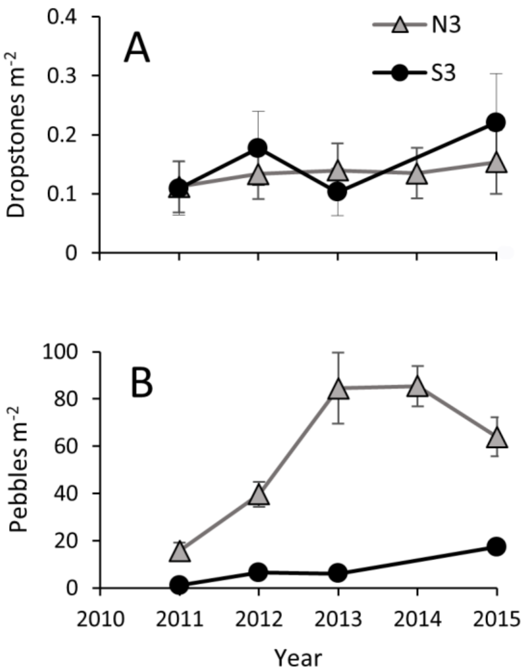

Fig. 12. A, density (m^{-2}) of dropstones; B, density of pebbles at stations N3 and S3 in the HAUSGARTEN observatory, 2011-2015. Error bars show 95% confidence intervals; error bars for pebbles at S3 are small enough to not be visible.

size of a dropstone is not related to its position on the seafloor, so stone size can be considered as an independent factor potentially influencing the biotic communities.

About 71% of all dropstones were inhabited by at least one individual. Most morphotypes found on dropstones were sponges or cnidarians, and about 96% of dropstone fauna were suspension feeders (Table 5). Examples of dropstone communities from each station are shown in Fig. 13, and morphotypes found on dropstones are depicted in Figs. 14-20.

Relationship of stone size to the biotic community

Larger dropstones were inhabited by more individuals and had higher morphotype diversity. The number of individuals (N), species richness (S), Margalef richness (d),

Table 5. Number of morphotypes and proportion of individuals in each phylum and in each trophic group on dropstones in the Fram Strait.

Phylum	**No. morphotypes**	**% individuals**
Porifera	35	83.2
Cnidaria	7	11.9
Mollusca	1	0.1
Arthropoda	5	3.5
Annelida	2	0.1
Echinodermata	5	0.9
Unknown	1	0.3
Trophic group	**No. morphotypes**	**% individuals**
Suspension feeder	45	96.3
Predator/scavenger	9	3.4
Deposit feeder	1	0.0
Unknown	1	0.3

evenness (J'), and diversity (H') of the fauna on a particular stone all showed a logarithmic relationship to the stone size (Fig. 21A – E). The relationship was strongest for H' (R^2 = 0.57) and S (R^2 = 0.53) and weakest for N (R^2 = 0.38). A log-log transformation of the species-area plot is commonly reported for terrestrial islands (MacArthur and Wilson 1967, Rusterholz and Howe 1979), and a similar transformation of the dropstone data also revealed a log-log relationship of species richness and stone area (R^2 = 0.52; Fig. 21F). Hypothesis 1 (see introduction) was thus supported.

Despite the higher diversity observed on larger stones, there was not a significant correlation between the composition of the biotic community (represented in a Bray-Curtis similarity matrix) and the size of the stone (Euclidean distance matrix) (Mantel test, $z = 8.8 \times 10^8$, p = 0.469). In other words, stones of the same size did not necessarily

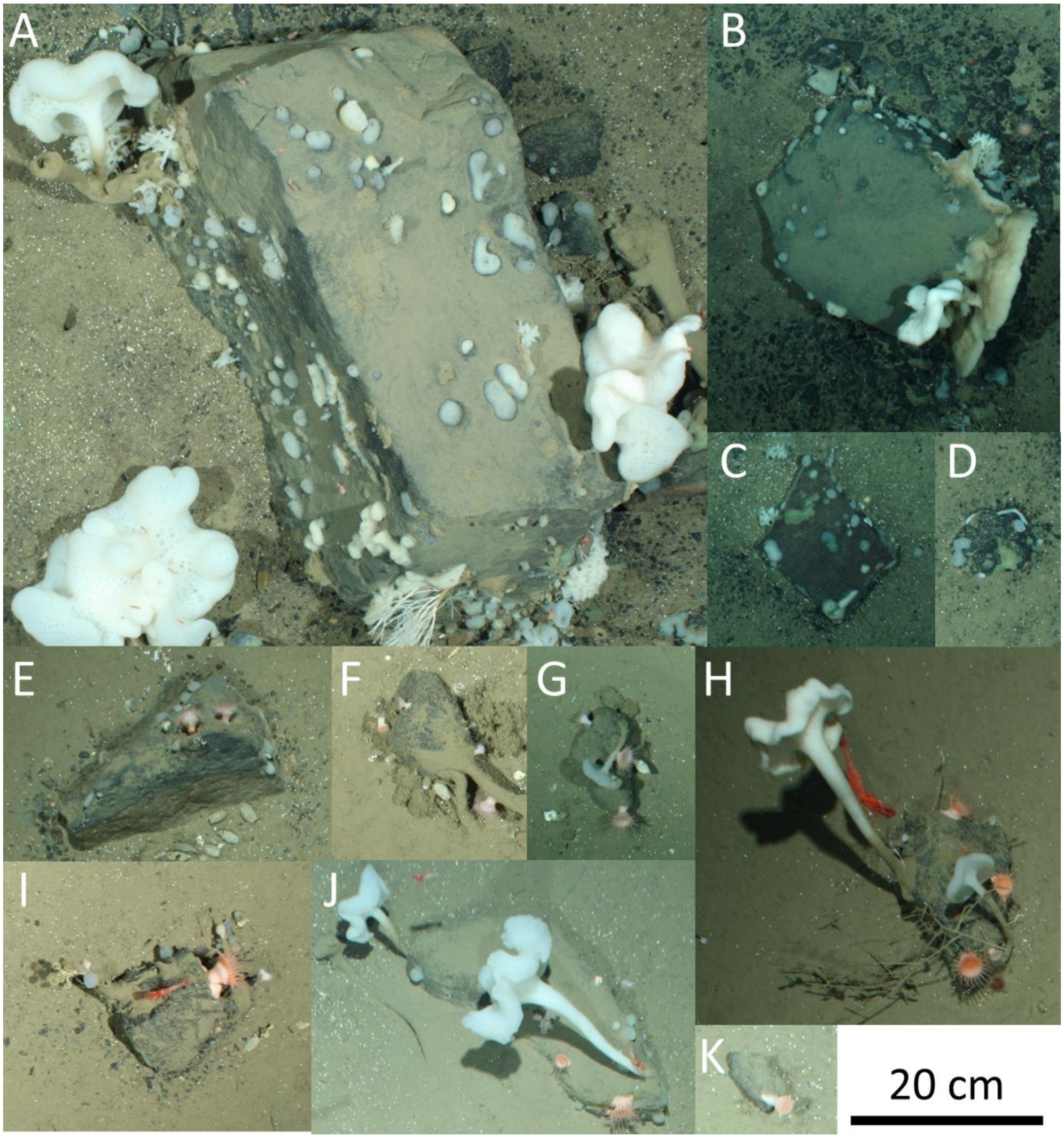

Fig. 13. Examples of dropstone communities on stones of varying size and at different stations. A-D, Senke; E-G, HG IV; H, N5; I, N3; J-K, S3.

have similar faunal composition. This result means there was no evidence of "incidence functions" (hypothesis 2) for dropstone communities.

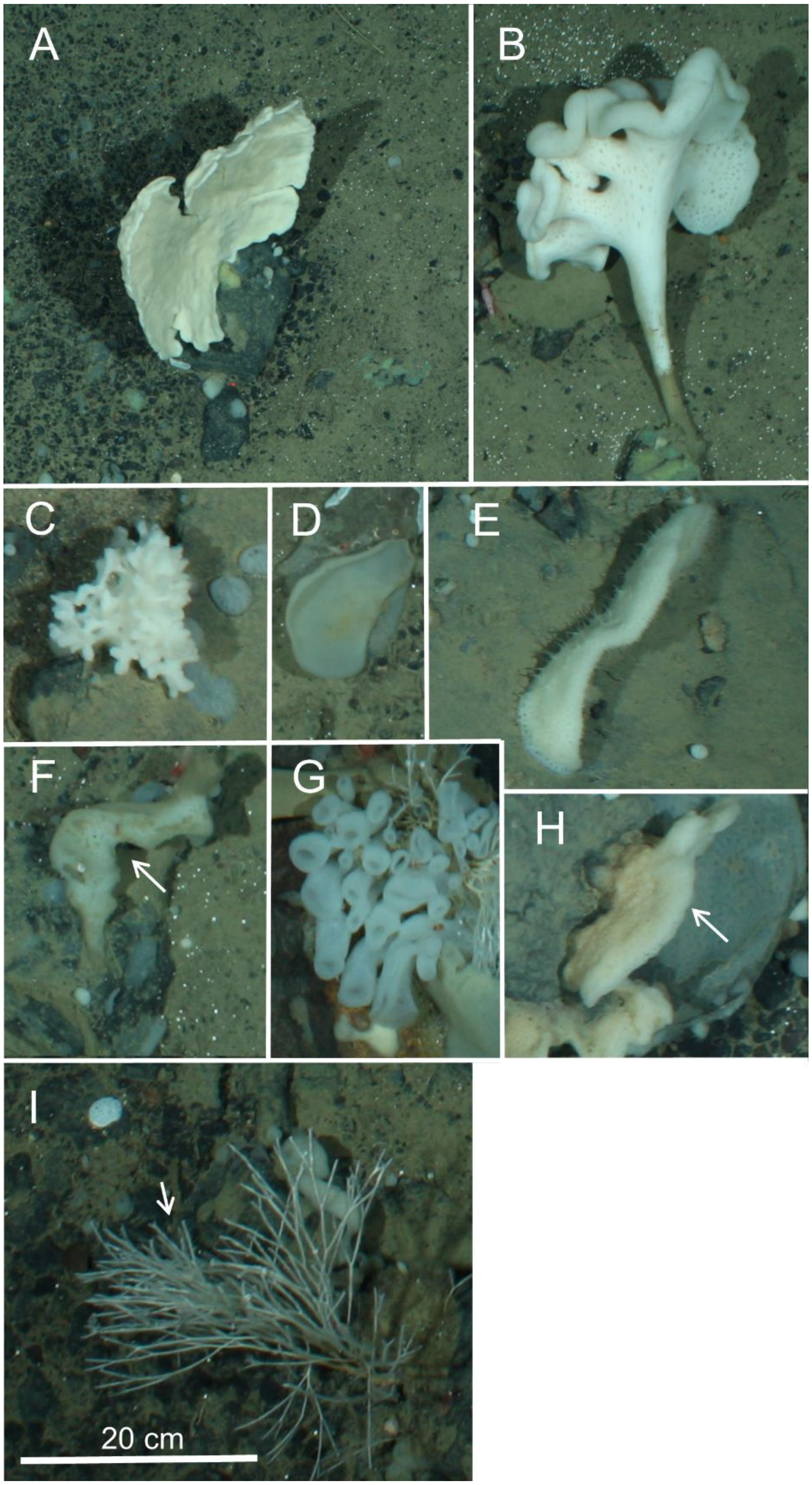

Fig. 14. Large sponges found on dropstones in the HAUSGARTEN observatory. A, *Phakellia* sp.; B, *Caulophacus arcticus*; C, *Lissendoryx complicata*; D, transparent gray sponge; E, hairy white sponge; F, asymmetrical white sponge; G, cup sponge; H, wall sponge; I, *Cladorhiza* cf. *gelida*.

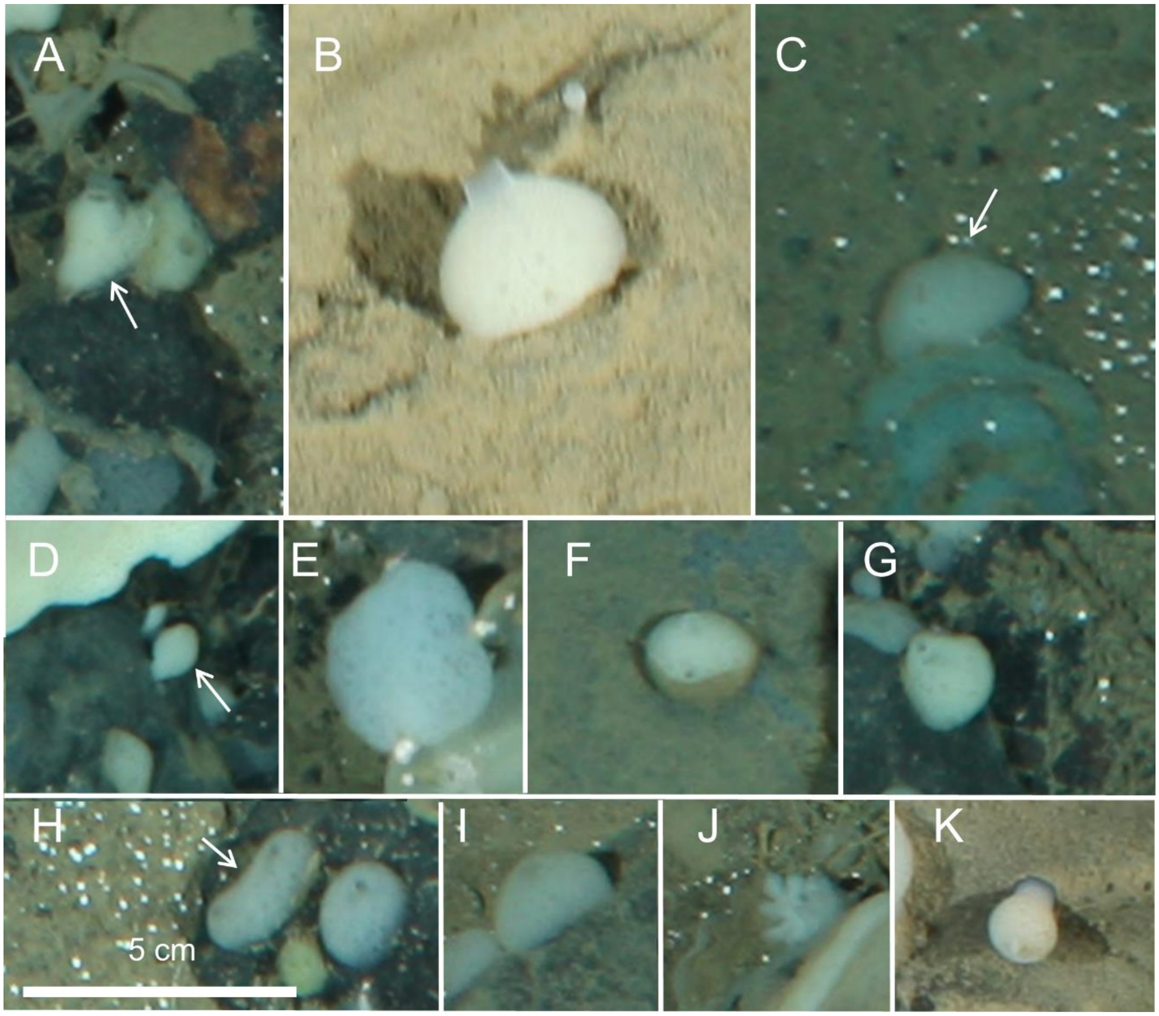

Fig. 15. Small sponges found on dropstones in the HAUSGARTEN observatory. A, vase sponge; B, *Polymastia* sp.; C, lollipop sponge; D, lobe-like sponge; E, bubble sponge; F, half-and-half sponge; G, cannonball sponge; H, gray dome sponge; I, white dome sponge; J, flame sponge; K, *Tentorium semisuberites*.

Relationship of dropstone distribution to the biotic community

Dropstone fauna had an overdispersed (clumped) distribution. The frequency-distribution of N (number of individuals on a stone) differed significantly from a Poisson distribution (G-test, $G = 1.5 \times 10^4$, $p < 0.001$; Fig. 22), with a variance-to-mean ratio of 87.8. This was the case for every morphotype (heterogeneity $G = 0$, $p = 1$). A significant

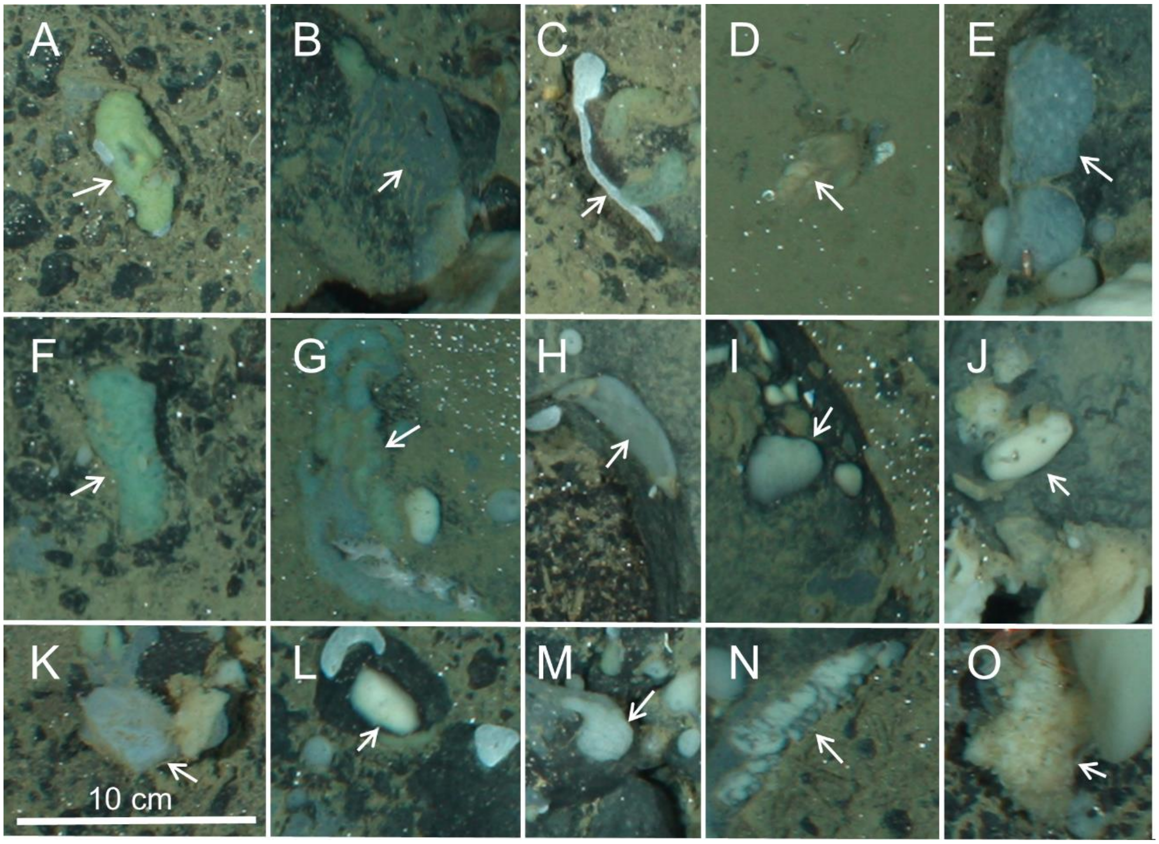

Fig. 16. Encrusting morphotypes found on dropstones in the HAUSGARTEN observatory. A, yellow encrusting sponge; B, gray encrusting sponge 1; C, thin white encrustment; D, orange-yellow encrustment; E, myxillinid sponge; F, laminar bryozoan; G, gray-yellow puffy encrustment; H, gray encrusting sponge 2; I, pancake sponge; J, puffy white encrustment; K, gray encrusting sponge 3; L, white pancake sponge; M, swirly white encrustment; N, white bulbous encrustment; O, sheet of papillae.

spatial auto-correlation was found for dropstone faunal composition (Mantel test using Bray-Curtis similarity matrix based on the biotic data and Euclidean distance matrix based on latitude/longitude, $z = 4.3 \times 10^6$, $p = 0.001$), meaning that stones closer to one another in space had more similar biotic communities. Even when a presence-absence transformation of the biotic data was used, a significant spatial auto-correlation was found (Mantel test, $z = 5.5 \times 10^6$, $p = 0.001$), which means that differences in the biotic

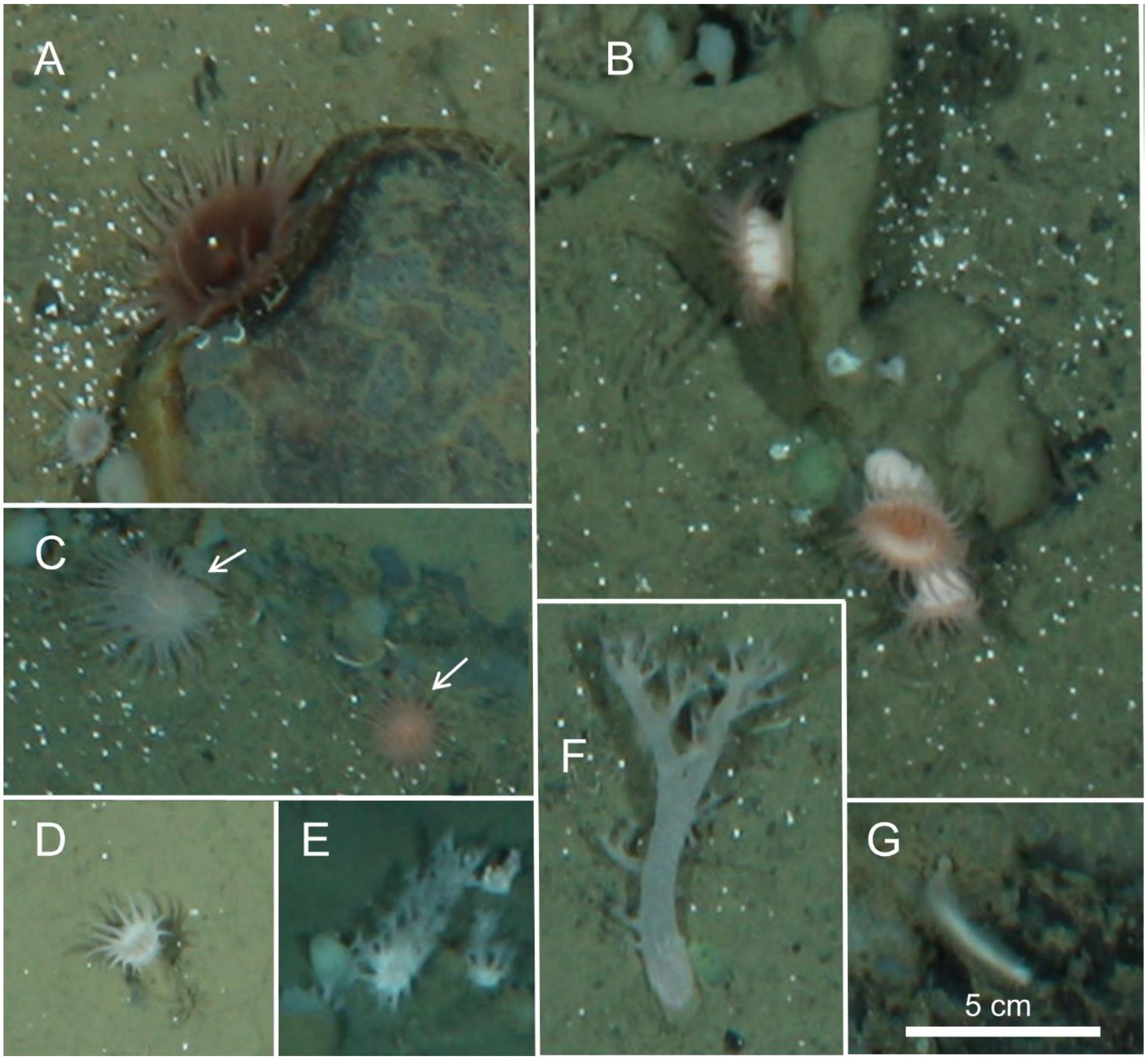

Fig. 17. Cnidarians found on dropstones in the HAUSGARTEN observatory. A, large red anemone; B, Hormathiidae; C, Pink/white anemone; D, *Bathyphellia margaritacea*; E, fringe anemone; F, *Gersemia fruticosa*; G, sea pen.

communities in different parts of the study area were due to the presence or absence of morphotypes and not just their relative abundances.

The highest richness, abundance, evenness, and diversity of dropstone fauna was found at station Senke, located at the foot of the rocky reef. A range of values was found at each station, though greater maximum values for richness, abundance, and diversity were found at stations closer to the reef. Abundance, richness, evenness, and diversity

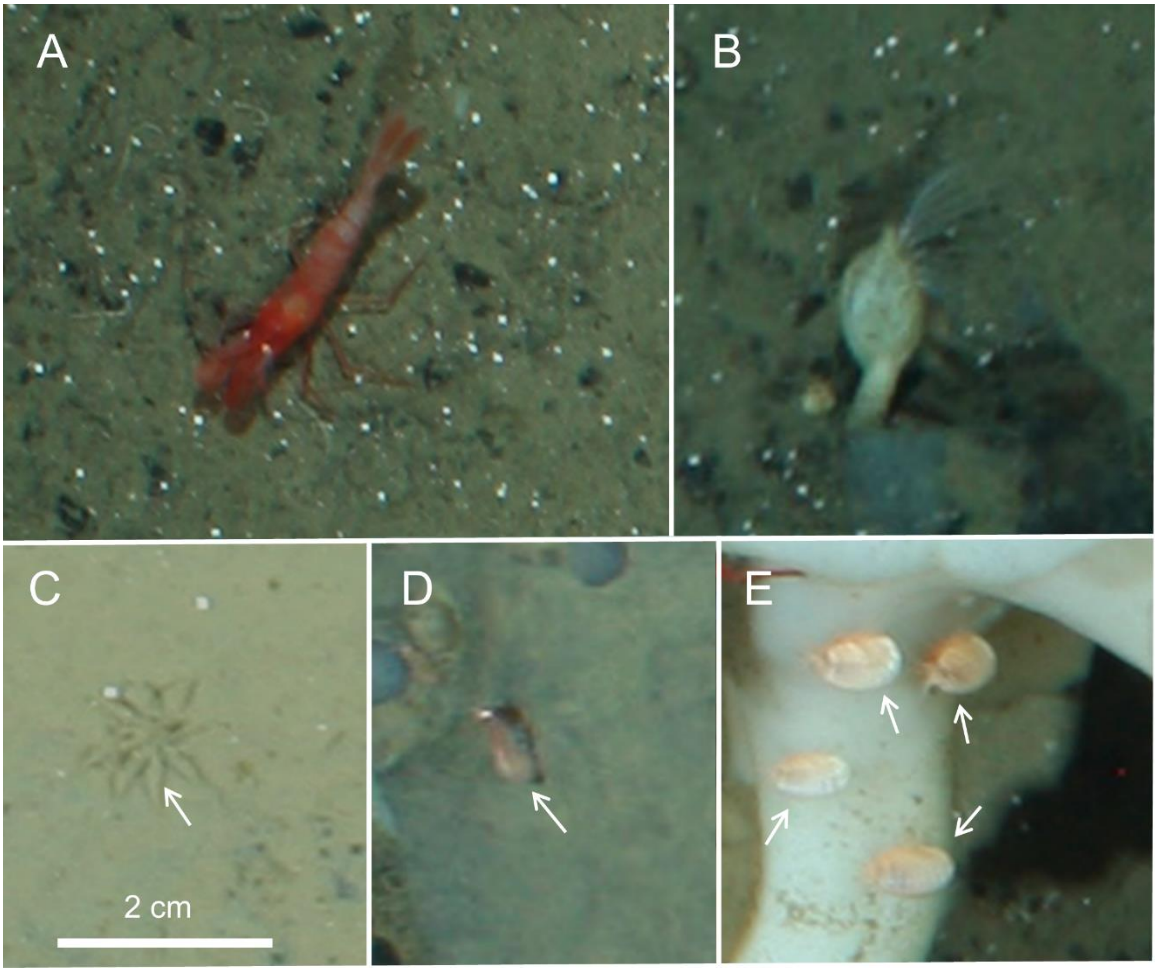

Fig. 18. Arthropods found on dropstones in the HAUSGARTEN observatory. A, *Bythocaris* cf. *leucopis*; B, *Verum striolatum*; C, pycnogonid; D, Lyssianasidae sp. 1; E, amphipod.

each showed a significant negative correlation to distance from the rocky reef (Fig. 23). Hypothesis 3 was thus supported.

Dropstone fauna showed no evidence of a nested distribution among stations. The N_1 (52) and BR (32) indices both fell within the 95% confidence interval ranges (39-53 and 32-38, respectively). Therefore, hypothesis 4 was not supported.

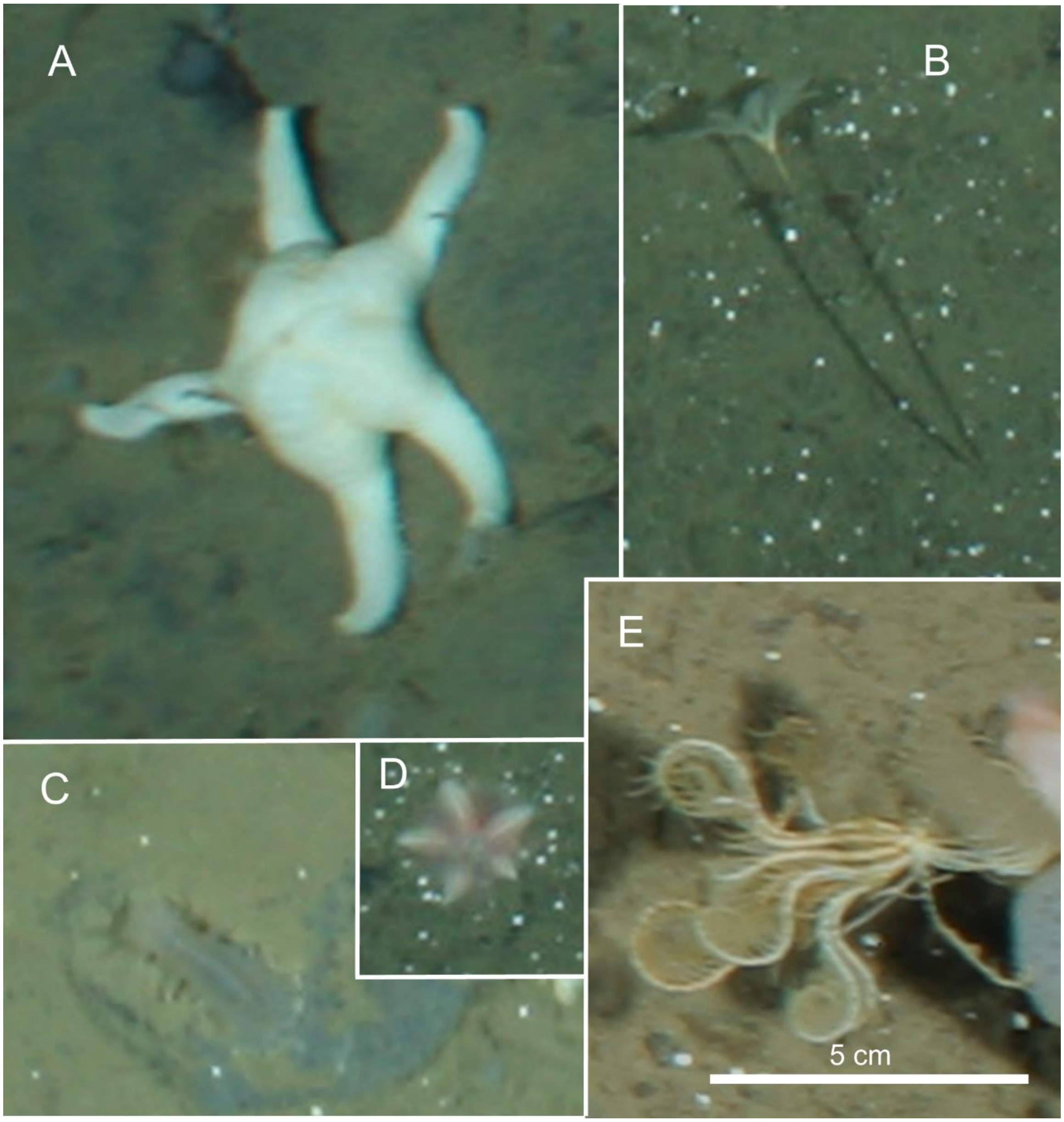

Fig. 19. Echinoderms found on dropstones in the HAUSGARTEN observatory. A, *Poraniomorpha hispida*; B, *Bathycrinus carpenterii*; C, *Kolga hyalina*; D, *Hymenaster pellucidus*; E, *Poliometra prolixa*.

Interactions between morphotypes

The data revealed patterns of non-random co-occurrence at three of the five stations: Senke, HG IV and N3 ($C > e$, $p < 0.001$). Only random co-occurrence patterns

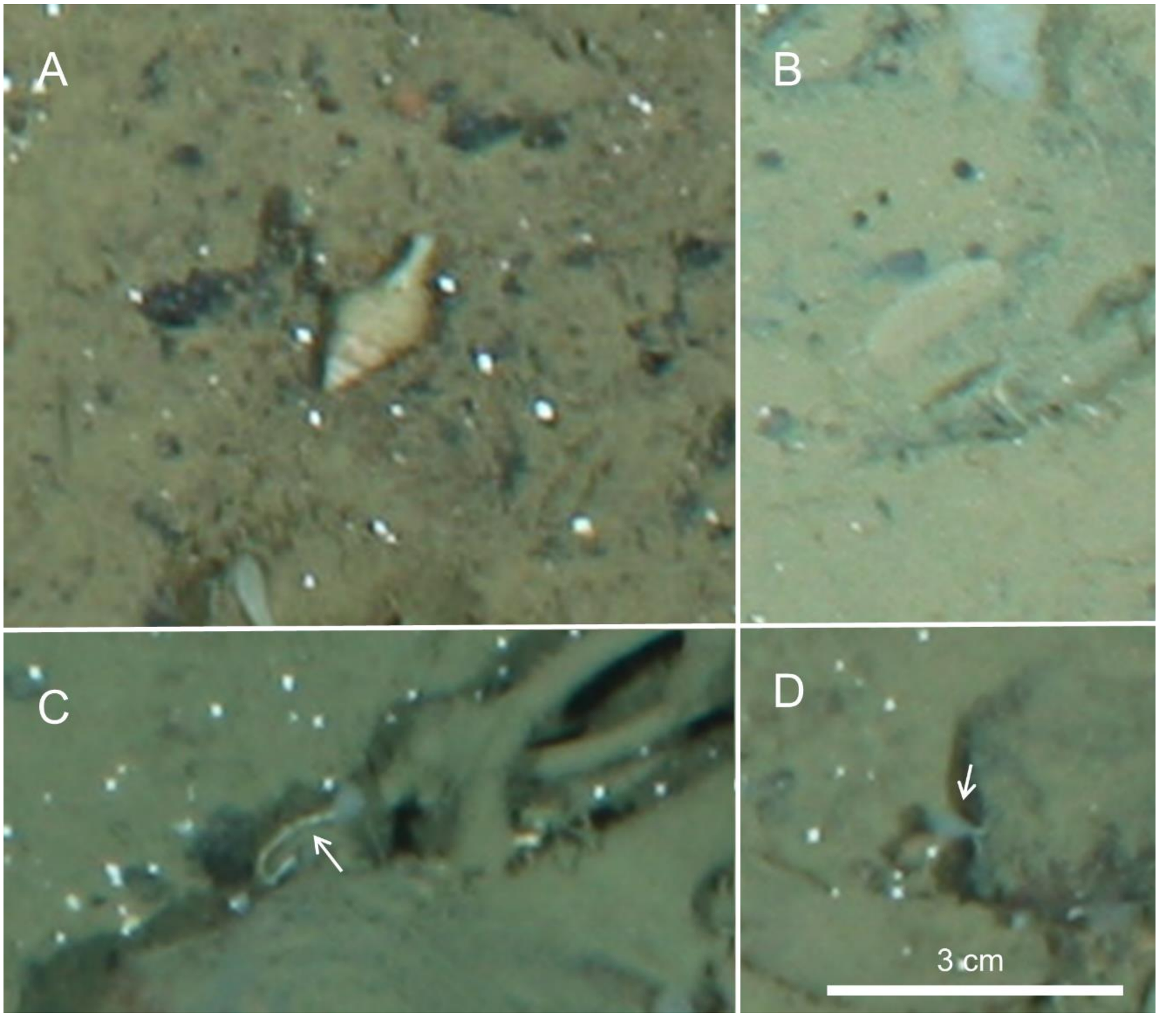

Fig. 20. Miscellaneous species found on dropstones in the HAUSGARTEN observatory. A, *Mohnia* cf. *mohnia*; B, *Byglides groenlandia*; C, serpulid polychaete; D, unknown morphotype.

were found for stations N5 and S3 ($p = 0.12$ and 0.09, respectively). Hypothesis 5 was thus partially supported.

Pairwise tests showed only a small number of non-randomly co-occurring morphotype pairs at each station (Table 6). A total of 12 morphotype pairs (of 1540 possible pairs) at four stations were found to co-occur less often than expected by random

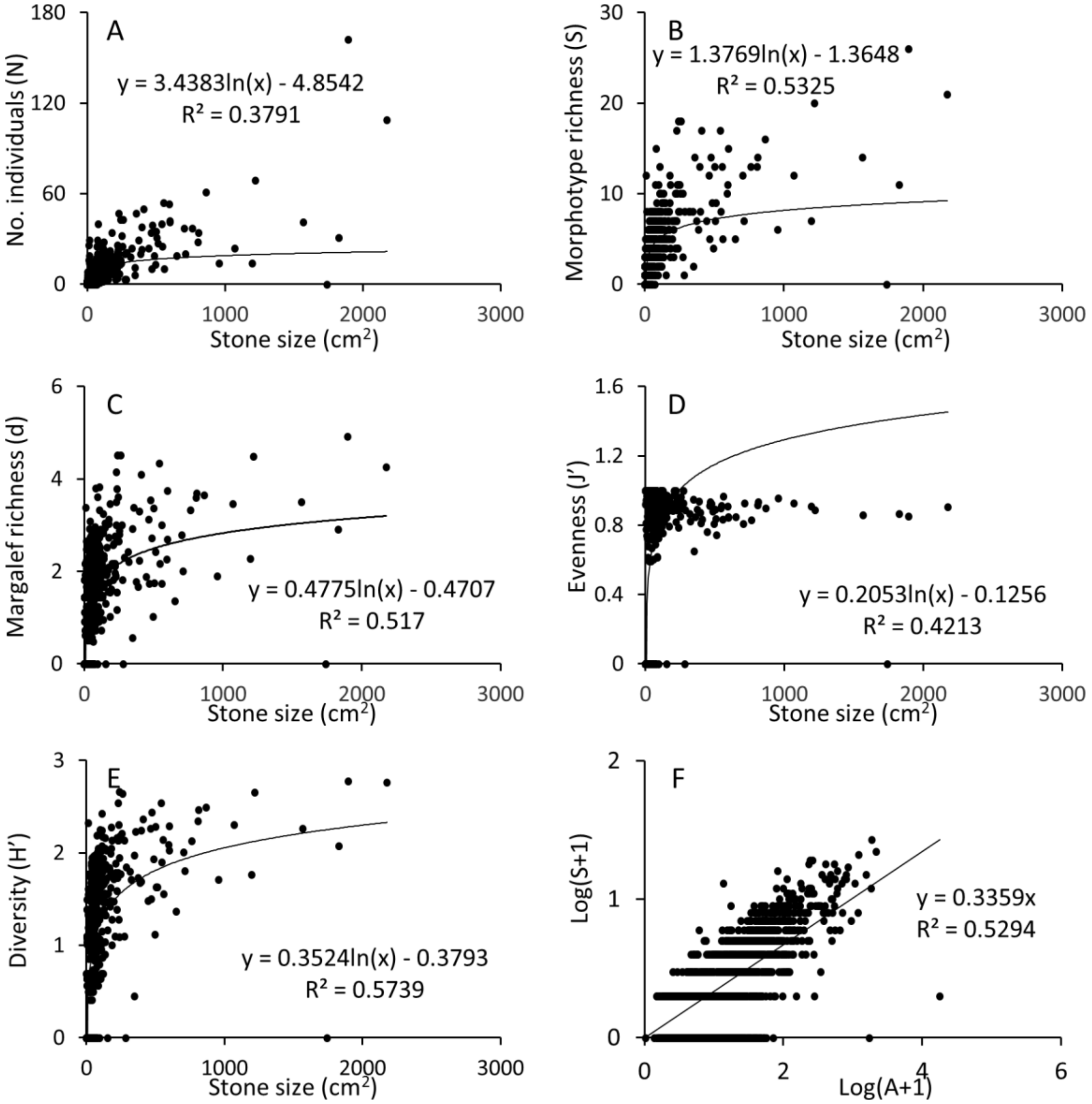

Fig. 21. A-E, biotic parameters (abundance, richness, evenness, and diversity of fauna) on a dropstone versus the size (surface area visible in downward-facing view); F, morphotype richness on a dropstone versus the size of the stone, with each axis log(x+1)-transformed to show the log-linear species-area relationship common among island systems in the classical literature.

chance. An additional eight pairs of morphotypes at three stations were found to non-randomly co-occur more often than expected by random chance (Table 6).

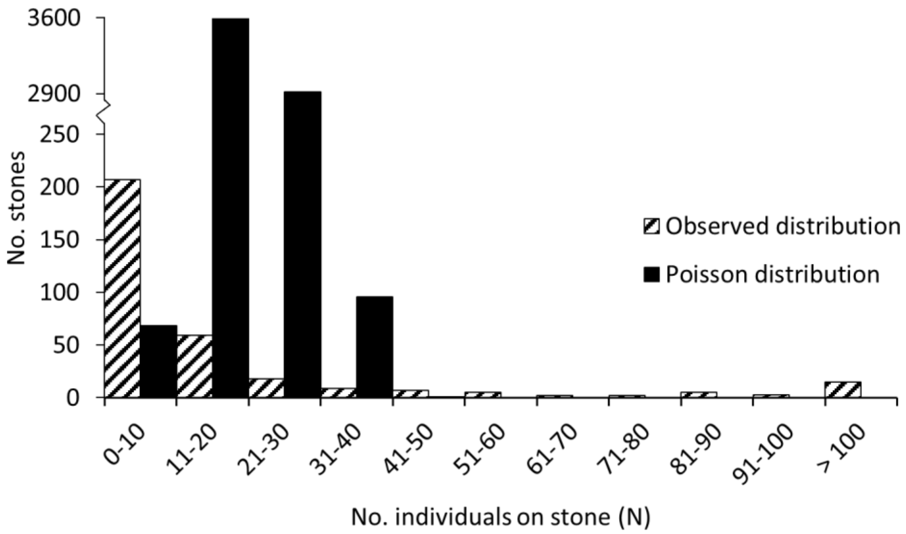

Fig. 22. Frequency distribution of the number of individuals on a dropstone (N), and a Poisson distribution with the same mean. A significant difference between the two distributions (see text) indicates that dropstone fauna have a clumped distribution.

DISCUSSION

Dropstones as habitats

The clumped distribution of dropstones probably reflects their origin in icebergs. A single iceberg may have carried many stones accumulated in clumps, which were released at the same time as the iceberg melted. There is the potential for some stones to have broken off from the rocky reef and rolled down the adjacent slope (Meyer et al. 2014); however, it does not appear that this is the primary force affecting the distribution of dropstones because clusters of stones were distributed randomly on the seafloor, without regard for distance to the rocky reef.

The size and location of dropstones correlated with the biotic community, with higher richness, abundance, and diversity of fauna on larger stones. The fact that these two factors, stone size and proximity to the reef, both independently and significantly

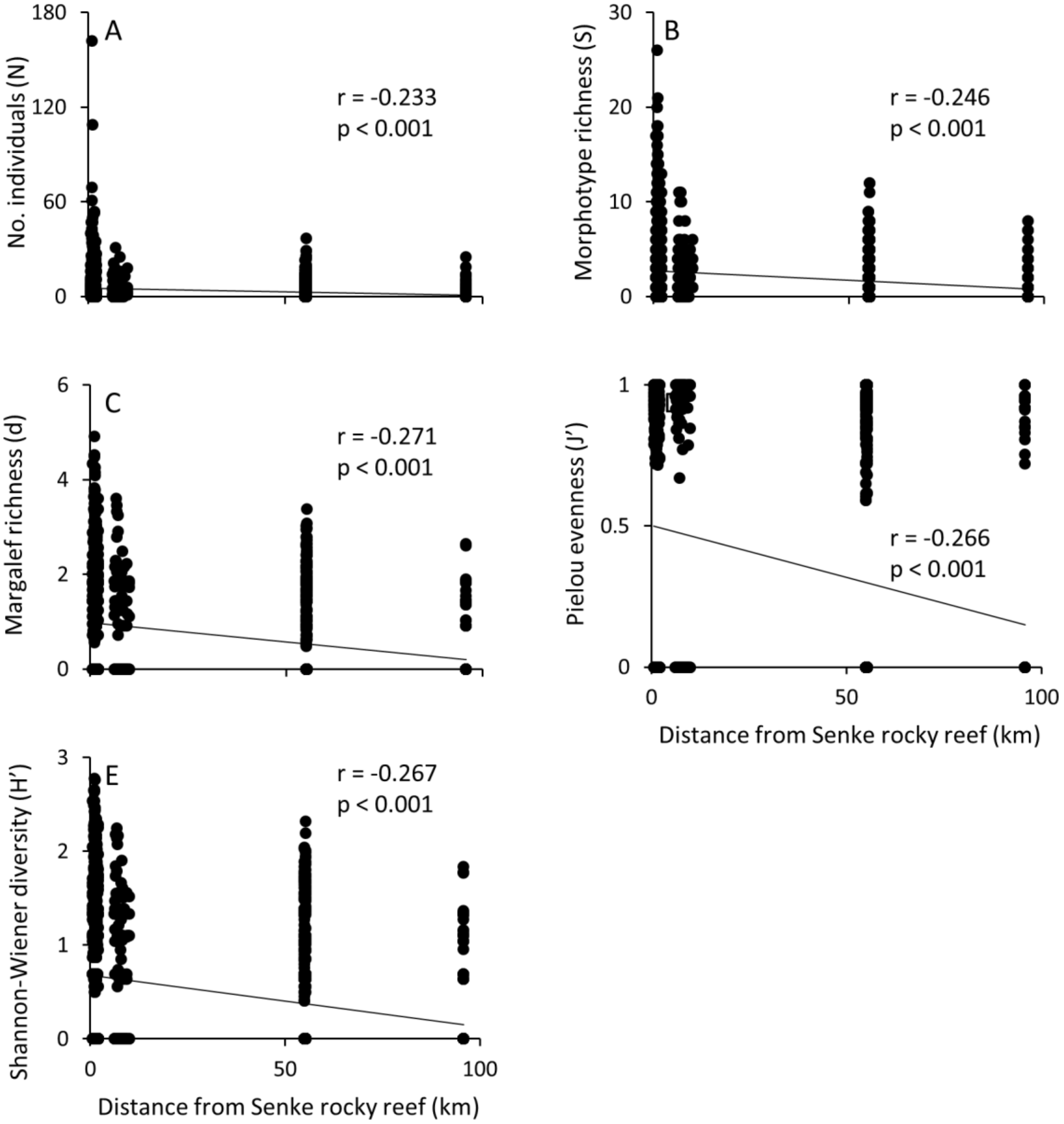

Fig. 23. Biotic parameters (abundance, richness, evenness, and diversity of fauna) on dropstones versus distance to the foot of the Senke rocky reef. Best-fit linear curves and non-parametric correlation results shown.

impacted the biotic community is reminiscent of MacArthur and Wilson's (1967) classical island biogeography theory, which pointed to the influence of island area and distance from a source population on island fauna. Even though the observable patterns in dropstone communities resemble classical islands, the mechanisms driving these patterns

Table 6. Morphotype pairs at each station that co-occur more or less often than expected by random chance.

Station	**Morphotype 1**	**Morphotype 2**	**Less or more often than by chance?**
S3	Gray encrusting sponge 1	Myxillinid sponge	Less
S3	Gray encrusting sponge 1	Puffy white encrustment	Less
S3	*Bathyphellia margaritacea*	Gray dome sponge	Less
S3	*Bathyphellia margaritacea*	Myxillinid sponge	Less
S3	Hormathiidae	*Bythocaris* cf. *leucopis*	More
S3	Hormathiidae	*Cladorhiza* cf. *gelida*	More
S3	Lobe-like sponge	Pycnogonid	More
HG IV	*Bathyphellia margaritacea*	*Poliometra prolixa*	Less
HG IV	*Bathyphellia margaritacea*	Lobe-like sponge	Less
HG IV	*Bathyphellia margaritacea*	*Gersemia fruticosa*	Less
HG IV	*Polymastia* sp.	White pancake sponge	More
HG IV	*Poliometra prolixa*	*Bythocaris* cf. *leucopis*	More
HG IV	*Poliometra prolixa*	Amphipod	More
Senke	Yellow encrusting sponge	*Phakellia* sp.	Less
Senke	Asymmetrical white sponge	Gray encrusting sponge 1	Less
N5	Myxillinid sponge	Gray encrusting sponge 1	Less
N5	*Bathyphellia margaritacea*	Myxillinid sponge	Less
N5	Gray encrusting sponge 1	Puffy white encrustment	Less
N5	Hormathiidae	*Bythocaris* cf. *leucopis*	More
N5	Hormathiidae	*Cladorhiza* cf. *gelida*	More

may not be the same as have been suggested for classical islands or habitat islands. The possible mechanisms structuring dropstone communities are discussed in more detail below.

Relationship of stone size to the biotic community

Our results showed higher species richness on larger stones. Dropstone fauna may thrive on larger stones because of elevated food supply. Larger stones extend higher in the benthic boundary layer, where they are exposed to faster currents that bring particulate food for suspension feeding (Vogel 1996). Suspension feeders are well-known to inhabit elevated substrata on seamounts (Clark et al. 2010) and fjord sills (Mortensen et al. 2001), and on a smaller scale, suspension-feeding foraminifera inhabit glass sponge stalks (Beaulieu 2001) and manganese nodules (Mullineaux 1988). Dropstone megafauna may gain an advantage for suspension feeding by inhabiting larger stones (Schulz et al. 2010).

Larger dropstones may be older, as they would take longer to be covered by sedimentation. This means it is possible that the older stones have higher diversity, abundance, and richness of fauna because they have been underwater for longer and therefore harbor communities in a state of more advanced succession. However, this explanation ignores the fact that new dropstones are being deposited in the study area in modern times. All stations except S3 are seasonally covered by sea ice. Glaciers in west Svalbard fjords have been known to calve icebergs carrying terrestrial material in modern times (Hagen et al. 2003), and ice is also advected into the Fram Strait from the Laptev and Kara seas (Bergmann, unpubl. data). Our data show a significantly higher density of dropstones at S3 in 2015 (Fig. 12), and both dropstone and hard substratum density increased significantly at HG IV between 2002 and 2011 (Bergmann, unpubl. data).

On terrestrial islands, habitat diversity, disturbance level and primary productivity are all correlated with island size and have been put forth as explanations for the higher richness of fauna on larger islands (Gotelli and Graves 1996). However, these factors probably have little effect on dropstone communities. Habitat heterogeneity on terrestrial islands includes mountains, forests and beaches; on dropstones, habitat is the rock surface. Larger stones may have more complex surfaces and microhabitats, but the difference in heterogeneity between small and large stones is much less than the difference in heterogeneity between small and large terrestrial islands. Primary production also does not occur locally at the depth of the dropstones, and physical disturbance is relatively rare compared to terrestrial islands (though predators i.e., *Hymenaster pellucidus*, *Lycodes frigidus* may be a source of disturbance on dropstones). In shallow water, larger stones have higher diversity because they are less subject to disturbance by waves (Sousa 1979, Kukliński 2009). However, with a bottom current of approximately 5 cm s^{-1} in the study area, dropstones are very unlikely to be overturned. The higher diversity on larger dropstones must thus be the result of another mechanism.

Based on our data, the most parsimonious explanation for the higher richness and abundance of fauna on larger stones is the “passive sampling” hypothesis (Gotelli and Graves 1996). This hypothesis states that larger islands (stones) are colonized by more organisms simply because they are larger targets for dispersing propagules. Larger substrata have more surface area and can accumulate more species in that area as succession proceeds (Abele and Patton 1976, Schoener and Schoener 1981). Larger stones are also exposed to faster bottom currents, where the larval flux is probably greater. A greater variety of microhabitats with different flow velocities and shear stresses may be available on larger stones. It would be desirable to separate the effects of habitat heterogeneity and boundary layer current regimes on dropstones experimentally, to understand how these mechanisms structure dropstone communities.

It should be especially noted that there was no significant correlation between the size of dropstones and the composition of the biotic communities inhabiting them. This means that there is not one community of organisms inhabiting smaller stones (such as opportunists on intertidal boulders) and a separate community inhabiting larger stones.

These “incidence functions” were first suggested by Diamond (1975a) for avifauna on terrestrial islands. Instead, the morphotypes present on each stone are a random sub-set of the available morphotypes, and the fauna on larger stones happen to be more diverse because they are a larger sub-sample of the available fauna.

The relationships between biotic parameters (N, S, d, J', H') and the size of a stone were asymptotic, so an infinitely large stone would not be able to host an infinitely large number of individuals or species. This asymptotic relationship may indicate that there is a maximum carrying capacity for a stone (asymptotic relationship to N) or that there is a finite pool of morphotypes from which these individuals can be drawn (asymptotic relationship to S, morphotype richness). The mathematical relationship between morphotype richness and stone area was linear when each of these variables was log-transformed; a pattern commonly found in classical island literature (MacArthur and Wilson 1967). Therefore, it is possible that this oft-discussed classical pattern is merely the result of species on a particular island or habitat island being a sub-sample from a finite pool of available species.

Thus, if the fauna on a stone is considered a sub-sample of the available finite pool of morphotypes, logic dictates that a sufficiently large stone should host the majority or even all of the available morphotypes, and the communities would begin to converge, showing greater similarity at larger stone sizes. However, this is not observed to be the case for dropstone communities, as there was no correlation between stone size and biotic community composition. It is possible that the stones in the present study are simply not large enough to host all available morphotypes of fauna; the maximum morphotype richness on a single stone was 26, less than half of the 56 available morphotypes found on all dropstones. By contrast, 45 morphotypes inhabit the Senke rocky reef (Meyer et al. 2014 Table S1, excluding soft-bottom species).

Relationship of dropstone distribution to the biotic community

Dropstone fauna were spatially auto-correlated and had a clumped distribution, which may be a result of dispersal via a planktonic larval stage. It is unknown how long dropstone fauna persist as larvae in the water column or how far they disperse; however, the dropstone fauna consist of mostly encrusting, clonal species, which generally tend to have short-duration larvae (Jackson 1986). Short pelagic larval duration would restrict the dispersal of dropstone fauna to the stones in a small area surrounding natal stones, resulting in a clumped distribution. Many marine hard-bottom species in fact disperse < 1 km, which may be an evolutionary stable strategy to ensure competent larvae find a suitable substratum for recruitment (Grantham et al. 2003, Shanks et al. 2003). At a bottom current speed of 5 cm s^{-1}, a larva in the water column for one day in our study area would travel 4.32 km, if its path of motion were linear. However, dropstones cause turbulent eddies on the seafloor (Hasemann et al. 2013), so a larva released from a dropstone is unlikely to have a linear path of motion, and its net distance traveled may be much less.

The rocky reef has the potential to serve as a source population for hard-bottom fauna on dropstones, given its dense populations of sessile fauna and its upstream location from 4 of the 5 dropstone stations in this study (Meyer et al. 2014). It indeed appears that increased larval supply from the rocky reef may affect dropstone communities, based on the higher abundance, richness, and diversity of fauna found on stones nearer to the reef (Fig. 23). However, we cannot conclude that the rocky reef is the sole or even the primary source of larvae to the dropstones. If this were the case, one would also expect a nested pattern of the fauna, in which the most morphotypes would be present nearer the reef (at station Senke), and nested sub-sets of the fauna would be present at stations further away from the reef. However, our data showed no evidence of nestedness among stations. In fact, dropstones at station S3, south of the reef, featured fauna not significantly different in abundance, richness, and diversity from station HG IV, located equidistant but upstream of the reef (Fig. 23).

In some cases, hard-bottom fauna dispersing to widely-spaced substrata may have to delay metamorphosis (Marshall and Keough 2003), which may affect colony growth or recruits' performance as adults (Marshall and Keough 2004). However, we have no reason to believe that hard-bottom fauna on dropstones would be incapable of reproducing and therefore reliant on the rocky reef as a source of larvae. It is more likely that larvae disperse from both colonized dropstones and the densely-populated reef, resulting in the patterns observed in our data: clumped distribution of dropstone fauna, and higher abundance, richness, and diversity of fauna closer to the rocky reef.

Interactions between morphotypes

We found that morphotypes co-occurred non-randomly at three of five stations. For those pairs co-occurring less often than expected by random chance, it cannot necessarily be concluded that competitive exclusion is the cause, as is traditionally concluded for terrestrial islands (Diamond 1975a). Many dropstone morphotypes are encrusting forms, primarily sponges. In fact, nine of the twelve morphotype pairs found to have negative non-random co-occurrence included at least one encrusting form. If these encrusting morphotypes were truly competing, we would expect them to occupy larger portions of the dropstone surface area and even overgrow each other, such as is commonly observed for competing encrusting species in shallow water environments (Sebens 1986, Oschmann 1990). Large portions of the available space on dropstones were in fact left uncolonized (Meyer, unpubl. data, Oschmann 1990). While it is possible that already-established fauna on a stone may consume larvae of potentially-settling species, experimental evidence from shallow water has shown larval predation does not significantly affect recruitment (Young and Gotelli 1988, Young 1989, Young and Cameron 1989).

Rather than competitive exclusion, pairs of morphotypes may non-randomly co-occur on dropstones as a result of their own distribution. A significant spatial auto-correlation was found for the dropstone fauna, even when a presence-absence transformation of the biotic data was used, indicating that the absence of some morphotypes from parts of the study area leads to the observed patterns in the biotic data. If two species occur in different parts of the study area or are most abundant in different parts of a particular station, they would seldom be found together. It is not necessary to invoke interspecific competition to explain non-random co-occurrence of dropstone fauna; the observed patterns may just be a result of the clumped distribution of fauna. Further support for this hypothesis stems from the fact that on the rocky reef, a continuous habitat, morphotypes co-occur randomly (Meyer, unpubl. results).

We also found that eight morphotype pairs co-occurred more often than expected by random chance. For example, “Hormathiidae” (Fig. 17B) and *Cladorhiza* cf. *gelida* (Fig.

14I) had positive non-random co-occurrence at stations S3 and N5. Large erect species such as *C.* cf. *gelida* and *Caulophacus arcticus* (Fig. 14B) were commonly observed in the images being surrounded by mobile crustaceans including *Bythocaris* cf. *leucopis* (Fig. 18A) and "amphipod" (Fig. 18E). Individuals of *C.* cf. *gelida* also in many cases had one or more anemones, "Hormathiidae," living on them (Fig. 24). Epibionts may be outcompeted on primary substrata and thus be forced to occupy secondary substrata. We also find it likely that these epibiotic species take advantage of the elevated structure provided by large structural basibionts. "Hormathiidae" and *Poliometra prolixa*, a comatulid crinoid, are suspension feeders (Bergmann et al. 2009). A number of species live on or are associated with large structural coral species in the deep sea (Cordes et al. 2008), and deep-sea suspension feeders climb on stones, sponges, or the spines of sea urchins to elevate themselves off the seafloor and expose themselves to better currents (Gutt & Schickan 1998). "Hormathiidae" is very likely elevating itself for suspension feeding by living atop *C.* cf. *gelida*, and it also inhabits stalks of the crinoid *Bathycrinus carpenterii* (Fig. 19B; Bergmann, unpubl. data). Similar epibiotic relationships have been found for Antarctic fauna and are mostly likely commensal (Gutt and Schickan 1998). Morphotypes that utilized large structural basibionts also had positive non-random co-occurrence ("Hormathiidae" – *B.* cf. *leucopis* at stations S3 and N5, *Poliometra prolixa* – *B.* cf. *leucopis* and *Poliometra prolixa* – "amphipod" at HG IV). It is not entirely clear what advantage *B.* cf. *leucopis* and the amphipod gain by resting on large sponges, though they may be protected from predators or gain some advantage in feeding.

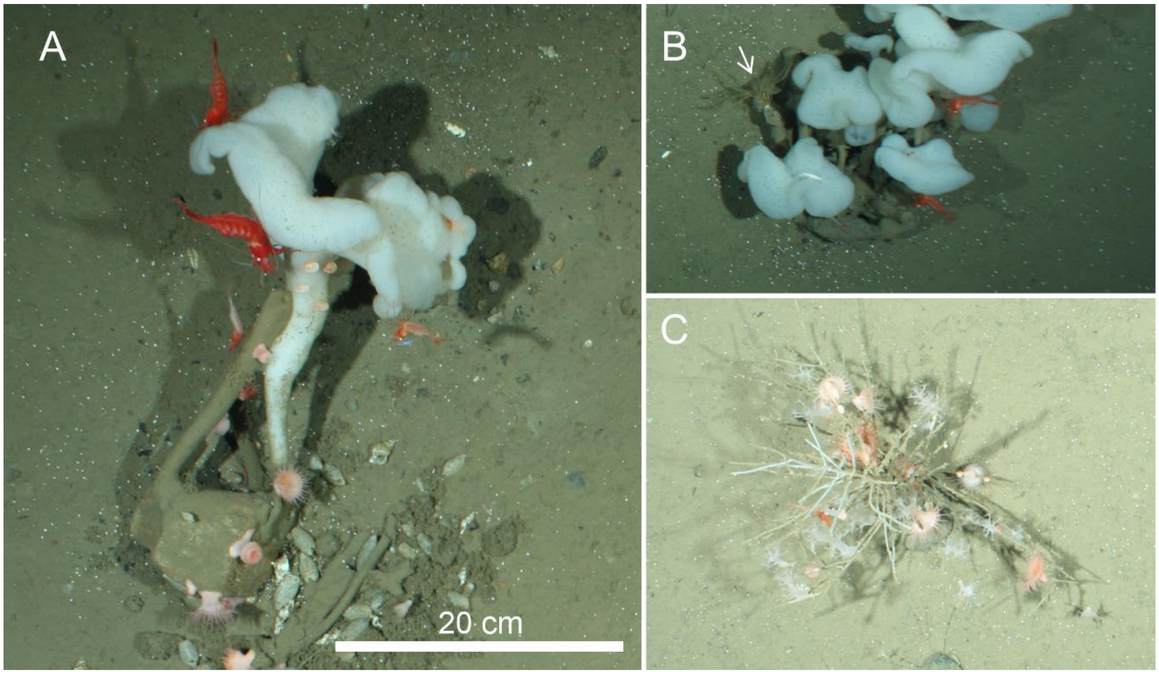

Fig. 24. A, Crustaceans including *Bythocaris* cf. *leucopis* and “amphipod” resting on *Caulophacus arcticus*; B, *Poliometra prolixa* (white arrow) and *B.* cf. *leucopis* on *C. arcticus*; C, “Hormathiidae” as an epibiont on *Cladorhiza* cf. *gelida*.

Other pairs of species co-occurred more often than expected, though the reason is not so obvious. In the case of “lobe-like sponge” (Fig. 15D) and “pycnogonid” (Fig. 18C) at S3, perhaps one is the prey of the other. For the pair *Polymastia* sp. (Fig.15B) – “white pancake sponge” (Fig. 16C) at HG IV, we are unable to conjecture a reason. Our results demonstrate that some morphotype pairs co-occur more often than expected by random chance because of epibiontism.

CONCLUSION

Dropstones constitute island-like habitats for hard-bottom fauna at high latitude. While the patterns observed in dropstone communities bear some resemblance to classical island systems, the mechanisms causing these patterns are not necessarily the same. Differences in primary productivity, habitat diversity, and physical disturbance are not satisfactory explanations for the distributions of dropstone fauna; rather, simple mechanisms such as hydrodynamics and larval dispersal offer parsimonious explanations. This study is to our knowledge the first time that positive non-random co-occurrence patterns have been shown for island-like fauna. An understanding of dropstone communities provides new insights for studies in other island-like habitats.

BRIDGE III

The studies on shipwrecks and dropstones presented in Chapters III and IV are based on data from a single time-point. However, communities on isolated hard substrata develop and undergo succession over time. They are also impacted by abiotic factors such as temperature and glacial sedimentation that vary temporally. Greater influxes of warm, saline Atlantic water to the Fram Strait via the West Spitsbergen Current have caused warming bottom temperatures over the past ten years (Soltwedel et al. 2016). Warming and penetration of Atlantic water into Svalbard fjords has also allowed the establishment of typically Atlantic fauna in Svalbard waters in recent years (Berge et al. 2005, Renaud et al. 2012). In the next chapter, I consider the benthic communities in Svalbard fjords, in order to understand how abiotic factors impact high Arctic benthos and how observations in the present can help predict future changes.

CHAPTER V

ENVIRONMENTAL FACTORS STRUCTURING ARCTIC MEGABENTHOS – A CASE STUDY FROM A SHELF AND TWO FJORDS

Kirstin S. Meyer, Andrew K. Sweetman, Craig M. Young, and Paul E. Renaud

INTRODUCTION

The interplay between regional- and local-scale factors is an important determinant of diversity in biotic communities (Ricklefs 1987), and marine benthic diversity can be influenced by factors at a variety of spatial scales (Gage 2004, Gutt and Piepenburg 2003, Robert et al. 2014). In the Arctic, environmental drivers such as depth, benthic food supply, and bottom oxygen affect megabenthic communities at regional scales, but factors such as substratum type and disturbance may be just as important in structuring communities on more local scales (Kukliński et al. 2006a, Roy et al. 2014). Sensitivity of benthic communities to abiotic factors, therefore, will vary in different ways across these different scales, and this must be considered when monitoring programs are designed and their findings are interpreted.

Benthic communities off the Norwegian archipelago of Svalbard are influenced by a variety of factors, including water mass distribution, sedimentation, climate forcing, availability of biotic and abiotic substrata, disturbance, and food input (Bałazy and Kukliński 2013, Carroll and Ambrose 2012, Kędra et al. 2012, Kortsch et al. 2012, Kukliński et al. 2006b, Piepenburg et al. 1996, Ronowicz et al. 2013). Despite recent research efforts (Sswat et al. 2015), our understanding of how abiotic factors influence the megabenthos around Svalbard remains limited. As future climatic changes are likely to be more dramatic in the Arctic than in other regions (ACIA 2006, Mora et al. 2013), it is especially important to understand what factors influence these communities (Bergmann et al. 2011a, Nephin et al. 2014).

Fjords are geologically young basins heavily influenced by terrestrial input (Syvitski et al. 1987). Fjord fauna are often considered to be subsets of shelf fauna, but recent evidence suggests this is not always the case (Włodarska-Kowalczuk et al. 2012). Generally, a decline in diversity is observed from outer to inner fjords, and this is usually attributed to gradients of glacial sedimentation (Görlich et al. 1987, Włodarska-Kowalczuk et al. 2005, 2012). Benthic megafaunal biomass and diversity are also generally lower in Arctic fjords compared to the shelf, a pattern that again is attributed to inorganic sedimentation (Grange and Smith 2013, Piepenburg et al. 1996, Syvitski et al. 1989).

In the present analysis, we describe from photographic images the benthic megafaunal communities in two Svalbard fjords and on the north Svalbard shelf, as well as the dominant abiotic factors that appear to structure these communities. We focus in particular on functional traits of the benthic fauna.

Functional traits describe what organisms actually do in a community rather than their taxonomic classifications (Petchey and Gaston 2002). Communities with greater functional diversity may be more resistant to invasion, have greater productivity or more efficient resource use, and provide a wider array of ecosystem services than those with lower functional diversity (Mason et al. 2005, Petchey and Gaston 2006). Functional traits of the fauna may be more useful in explaining ecosystem processes than taxonomic analyses alone (Bremner et al. 2013, Mokany et al. 2008). Evenness of functional guilds has been found to decline from outer to inner regions of Svalbard fjords, with fewer suspension feeders and more mobile, deposit-feeding organisms found in inner fjords (Włodarska-Kowalczuk 2007, Włodarska-Kowalczuk et al. 2012). This most likely influences the complexity of ecosystem processes carried out by the benthos along the fjord gradient.

We set out to discern how the abiotic factors of depth, water temperature, availability of hard substrata, stone size heterogeneity, and inorganic sedimentation are related to megabenthic communities in north Svalbard fjords and on the nearby shelf. On the basis of previous studies, we expected that sedimentation would have a dominant effect on macrofaunal abundance and diversity. We also expected that assemblages of organisms with different functional traits would be found in different areas – shelf and inner and outer fjords – as a result of the influence of abiotic factors. We investigated different spatial scales by comparing stations among and within fjord and shelf areas.

METHODS

Study area

Photographs of the seafloor were recorded in Raudfjorden, Rijpfjorden, and on the north Svalbard shelf (Fig. 25). Raudfjorden and Rijpfjorden are both predominantly north-facing fjords in the northern part of the Svalbard archipelago. Both have a

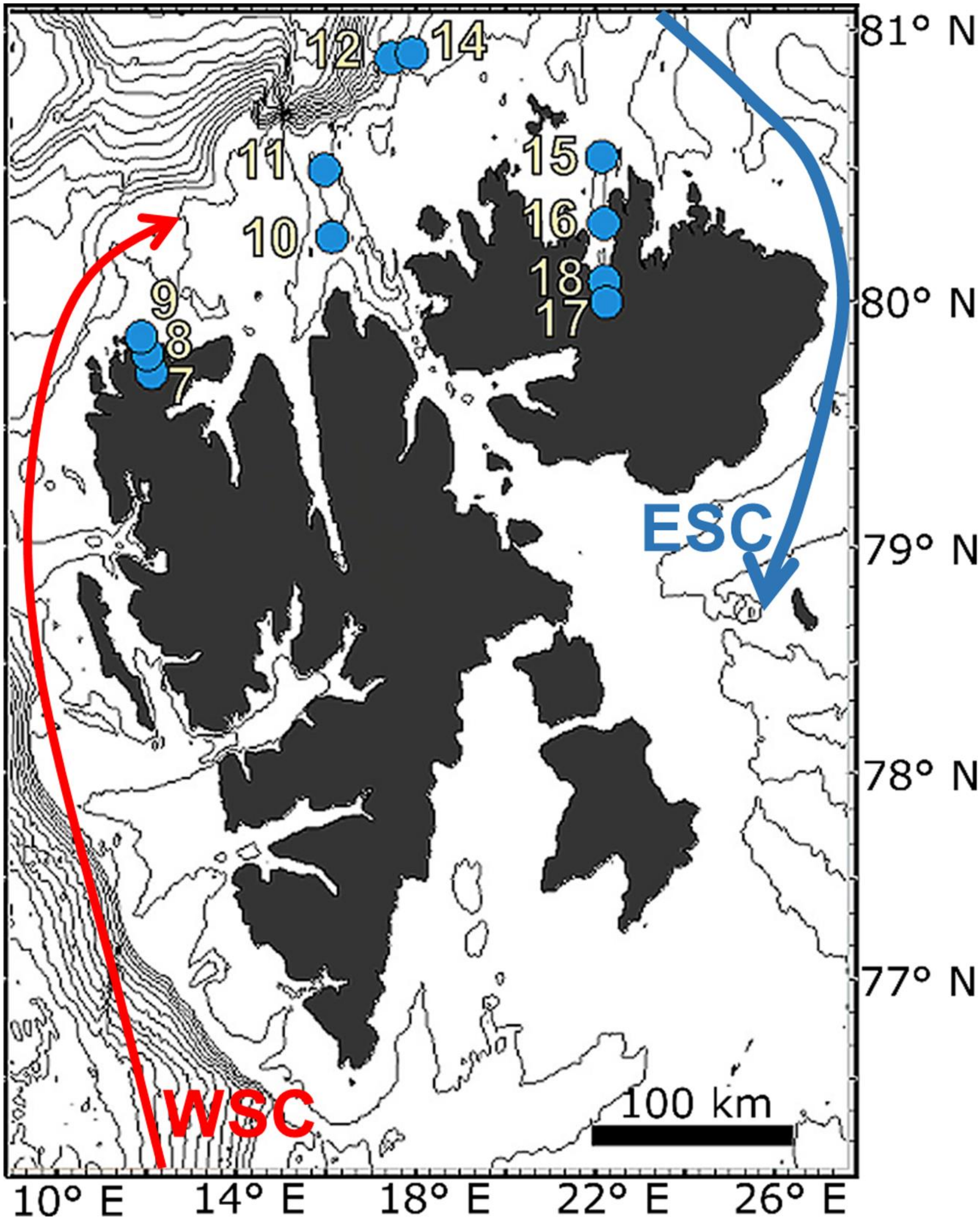

Fig. 25. Map of sampling stations in north Svalbard. Depth contours are shown every 150 m. WSC, West Spitsbergen Current (Atlantic Water); ESC, East Spitsbergen Current (Arctic Water).

maximum depth between 200 and 250 m (Holte and Gulliksen 1998, Wang et al. 2013). Raudfjorden consists of a single basin and has a sill at the fjord mouth that rises to a depth of 130 m (Holte and Gulliksen 1998). Rijpfjorden has a sill halfway down its length but opens widely onto a shallow shelf at 100-200 m depth (Ambrose et al. 2006, Wang et al. 2013).

Raudfjorden is largely influenced by Atlantic Water, a warm, saline water mass that continues onto the north Svalbard shelf (Holte and Gulliksen 1998, Muench et al. 1992, Rudels et al. 2005). It also experiences a relatively high rate of inorganic sedimentation at 0.1 – 0.2 cm year^{-1} in the outer part of the fjord (Elverhøi et al. 1983), with sedimentation rate increasing toward the fjord head (Holte and Gulliksen 1998).

In contrast, Rijpfjorden is a “true” Arctic fjord as it is primarily influenced by Arctic water and remains covered by ice for most of the year, from October to June or July (Morata et al. 2013). The melting process is dynamic, with snowmelt re-freezing as ice in the late spring (Wang et al. 2013). Even after landfast ice in Rijpfjorden has melted, ice floes are brought into the fjord by surface currents from the northeast, with the result that Rijpfjorden is covered by sea ice in various forms for most of the year (Ambrose et al. 2006, Leu et al. 2011). Because of its “true” Arctic character, Rijpfjorden has been the site of several studies designed to predict the effects of climate change on Arctic communities (Ambrose et al. 2006, Leu et al. 2011, Morata et al. 2013, Wallace et al. 2010).

The north Svalbard shelf stations included in this case study are located between 80 and 81° N. The north shelf is influenced by cooling AW at intermediate depth, though bottom water may be formed as dense plumes of cold brine that spill over the shelf following sea ice formation (Quadfasel et al. 1988, Rudels et al. 2005). The stations included in this case study are close to the winter ice edge, though the ice edge is dynamic and has retreated to the northeast since 1979 (Onarheim et al. 2014, Piechura and Walczowski 2009). The stations in this case study are also in an area that may be subject to fishing activity (Norsk Fiskeridirektoratet).

Image collection

Photographs were recorded using a downward-facing digital drop camera, as described by Sweetman and Chapman (2011). Photos were recorded at an altitude of approximately 2.5 m and were spaced about 10 m apart. Fixed laser points were used for size reference. All footage was recorded in September 2011 from the R/V *Helmer Hanssen*.

Image analysis

Images that were too dark, too turbid, showed evidence of fishing activity, or were at an anomalous altitude were considered ineligible for analysis. Of the eligible photos, 15 were randomly sub-selected from each station and analyzed using the cell counter function in ImageJ (National Institutes of Health, USA). Percent cover of hard substratum was quantified as the number of random dots out of 100 overlying rock when projected on the image. Stone size heterogeneity was calculated as the coefficient of variation of the surface areas of 15 randomly sub-selected stones in each image (or all stones, if fewer than 15 were present).

Abiotic factors

Water temperature and turbidity were recorded with a Seabird SBE9/11+ CTD and attached turbidity sensor (Seapoint). Measurements were recorded at each station in August – September 2011 aboard the R/V *Helmer Hanssen*. Bottom temperature and bottom turbidity used for analysis in this case study are averaged over the bottom 10 m of the water column.

Statistical analyses

A conceptual outline of the statistical analyses in this study is shown in Figure 26. Biotic indices including total number of individuals (N), total number of species (S), Shannon-Wiener diversity (H' based on natural log, Shannon and Weaver 1963), Pielou evenness (J', Pielou 1969), and Margalef richness (d, Margalef 1968), were calculated using Primer v6 (Clarke and Gorley 2006). Margalef richness was considered a more appropriate index of species richness than the number of species per image because the number of individuals per image varied widely among stations. Abiotic factors and biotic indices were compared among stations with a non-parametric analysis of variance (Kruskal-Wallis test, K-W) because data violated the assumption of homoscedasticity, even after log transformation. Dunn’s test was used for post-hoc pairwise comparisons. Multivariate analysis of similarity (ANOSIM) for all fauna was conducted based on a Bray-Curtis similarity matrix in Primer. A DISTL-M procedure was used to discern the influence of abiotic factors on the fauna, and a dbRDA plot was constructed to visualize the fit of the DISTL-M model to the biotic data using the PERMANOVA+ add-on to Primer v6 (Anderson et al. 2008).

Functional traits

In order to understand how abiotic factors related to the functional traits of organisms in the fjords and on the shelf, we constructed a “functional trait matrix” in which the abundance of individuals possessing each functional trait was listed instead of abundance of each morphotype. Functional traits included size, morphology (flat, mound, oblong, with walking legs, upright and simple, upright and branched), mobility (sessile, swimming, crawling), colonial/solitary (colony of zooids, sponge, single individual), and feeding mode (photosynthetic, suspension feeder, deposit feeder, predator, scavenger/opportunist). Because the functional traits we chose were categorical, it was not possible to use many of the indices which have been developed to measure functional diversity (Schleuter et al. 2010). We instead used multivariate statistical techniques and conducted the same analyses as we had done for the fauna sensu Bremner et al. (2013). A resemblance matrix was constructed based on Euclidean distances and was used as the basis for multivariate DISTL-M and dbRDA analyses (Fig. 26).

RESULTS

Abiotic factors

Bottom temperature was highest (+4.5˚ C) at station 7, in inner Raudfjorden, lower at the north shelf stations 11, 12, and 14 (2.92 – 3.25˚ C), and lowest in Rijpfjorden (-1.8 – 0.5˚ C; Fig. 27). These values indicate greater influence of Atlantic water on stations in Raudfjorden and on the shelf and greater Arctic-water influence in Rijpfjorden. Turbidity was highest at station 7, in Raudfjorden, and was generally much higher at stations in this fjord than at stations on the shelf. Rijpfjorden stations showed

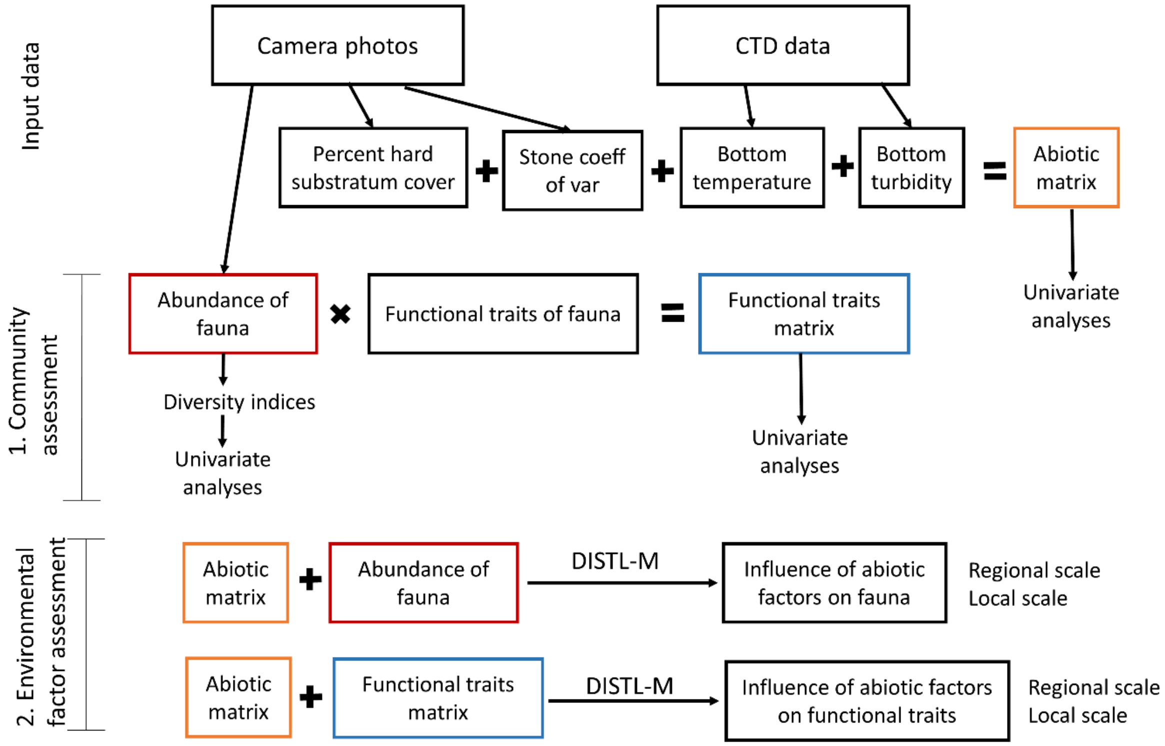

Fig. 26. Conceptual outline of statistical analyses conducted in this study.

intermediate turbidity, with more turbid water being present at stations 17 and 18, in the inner part of the fjord (Fig. 27).

Percent hard substratum cover and stone size heterogeneity were found to be significantly different among stations (Table 7). A sample photo from each station is shown in Fig. 28. Mean percent hard cover was highest at stations 7, in inner Raudfjorden (33.0 ± 28.5, mean ± standard deviation), and 14, on the north Svalbard shelf (38.3 ± 12.4), while stone size heterogeneity was highest at stations 7, 9, 12, and 14 (coefficients of variation 0.9 – 1.2, Fig. 29).

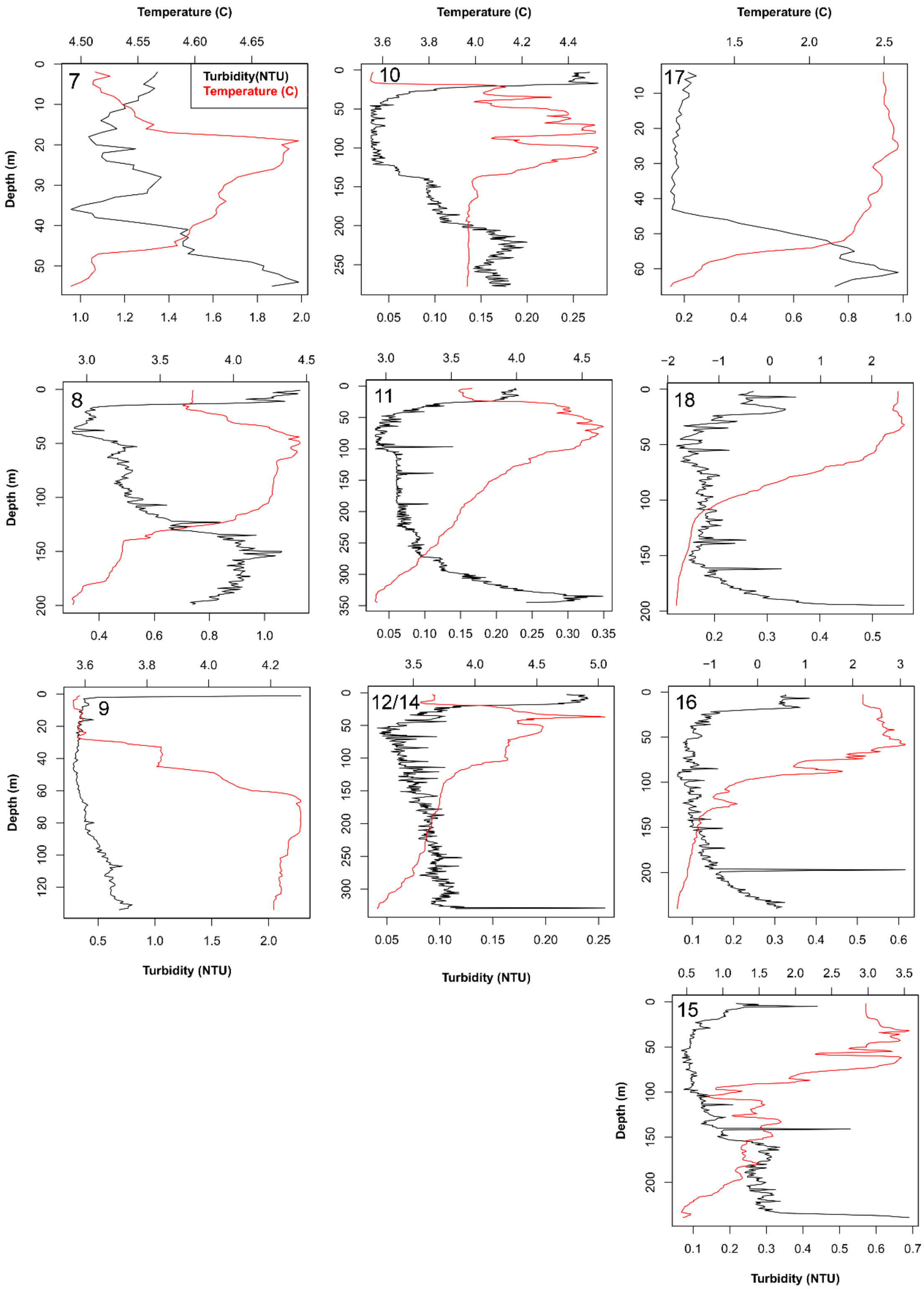

Fig. 27. CTD profiles showing temperature and turbidity of the water at each station. Numbers in bold indicate station. Note different scales of x- and y-axes.

Table 7. Results of Kruskal-Wallis tests for differences in biotic and abiotic factors among stations. Results of pairwise post-hoc tests are shown in Fig. 29 and 30.

Factor	**K**	**df**	**P**
% hard cover	122.759	10	<0.001
Stone heterogeneity	98.635	10	<0.001
N	136.455	10	<0.001
S	111.426	10	<0.001
H'	131.669	10	<0.001
J'	105.321	10	<0.001
d	109.815	10	<0.001

Differences in richness and diversity among stations

Multivariate analysis of similarity revealed overall significant differences among stations (ANOSIM, Global R = 0.827, p = 0.001). Significant differences were revealed for each of the indices N, S, H′, J′, and d among stations (Table 7). The highest average number of individuals (465.3 ± 68.9) was at station 17, in inner Rijpfjorden, and this was significantly different from every other station except station 18 in post-hoc analysis. However, the highest average number of species per image (13.6 ± 1.5) and the highest average H′ index (2.1 ± 0.2) were both found at station 14, on the north Svalbard shelf. Station 14 also showed the highest average Margalef richness (2.5 ± 0.3), though this was not significantly different from stations 12, 15, 16, or 18, on the outer shelf and in Rijpfjorden. Pielou evenness was significantly lower (0.15 – 0.19) at stations 10, 17, and 18, than all other stations except station 8 (0.41 ± 0.07) in mid Raudfjorden (Fig. 30).

Because species-accumulation curves were not found to reach an asymptote for any station, we compared Chao1 richness values for each station using individual photos

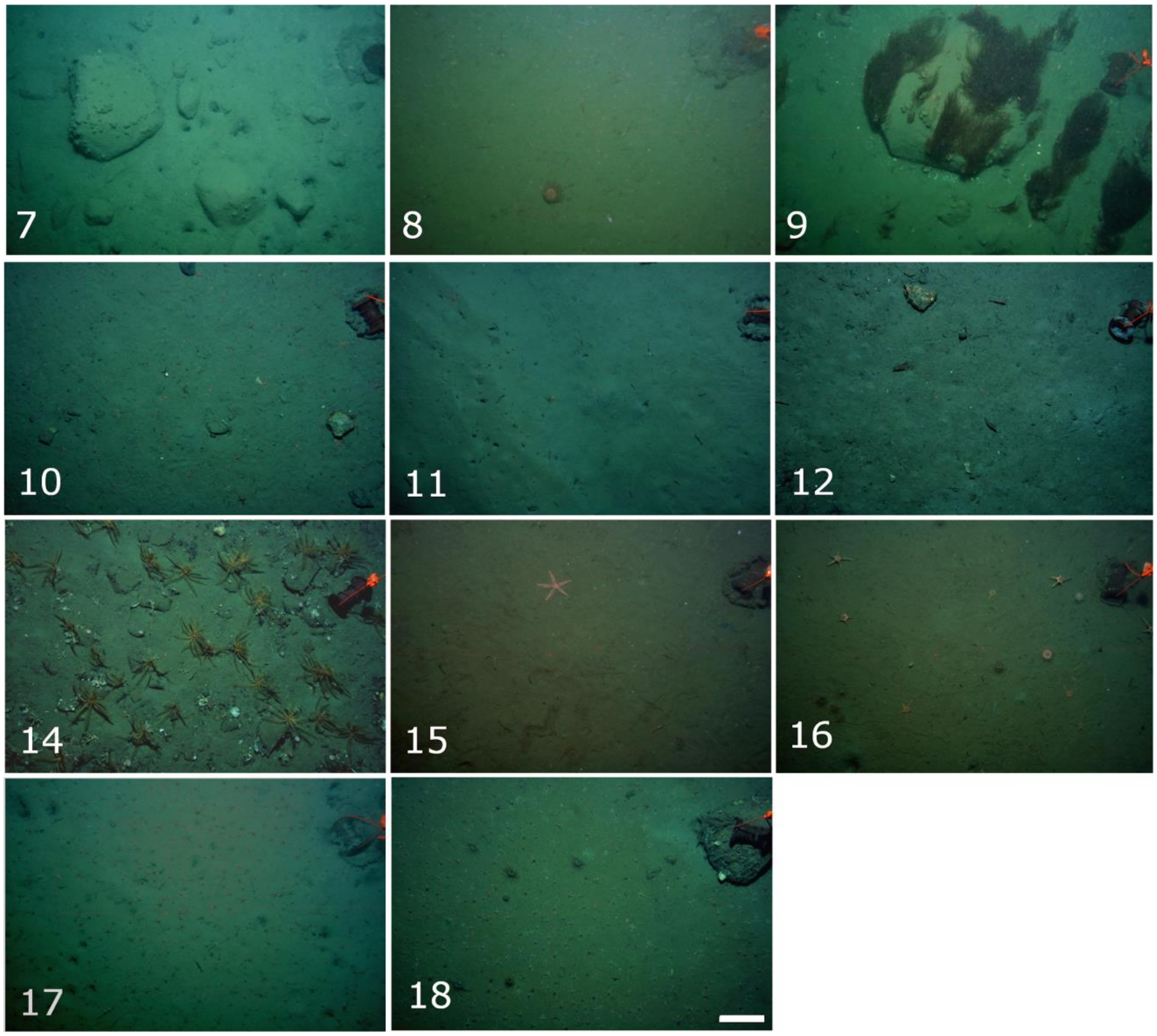

Fig. 28. An example photo from each station in north Svalbard.

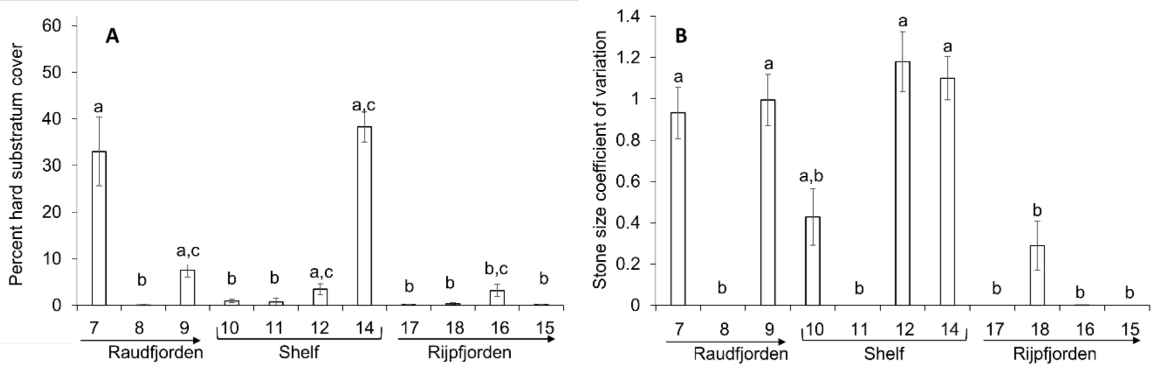

Fig. 29. Abiotic factors at each north Svalbard station. A, average percent hard substratum cover per image; B, average stone size heterogeneity (coefficient of variation) per image. Error bars represent standard error. Stations without any letters in common were found to be significantly different from each other in pairwise post-hoc analysis. Arrows point toward fjord mouth.

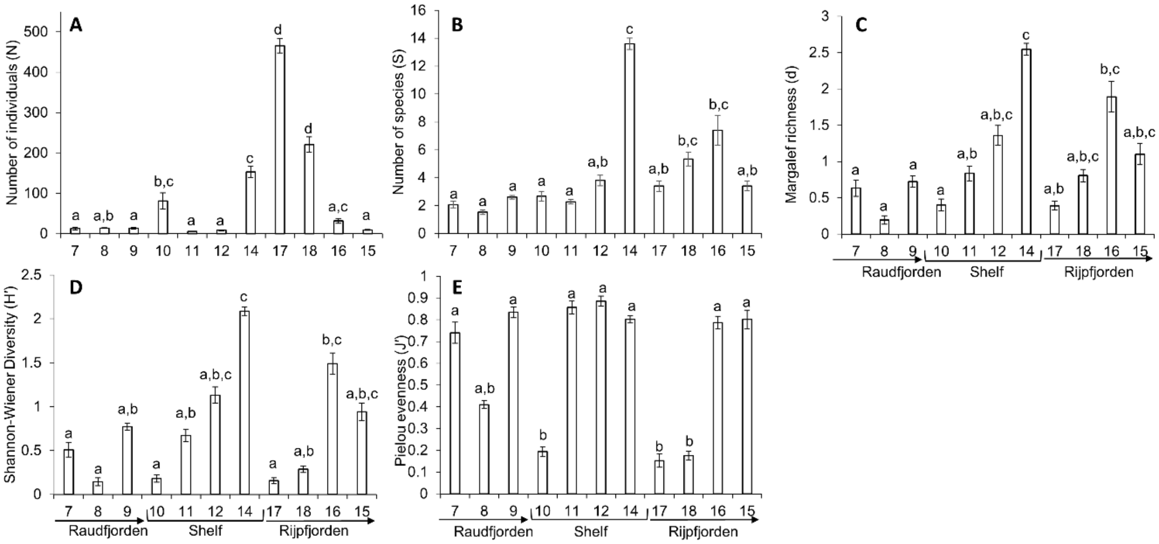

Fig. 30. Biotic indices of richness, evenness, and diversity at each station in north Svalbard. A, average number of individuals per image; B, average number of species per image; C, Margalef richness; D, Shannon-Wiener diversity index; E, Pielou evenness index. Error bars represent standard error. Stations without any letters in common were found to be significantly different from each other in pairwise post-hoc analysis. Arrows point toward fjord mouth.

as replicates. Chao1 is a diversity index based on the number of rare species in a sample, designed to estimate species richness under the assumption that not every species present has been captured. Within Raudfjorden, station 7 in the inner fjord was found to have the highest estimated richness (13.5 ± 7.2), while station 8, in mid-Raudfjorden, had the lowest (5.0 ± 2.7). On the shelf, stations 11 and 10, closer to land on the inner shelf, were found to have the lowest Chao1 richness (6.0 ± 2.7 and 19.3 ± 7.5, respectively), while stations 12 and especially 14 had the highest (26.2 ± 8.3 and 36.0 ± 10.2, respectively). Within Rijpfjorden, stations 17 and 18, in the inner fjord, had the lowest richness (14.5 ± 7.2 and 22.0 ± 5.3, respectively), but outermost station 15 also had similarly low richness (17.1 ± 2.5). It should be noted that the Chao1 richness values for these stations were still higher than for other stations in Raudfjorden and on the shelf, specifically 8, 9, and 11.

Station 16 had the highest Chao1 richness within Rijpfjorden and indeed of all stations (53.5 ± 31.1; Fig. 31). When Chao1 was calculated on a regional scale, with all Raudfjorden, shelf, and Rijpfjorden values combined, Rijpfjorden had the highest richness, though it was not significantly different from the shelf (Fig. 31).

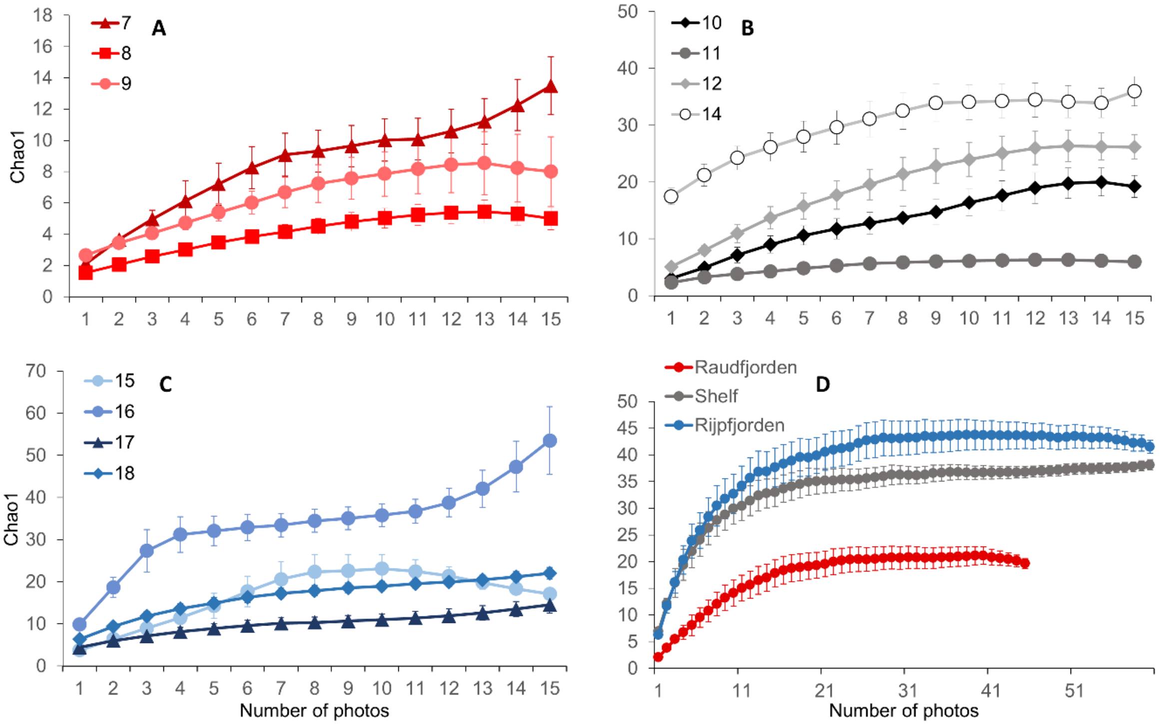

Fig. 31. Chao1 species richness estimates. A, stations in Raudfjorden; B, stations on the north Svalbard shelf; C, stations in Rijpfjorden; D, fjord and shelf regions combined. Error bars represent standard error.

Relationships between biotic and abiotic factors

DISTL-M analysis revealed that each of the abiotic factors tested had a significant effect on the biotic data cloud (p = 0.001 for each factor in marginal tests). The abiotic factor that accounted for the highest proportion of variability in the biotic data was depth, with an R^2 value of 0.11, followed in order by bottom temperature ($R^2 = 0.10$), bottom turbidity ($R^2 = 0.08$), percent hard substratum cover ($R^2 = 0.05$), and stone size heterogeneity ($R^2 = 0.03$). The best-fit forward-selected model included all abiotic variables and had an R^2 value of 0.36, indicating that all abiotic factors together explained approximately 36% of the variability in the biotic data.

The accompanying dbRDA graph shows that stations separate along the axes of bottom temperature, bottom turbidity, and depth, indicating that these factors influence the differences in benthic communities among stations (Fig. 32). Points belonging to the same station are spread out along the axes for percent hard substratum cover and stone size heterogeneity, indicating that these factors also influence the fauna but vary within stations. It should be noted that the y-axis captures much less (28%) of the variation in the data than the x-axis (40%). The four stations in Rijpfjorden are each represented by a close cluster of points, indicating lower intra-station heterogeneity of the community here than elsewhere. Points for Rijpfjorden are spatially separated from the other stations in the bottom left of the graph, indicating they are influenced by low temperature (Fig. 32).

Functional traits

An examination of the functional traits of the fauna at each station reveals that stations 17 and 18, in inner Rijpfjorden, are almost entirely dominated by small, mobile, scavengers (Fig. 33). Station 10 has a high proportion of mobile scavengers, while stations 8, 11, and 15 have high proportions of scavengers with various morphologies. Stations 7, 9, 12, 14, and 16 feature a high proportion of sessile suspension feeders, many of which are colonial (Fig. 33).

Results of a DISTL-M analysis show relationships between abiotic factors and the fauna at each station. All abiotic factors were found to be significantly related to the

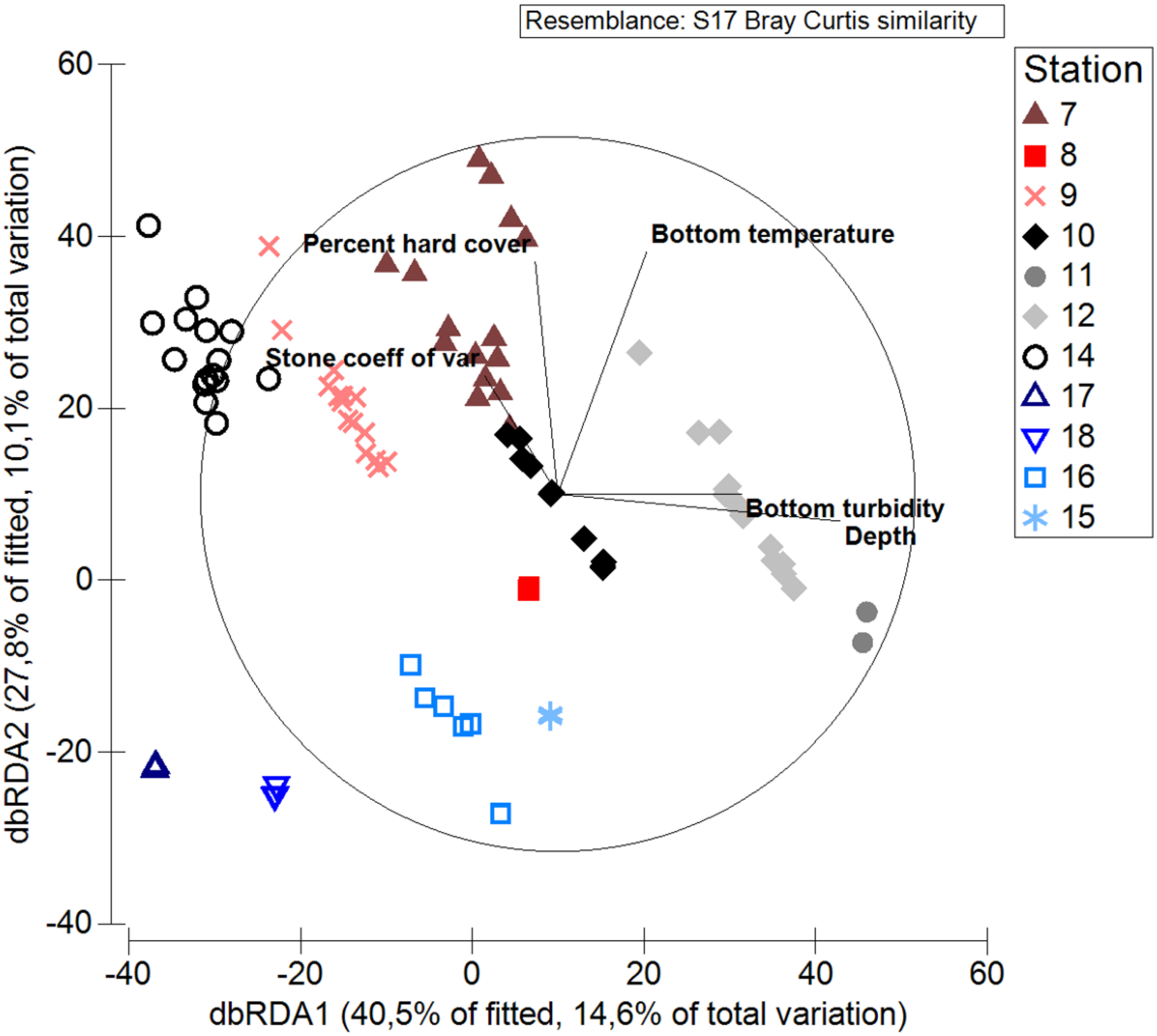

Fig. 32. dbRDA graph showing relationship of north Svalbard fauna to abiotic factors.

biotic data cloud (p = 0.001 in marginal tests) except for bottom turbidity (p = 0.203). The best-fit forward-selected model included all five abiotic factors and explained 56% of the variability in the functional trait data. Bottom temperature explained the largest amount of inter-station variability (36%; $R^2 = 0.36$). Depth explained the second-largest amount of variation (12%; $R^2 = 0.12$), and each of the other abiotic factors had R^2 values orders of magnitude lower (0.04, 0.04, and 0.002 for bottom turbidity, percent hard substratum cover, and stone heterogeneity, respectively). In the accompanying dbRDA

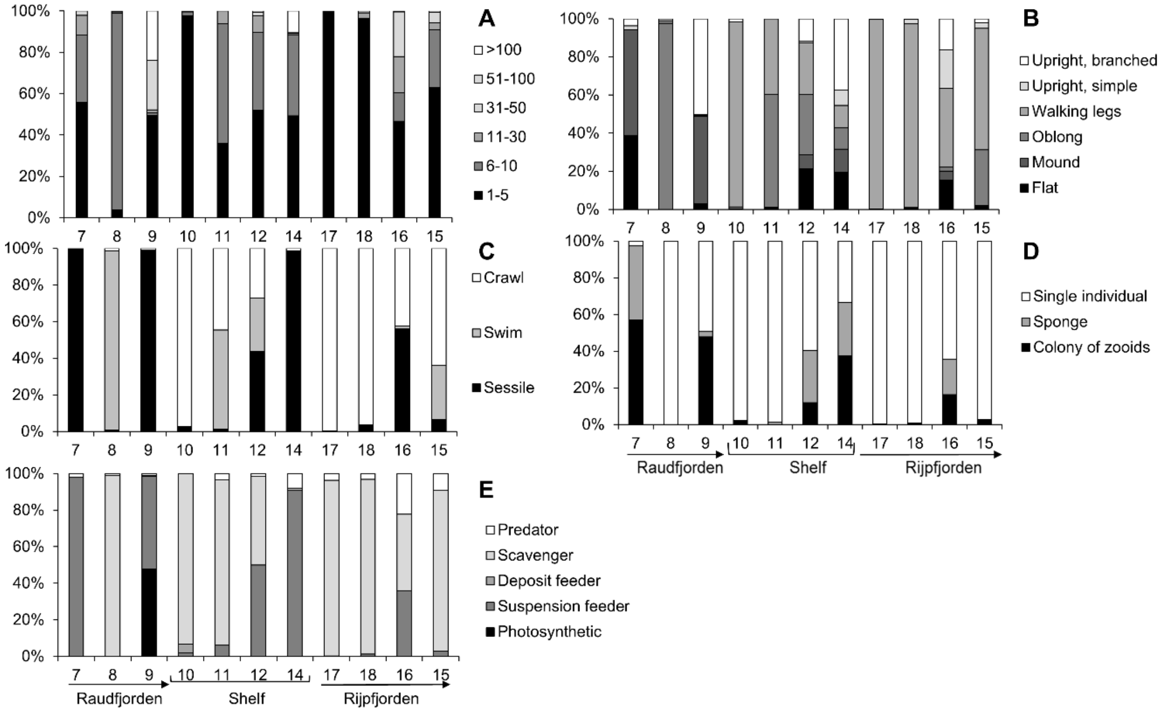

Fig. 33. Proportion of fauna at each north Svalbard station possessing different functional traits. A, size in vertically-facing view, cm; B, basic morphology; C, mobility; D, colonial/solitary; E, feeding mode. Arrows point toward fjord mouth.

based on functional traits, stations separated widely along the axes of bottom temperature and depth. Some separation occurred between points from the same station along the axes relating to percent hard substratum cover and bottom turbidity, though a much lower proportion of variability was captured by this second axis (Fig. 34).

Local versus regional scales

We also ran separate DISTL-M analyses for the shelf and each of the fjords. On this local scale, bottom temperature and depth were once again the strongest correlates of fauna within Raudfjorden, Rijpfjorden, and the north Svalbard shelf, as they explained the largest proportions of variation in the biotic data within each local area. In

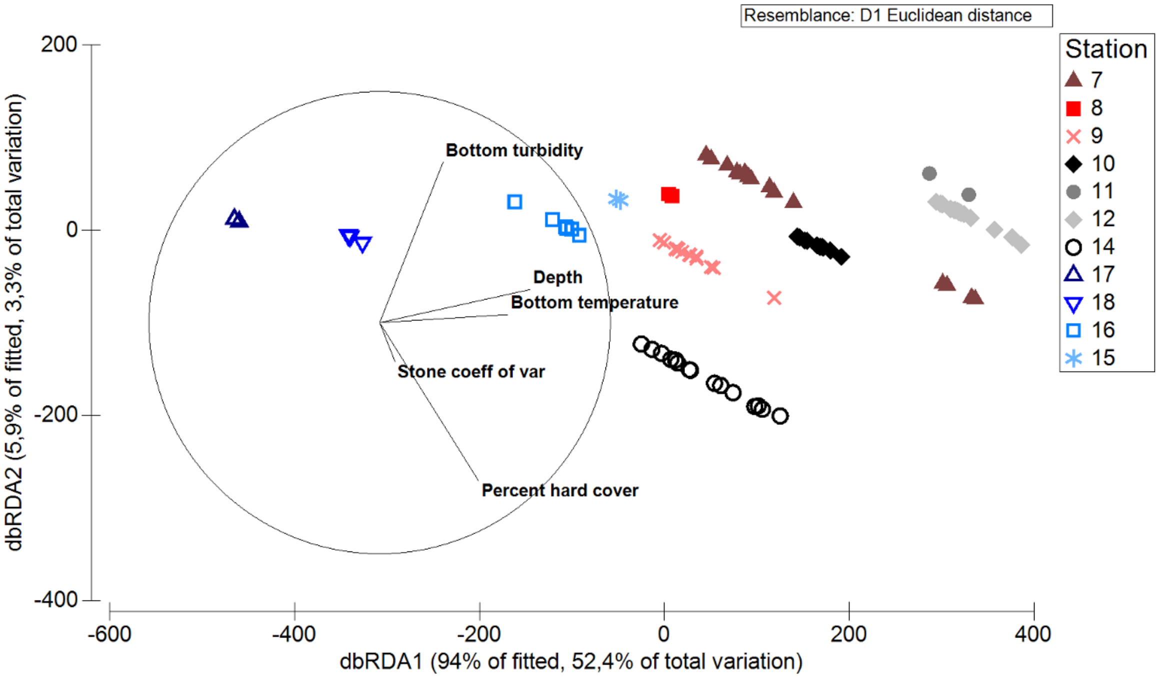

Fig. 34. dbRDA graph showing relationship of functional traits of north Svalbard fauna to abiotic factors.

Raudfjorden, R^2 values were 0.38 and 0.19 for bottom temperature and depth, respectively. On the shelf, depth explained 31% of the variation in the data ($R^2 = 0.31$) and temperature explained 27% ($R^2 = 0.27$), while in Rijpfjorden, depth explained 40% of the variation in the data ($R^2 = 0.40$) and bottom temperature explained 19% ($R^2 = 0.19$). No other abiotic factors were nearly as important in explaining the variation in the data, as their R^2 values were orders of magnitude lower (Fig. 35).

DISTL-M analysis of the functional traits on a local scale showed that functional traits of the fauna were influenced by different abiotic factors. For Raudfjorden, stone size heterogeneity explained 44% of the variability in the functional trait data cloud, and bottom temperature explained 13%. On the shelf, depth explained 38% of the variability in the functional trait data, and bottom temperature explained 20%. Depth was by far the

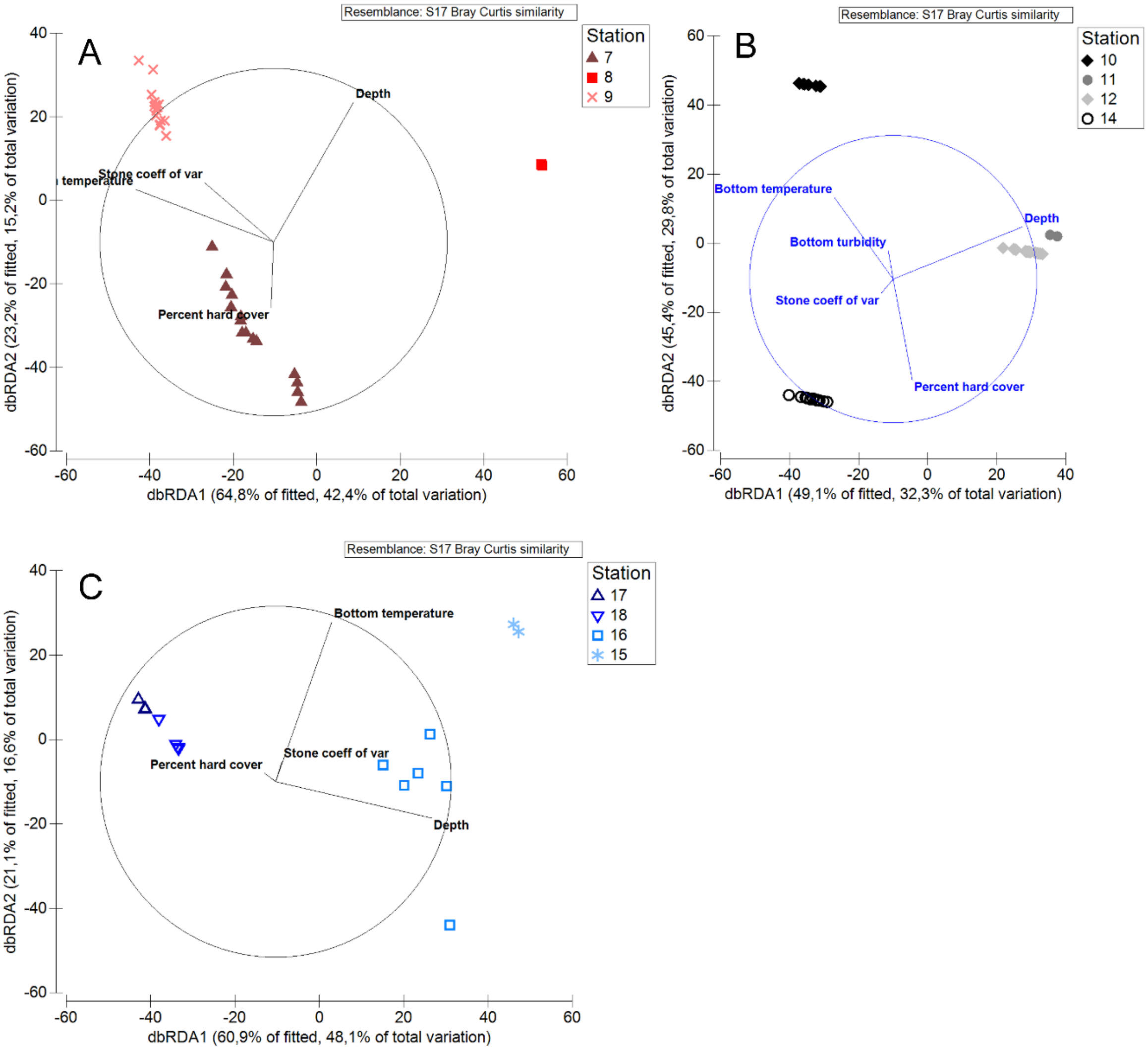

Fig. 35. dbRDA graph showing relationship of north Svalbard fauna to abiotic factors on a local scale. A, stations in Raudfjorden; B, stations on the north Svalbard shelf; C, stations in Rijpfjorden.

most important factor in Rijpfjorden, explaining 93% of the variation in the data (Fig. 36).

DISCUSSION

Our results indicated clear and significant differences in the benthic community within the same fjord, at stations spaced as little as 8 km apart. From this case study, we

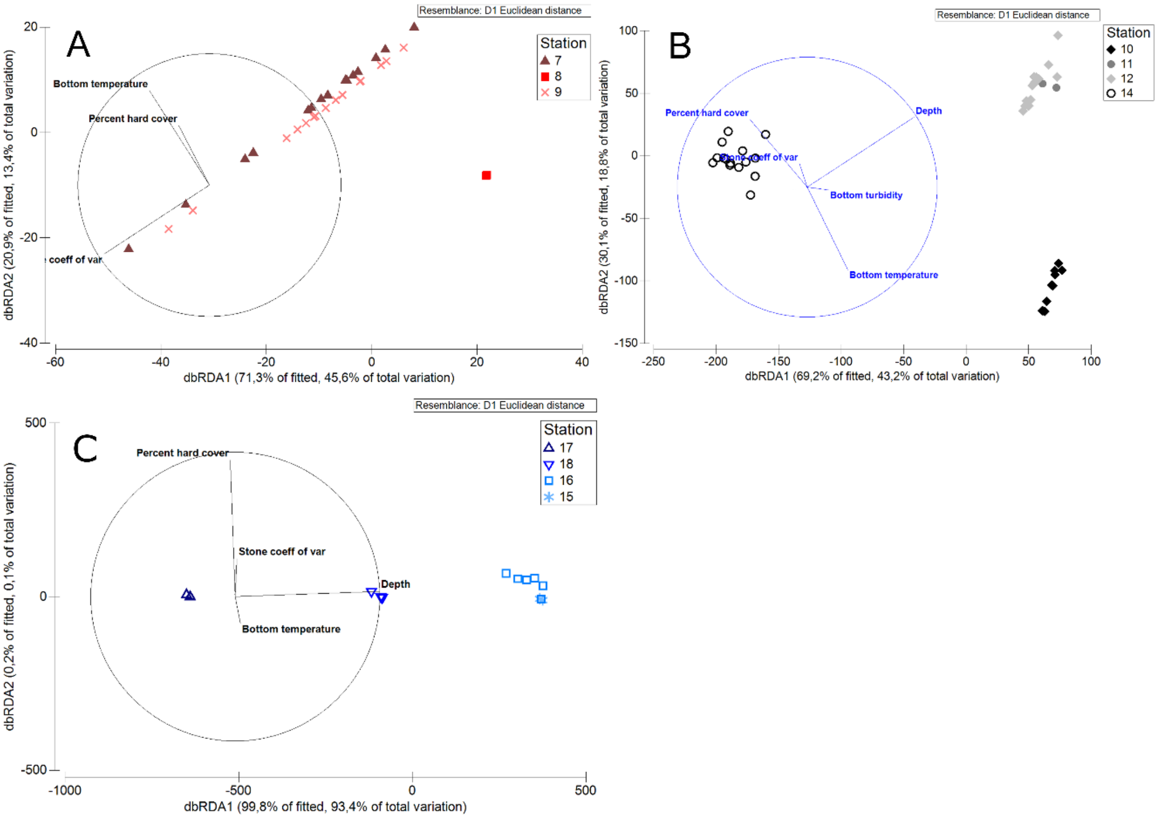

Fig. 36. dbRDA graphs showing relationship of functional traits of north Svalbard fauna to abiotic factors on a local scale. A, stations in Raudfjorden; B, stations on the north Svalbard shelf; C, stations in Rijpfjorden.

can therefore state that there was no single characteristic community for the fjords studied. Rather, distinct variations in the benthic community occurred along the fjord axis. Distributions of megafauna have seldom been documented for Svalbard fjords, so more research is required to determine if and to what extent patterns in the megafauna found in these fjords parallel patterns observed in other fjords and other major taxonomic groups (e.g., the macrofauna).

Roy et al. (2014) found that substratum type was more important in structuring benthic communities on local scales than on regional scales. However, in this case study, stone size heterogeneity explained only a small fraction of the variability in the local scale data, except for one case: the functional traits of fauna within Raudfjorden. Between fjords, stone size heterogeneity only explained a small fraction (3%) of the variability in the biotic data. While it is possible that habitat heterogeneity influences benthic megafauna on a larger spatial scale than was quantified here (~40 m, Robert et al. 2014), it was not possible to quantify habitat heterogeneity on larger spatial scales in this case study. Nevertheless, our results do highlight the importance of considering habitat heterogeneity on different spatial scales.

Bottom water temperature and depth were the most important abiotic factors structuring both composition and functional traits of the fauna in every case except for Raudfjorden mentioned above. The results will therefore be discussed here in the context of temperature and depth primarily. Depth explained 11% of the variability in the composition and 12% of the variability in the functional traits of north Svalbard fauna in this case study. Strong depth gradients in the megabenthos have also been observed in the Kara Sea and in East Greenland (Jørgensen et al. 1999, Mayer and Piepenburg 1996), though the latter case includes a greater range of depths than was quantified in this case study. In the Arctic, disturbance and competition have been shown to vary along depth gradients, but both factors are of little importance below ~40 m depth (Kukliński 2009, Barnes and Kukliński 2004). The sites included in this case study are located at 77-360 m, so of the factors correlated with depth, only benthic food supply is likely to be important. Food supply is generally negatively correlated with depth (Roy et al. 2014), but on local and meso-scales, structures such as polynyas and gyres can dramatically increase food supply to the benthos (Piepenburg 2005). Lateral advection is also responsible for local-scale patterns of benthic food supply (Mayer and Piepenburg 1996, Piepenburg 2005). In a recent study, Sswat et al. (2015) found that the north Svalbard shelf benthos was influenced by depth and substratum type, with higher diversity and abundance of sessile suspension feeders occurring at shallower stations. Station 14 in this case study had the highest abundance and diversity of suspension feeders and also the greatest availability of hard substrata (Fig. 29, 33). This station sits at shallower depth (192 m) compared to the adjacent station 12 (360 m). It is possible that bottom currents at shallower depth carry away fine particles to expose large stones and also bring particulate food to the suspension feeders at station 14. A similar pattern has been observed at Hopen in the NW Barents Sea (Cochrane et al. 2009). Arctic megabenthic communities may also change as a function of depth because of distinct water masses impinging on the seafloor at different depths. In the Canadian Arctic, colder, fresher water of Pacific origin overlies warmer, saline Atlantic water, and this gradient has been hypothesized as a major structuring factor for the megafauna there (Roy et al. 2014). Horizontal gradients in water masses have also been shown to affect the megabenthos in the Barents Sea, with higher abundance of megafauna being found at Atlantic-influenced southern stations, where productivity was higher (Cochrane et al. 2009). Our results also show high abundance of megafauna at Atlantic-influenced shelf stations (Fig. 30), but it cannot necessarily be stated that Atlantic water influence always leads to greater abundance and diversity of the megafauna, particularly in fjords because some Atlantic-influenced fjord sites in this case study showed low megafaunal abundance and diversity (e.g.,, Stations 7-9, Fig. 30).

Bottom water temperature (that was used as an indicator of Atlantic or Arctic water mass influence) at our sampling stations explained 10% and 36% of the variability in faunal composition and functioning, respectively. Stations in Raudfjorden were heavily influenced by Atlantic water masses (as indicated by the relatively higher temperatures, Fig. 27) and showed lower faunal diversity, plus a lower variety of functional traits (primarily mobile scavengers with rare sessile suspension feeders, Fig. 33). Stations in Raudfjorden had turbid bottom water (Fig. 27), indicating heavy disturbance from glacial sedimentation, re-suspension and/or terrestrial run-off. Inorganic sediment released by melting glaciers can smother organisms, clog filtering structures, dilute sediment organic material with inorganic particles, and reduce primary production by making the water column turbid, all of which can reduce biomass and diversity in glacial-influenced fjords (Włodarska-Kowalczuk et al. 2005). Stations in Raudfjorden had the lowest abundance of megafauna, indicating that it was difficult for more sedimentation-sensitive taxa to survive in this heavily-sedimented Atlantic-influenced fjord, such as sponges (that were dominant at the low turbidity station 14). Nevertheless, the dominant organisms at station 8 were shrimp of the species *Pandalus borealis*, which have been shown to be sensitive to inorganic particles in the water (Dale et al. 2008).

By contrast, the low bottom water temperature in Rijpfjorden indicated that the fjord is heavily influenced by Arctic water masses. The Rijpfjorden megabenthic community had high diversity, as shown by the high Chao1 index (Fig. 31) and also a wide variety of functional traits (e.g.,, predators, mobile scavengers, and sessile suspension feeders with various morphologies). A previous study at Arctic water mass-influenced stations in the Barents Sea has shown higher evenness and diversity of the megabenthos, despite lower abundance (Cochrane et al. 2009), and a body of recent research has shown that Arctic diversity is not as impoverished as previously believed (Piepenburg 2005). The high diversity observed at the outer Rijpfjorden stations is reminiscent of Antarctic fjord communities, which show higher faunal and functional diversity than shelf stations at similar depth (Grange and Smith 2013). Antarctic fjords are hypothesized to receive higher organic input than shelf stations in the form of macroalgal detritus, foraging krill, and whale excreta; however, the high diversity observed in Antarctic fjords more likely results from larval retention and lack of glacial sedimentation, because Antarctic fjords are at an earlier stage of warming than their Arctic counterparts (Grange and Smith 2013). In this case study, Rijpfjorden was found to be primarily influenced by Arctic water masses and to have high faunal diversity and a variety of functional and trophic groups and relative low water column turbidity. It could thus be considered more comparable with diverse Antarctic fjords, which are at an earlier stage of warming and not heavily influenced by glacial sedimentation.

Changes in ocean temperature and biogeochemistry are predicted to be more extreme in the Arctic compared to other regions of the world ocean (Mora et al. 2013). The Arctic shelf seas are predicted to experience an increase in water temperature of 2 – 4° C by 2100, and this is a greater temperature increase than is predicted for the Antarctic (Mora et al. 2013).

Food input to the seafloor may also increase in Arctic fjords with climate change if earlier ice break-up in spring leads to a mismatch between the spring bloom and the emergence of zooplankton, and tighter pelagic-benthic coupling (Zajączkowski and Legeżyńska 2001, Sokolova 1994, Leu et al. 2011). It is unclear how north Svalbard megafauna may respond to increased benthic carbon flux, but it is possible that greater food flux could boost megafaunal biomass (Smith et al. 2008). However, warming will also potentially increase glacier activity, calving, and sedimentation (Hodson and

Ferguson 1999, Włodarska-Kowalczuk and Węsławski 2001), which may in turn decrease megafaunal biomass and megabenthic functioning in north Svalbard. It is well documented that heavy inorganic sedimentation leads to reduced diversity and functional diversity of macrobiota (Syvitski et al. 1989, Piepenburg et al. 1996, Włodarska-Kowalczuk and Węsławski 2001, Włodarska-Kowalczuk 2007), and inorganic sedimentation can also reduce mesoscale heterogeneity of the benthic community (Włodarska-Kowalczuk and Węsławski 2008). The diverse communities at stations 15 and 16 in outer Rijpfjorden and at stations on the shelf have a variety of trophic groups. By contrast, in the more heavily-sedimented inner fjord stations in both Raud- and Rijpfjorden, the community consists almost entirely of mobile scavengers. An increase in sedimentation from rising temperatures and enhanced glacial melting may thus lead to a shift from suspension-feeding/detritivore communities to more necrophagous communities. If our results are representative for other fjords, warming temperatures could also lead to a reduction in megafaunal abundance and biomass. Much higher megafaunal abundances were observed at the colder (17 and 18), and less turbid (18) stations in inner Rijpfjorden compared to the warmer, more turbid station 8 in Raudfjorden (Fig. 30), even though all three stations were characterized by mobile scavengers and feature primarily soft substrata. Thus, warming and increased sedimentation, besides reducing functional diversity of the megabenthos, are likely to decrease the abundance and biomass. Such a reduction in abundance or biomass of the megabenthos may have major implications for Arctic fjord ecosystems (e.g.,, reducing energy transfer to predatory fishes and other higher trophic levels).

BRIDGE IV

Svalbard fjords are heterogenous environments, impacted by a variety of abiotic factors on multiple spatial and temporal scales. In the last chapter of this dissertation, I investigate how abiotic factors, particularly water temperature, affect recruitment in Svalbard fjords. This chapter returns to the theme of community assembly on isolated hard substrata, because recruitment is one of the first steps in community assembly. It also ties in closely with Chapter V by demonstrating the high degree of variability in Svalbard benthic communities, even within the same fjord. In Chapter VI, I show how recruitment in Svalbard fjords is affected by temperature, depth, season, and biotic interactions. I discuss the biology of the recruiting species to show that the first recruits to settlement plates in the high Arctic are generally fast-growing, poor-competitive pioneer species. I also test for one of the five common species distribution patterns on islands (Chapter II), non-random co-occurrence. Settlement plates constitute island-like habitats where the process of community assembly can be directly observed.

CHAPTER VI

RECRUITMENT IN HIGH ARCTIC FJORDS: RELATION TO TEMPERATURE, DEPTH, AND SEASON

Kirstin S. Meyer, Andrew K. Sweetman, Piotr Kuklinski, Peter Leopold, Daniel Vogedes, Jørgen Berge, Colin Griffiths, Craig M. Young, and Paul E. Renaud

INTRODUCTION

Hard-substratum habitats in the marine environment undergo a process of community assembly, which includes larval dispersal, recruitment, competition, predation, and succession (Chapter II). Community assembly is the process by which a new or uncolonized substratum comes to be inhabited by a mature benthic community. Recruitment is important in the process of community assembly, because the species that recruit first to a substratum can facilitate or inhibit the establishment of other species (Sutherland 1974, Osman and Whitlatch 1995a, Walters et al. 1997).

Hard-substratum habitats in the marine environment are often isolated, resembling "islands in a sea of mud" (Young 2009). Island-like substrata include natural (Oschmann 1990, Schulz et al. 2010), anthropogenic (Taylor et al. 2014), and biogenic structures (Gutt and Schickan 1998, Beaulieu 2001, Hétérier et al. 2008). Many marine island-like habitats have the same faunal distribution patterns as terrestrial islands, though the mechanisms are not necessarily the same (Abele and Patton 1976, Schoener and Schoener 1981, Huntington and Lirman 2012; Chapters III, IV). Biotic community composition on islands is related in the classical literature to island size, distance to a mainland, (MacArthur and Wilson 1967) and biotic interactions (Diamond 1975a).

At an isolated hard-substratum habitat in the Beaufort Sea, the Boulder Patch, (Konar and Iken 2005, Wilce and Dunton 2014), colonization of hard substrata by recruitment is very slow, with only 2% of experimentally-cleared boulders being covered after 4 years and 10% cover after 7 years (Konar 2007, 2013). Low recruitment (compared to temperate latitude) was also observed on experimental substrata in Isfjorden (Svalbard) (Barnes and Kukliński 2005, Kukliński et al. 2013a), and experimentally-cleared substratum patches in Kongsfjorden may take > 10 years to resemble undisturbed communities again (Beuchel and Gulliksen 2008).

Arctic fjords are heterogenous environments, with benthic communities that vary within and among fjords. The primary factors influencing benthic communities are depth and temperature, though substratum heterogeneity can be important on a local scale (Chapter V). Polar habitats also experience strong seasonal fluctuations in abiotic conditions that may influence the benthos. In this study, we seek to understand how recruitment on isolated hard substrata in Svalbard fjords is influenced by temperature, depth, season, and biotic interactions. Recruitment has been studied at single locations in Svalbard (Barnes and Kukliński 2005, Schmiing 2005, Kukliński et al. 2013a), but we present simultaneous data from three fjords: Isfjorden and Kongsfjorden, both in west Spitsbergen, and Rijpfjorden, on Nordauslandet (Fig. 37). Isfjorden and Kongsfjorden, home to the settlements of Longyearbyen and Ny-Ålesund, respectively, are Atlantic-influenced fjords, where warm, nutrient-rich waters from the West Spitsbergen Current penetrate (Svendsen et al. 2002). This North Atlantic water has facilitated colonization of

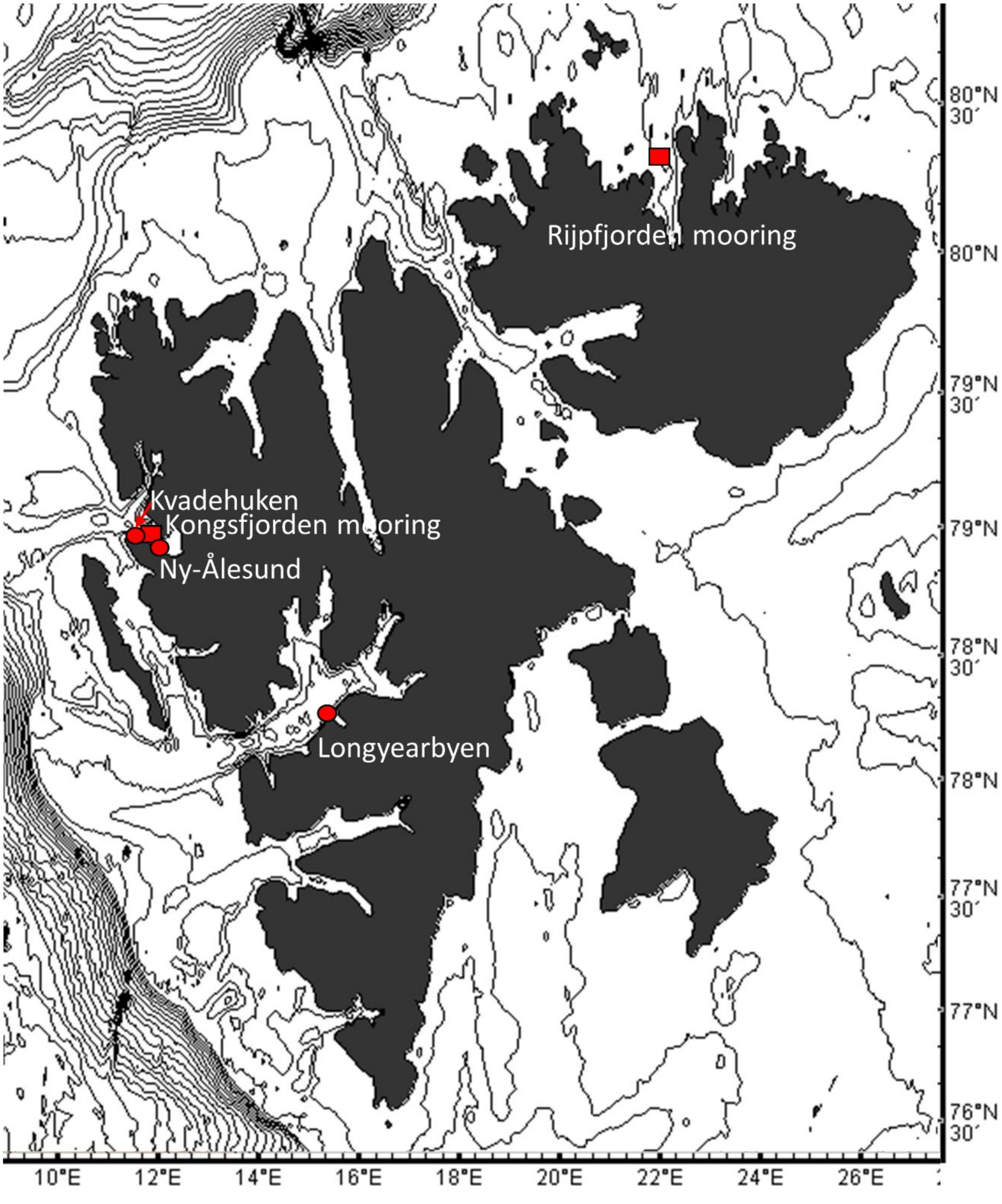

Fig. 37. Map of settlement plate deployment locations. Circles indicate shallow locations (7 – 15 m) reached by SCUBA; squares indicate moorings (30 and 195 – 215 m). Depth contours are shown every 100 m.

west Spitsbergen fjords by Atlantic fauna, including Atlantic cod (*Gadus morhua*) and blue mussels (*Mytilus edulis*) in recent years (Berge et al. 2005, Renaud et al. 2012).

Rijpfjorden, by contrast, is a “true” Arctic fjord, influenced primarily by cold, nutrient-poor waters (Wang et al. 2013).

In addition to the environmental and temporal variables (temperature, depth, and season) listed above, we consider how recruitment may be influenced by the specific biology of each species. The first colonists on isolated hard substrata (at temperate latitude) are typically fast-growing, poor-competitive pioneer species, such as acorn barnacles and spirorbid polychaetes (Dean and Hurd 1980, Chalmer 1982). Later in succession, slow-growing superior competitors dominate (Perkol-Finkel et al. 2005, 2006, Edwards and Stachowicz 2010). We hypothesize that the recruits to our experimental substrata will be primarily fast-growing, poor-competitive pioneers.

We also test for non-random co-occurrence patterns among the recruits in this study. Non-random co-occurrence refers to pairs of species being found together less (negative non-random co-occurrence) or more (positive non-random co-occurrence) than expected by chance, and it is a common species distribution pattern on islands and island-like habitats (Gotelli and McCabe 2002, Chapter II). Negative non-random co-occurrence patterns have been attributed to interspecific competition on islands (Diamond 1975a), though this interpretation has been heavily criticized (Connor and Simberloff 1979). For marine hard substrata, encrusting fauna may have negative non-random co-occurrence in the absence of interspecific overgrowth competition, indicating there is not necessarily a relationship between these two concepts for marine island-like habitats (Chapter IV). Positive non-random co-occurrence can be the results of epibiotic relationships (Chapter IV).

This study helps further an understanding of how hard-substratum habitats are structured in the high Arctic. We show how recruitment varies spatially and temporally and how it is potentially influenced by abiotic factors and biotic interactions.

METHODS

Deployment of settlement plates

Settlement plates were deployed in September-October 2014 from R/V *Helmer Hanssen*. Four frames of settlement plates were deployed at each of five locations: two moorings and three shallow locations reached by SCUBA (Table 8, Fig. 37). Moorings were deployed in Kongsfjorden and Rijpfjorden (Table 8, Fig. 37). Frames were affixed to the moorings in pairs, two as close to the seafloor as possible (~10 m altitude) and two at 30 m depth. Settlement plates deployed on moorings were recovered approximately one year after deployment, in September 2015.

Settlement plates (15 x 15 cm) were clear acrylic (0.32 cm thick) roughened with sandpaper. Plates were mounted on PVC frames (75 x 15 cm) with zip ties through holes drilled in each corner of the plates. Four settlement plates were mounted on each frame (Fig. 38).

At the shallow locations, four frames of settlement plates were deployed via SCUBA in September-October 2015. At Longyearbyen and Ny-Ålesund, plates were affixed to underwater structures associated with piers. At Kvadehuken, a hard-bottom site used for diving and long-term benthic studies (Beuchel and Gulliksen 2008, Kortsch et al.

Table 8. Deployment sites for all settlement plates in this study.

Deployment date	Recovery date	Location	Latitude (N)	Longitude (E)	Depth (m)	No. plates (No. frames)
10 Oct 2014	7 Jan 2015	Longyearbyen Bykaia	78° 13.77'	15° 36.00'	7	8 (2)
7 Jan 2015	7 Sep 2015	Longyearbyen Bykaia	78° 13.77'	15° 36.00'	7	8 (2)
10 Oct 2014	7 Sep 2015	Longyearbyen Bykaia	78° 13.77'	15° 36.00'	7	8 (2)
23 Sep 2014	14 Jan 2015	Ny-Ålesund Gamlekaia	78° 55.71'	11° 55.33'	7	8 (2)
14 Jan 2015	12 Sep 2015	Ny-Ålesund Gamlekaia	78° 55.71'	11° 55.33'	7	8 (2)
23 Sep 2014	12 Sep 2015	Ny-Ålesund Gamlekaia	78° 55.71'	11° 55.33'	7	8 (2)
25 Sep 2014	11 Sep 2015	Kvadehuken	78° 58.44'	11° 28.95'	15	12 (3)
26 Sep 2014	10 Sep 2015	Kongsfjorden mooring	78° 57.76'	11° 47.84'	30	8 (2)
26 Sep 2014	10 Sep 2015	Kongsfjorden mooring	78° 57.76'	11° 47.84'	215	8 (2)
30 Sep 2014	17 Sep 2015	Rijpfjorden mooring	80° 17.66'	22° 18.23'	30	8 (2)
30 Sep 2014	17 Sep 2015	Rijpfjorden mooring	80° 17.66'	22° 18.23'	195	8 (2)

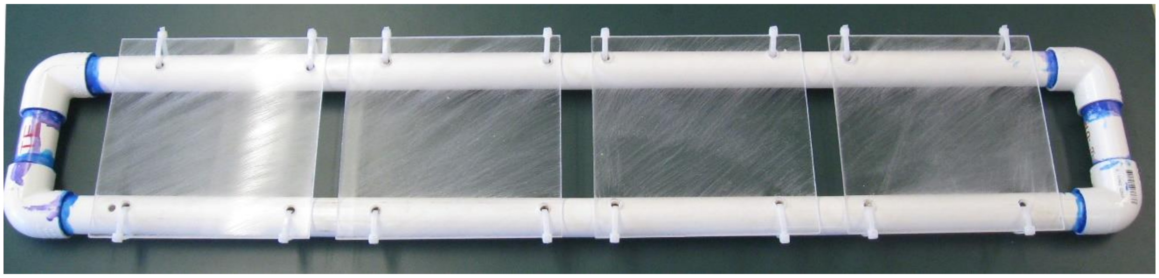

Fig. 38. Settlement plate deployment design. Individual plates are 15 x 15 cm.

2012) near the mouth of Kongsfjorden, frames were bolted directly to the bedrock. Settlement plates at all locations were oriented vertically in order to prevent recruits from being smothered by sedimentation and to ensure consistent orientation among sites.

Two frames of settlement plates were recovered from each shallow location in January 2015. Plates collected in January 2015 represent fall-winter recruitment and were replaced by two new frames of plates to capture spring-summer recruitment. The other two frames deployed in September-October 2015 were left undisturbed at each shallow location to capture recruitment over the entire year. The January 2015 dive at Kvadehuken had to be aborted because of logistical difficulty, and one frame of plates was lost over the deployment period. Therefore, only three year-long frames were obtained from this location (Table 8). All remaining settlement plates from both moorings and shallow locations were recovered in September 2015 during a cruise aboard R/V *Helmer Hanssen*.

Analysis of settlement plates

Immediately following recovery, all plates were held in cold (~4 °C) seawater aboard R/V *Helmer Hanssen*. Settlement plates were removed from their frames and examined under a dissecting microscope. Only one side of each plate, the side that had been roughened with sandpaper and was most exposed to the water column during the deployment, was examined. Sessile fauna present on each plate were counted and identified by referencing the pertinent taxonomic literature (i.e., Kluge 1975; Klekowski 1995) and by consulting taxonomic experts. Morphotype names were used for fauna that could not be identified, but only 8 of 48 observed taxa had to be labeled as morphotypes.

Species and morphotypes will be collectively referred to as “taxa.” Each taxon was photographed using a digital camera in conjunction with a dissecting microscope (Leica). For especially abundant taxa (i.e., *Semibalanus balanoides*, *Circeis armoricana*), settlement plates were sub-divided into 36 equal units using divisions on a clear acetate sheet visible behind the settlement plate. Six of these units were randomly sub-sampled for counting, and the number of individuals was then extrapolated to the full size of the plate. Deep (215 m) settlement plates deployed on the Kongsfjorden mooring were covered by the hydroid *Stegopoma plicatile*, including numerous entangled stolons on the plate, as well as upright, branched forms. For this species, it was impossible to determine the number of recruiting individuals, so the number of upright, branched forms was counted as an indirect proxy for recruitment.

Water temperature

TidbiT v2 temperature loggers (Onset, USA) were attached to one frame of settlement plates at each of the shallow locations. Water temperature was recorded every 15 minutes for the duration of the year-long deployment. The temperature logger was lost along with its frame at Kvadehuken (15 m), so instead, water temperature from a logger (SBE 56, Sea-Bird Electronics, USA) deployed at 13 m on the Kongsfjorden mooring was used to infer water temperature at this site.

Water temperature at the mooring locations was recorded every 12 minutes during the year-long deployment using temperature loggers (SBE 56) deployed near the settlement plates. Loggers were positioned near the settlement plates, at 33 m and 207 m in Kongsfjorden and at 32 m and 215 m in Rijpfjorden.

Statistical analysis of data

Settlement plates were pseudoreplicates, so we used Mann-Whitney U-tests (M-W) for univariate tests. Multi-variate statistics were conducted in Primer v6 (Clarke & Gorley 2006) following a log(x+1) transformation to reduce the effect of overly-dominant species. We tested for non-random co-occurrence in EcoSim (Entsminger 2014) using a fixed-fixed null model and the C-score index (Gotelli 2000). Tests for non-random co-occurrence were conducted for pseudoreplicate settlement plates only within a given location and season to avoid the compounding effects of seasonal and location-specific recruitment.

RESULTS

Water temperature

Water temperature at the shallow (7 – 15 m) locations varied between -2 and 9° C over the course of the year-long deployment (Fig. 39A). The lowest temperatures (-2 – 0° C) were observed in December 2014 – March 2015, though an influx of warmer water (1.5 – 1.8° C) appears at Ny-Ålesund and Kvadehuken (both in Kongsfjorden) in January 2015. The warmest temperatures at each site (6 – 8° C) occurred in June – August 2015 at Longyearbyen and Ny-Ålesund (both 7 m) and in September 2015 at Kvadehuken (15 m) (Fig. 39A).

Water temperature at the location of the Kongsfjorden mooring was 4.5 – 5° C in October 2014; the coldest temperatures (-0.8° C) at this location occurred in February 2015. The water gradually warmed throughout the spring and summer, reaching a maximum of 6° C at 33 m and 3° C at 207 m in August 2015 (Fig. 39B). In Rijpfjorden,

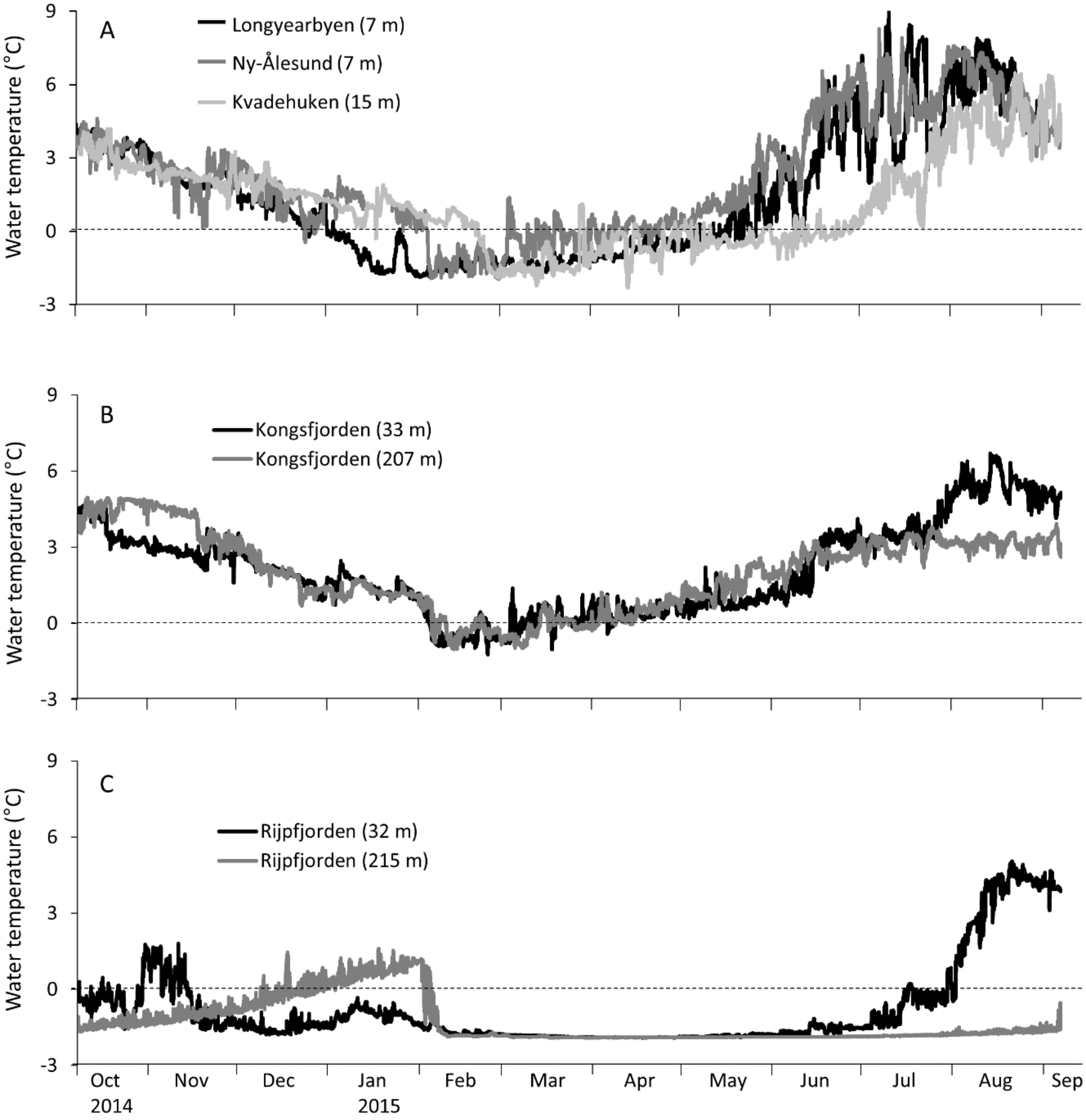

Fig. 39. Water temperature at settlement plate deployment sites. A, shallow dock sites; B, Kongsfjorden mooring; C, Rijpfjorden mooring.

water temperature in Oct 2014 was 0° C at 32 m and -1.5° C at 215 m (Fig. 39C). The bottom water gradually warmed to reach 1° C in January 2015 before dropping below 0; the temperature at both depths remained -2 – -1° C from February to June 2015. The water at 32 m reached a maximum of 4° C in September 2015, while the bottom water (215 m) remained at -1° C (Fig. 39C).

Seasonal patterns in recruitment

During fall-winter, there was significantly higher recruitment per plate at Ny-Ålesund than at Longyearbyen (M-W, U = U = 4.00, p = 0.002), but the number of morphotypes recruiting to plates at each location was not significantly different (U = 24.0, p = 0.442) (Fig. 40). High recruitment of the spirorbid *Circeis armoricana* (Fig. 41) occurred at each location, with up to 862 individuals being found on a single plate at Ny-Ålesund. Bryozoans *Celleporella hyalina* and *Callopora craticula* (Fig. 41) were also common recruits on the fall-winter plates.

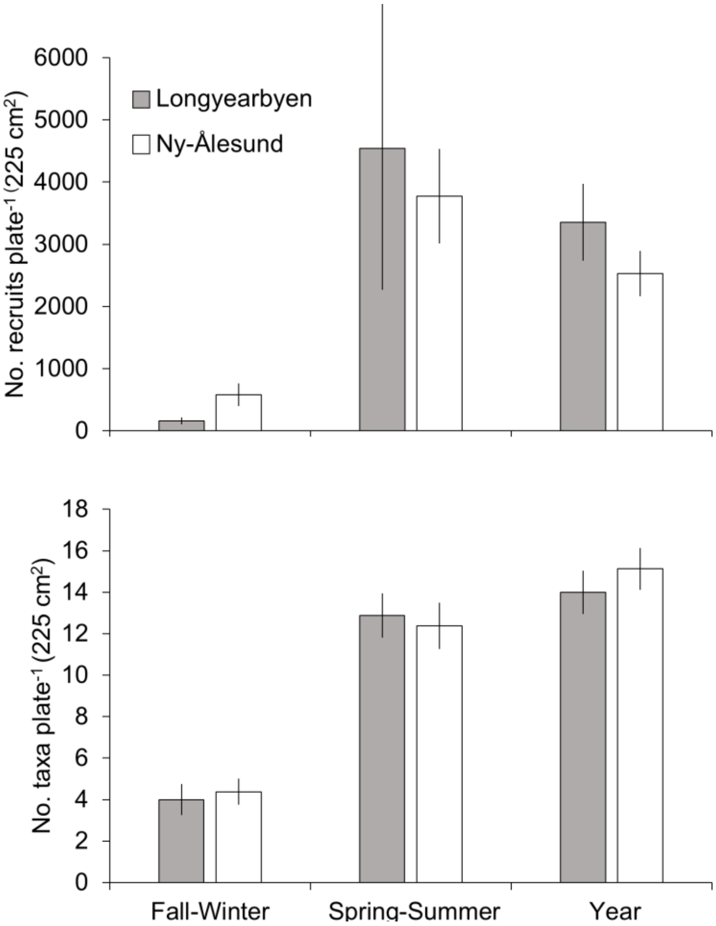

Fig. 40. Seasonal recruitment (225 cm^{-2}) at 7 m depth at Longyearbyen and Ny-Ålesund piers. Error bars show 95% confidence intervals.

Significantly higher recruitment was observed at both Longyearbyen and Ny-Ålesund for spring-summer than fall-winter (Longyearbyen, U = 0.00, p = 0.001; Ny-Ålesund, U = 0.00, p = 0.001), with thousands instead of hundreds of individuals recruiting to each plate (Fig. 40). The number of taxa recruiting to each plate was also significantly higher in the spring-summer than fall-winter at both locations (Longyearbyen, U = 0.00, p = 0.001; Ny-Ålesund, U = 0.00, p = 0.001) (Fig. 40). There were more recruits per plate in the spring-summer at Longyearbyen than Ny-Ålesund, though this difference was not significant (U = 31.00, p = 0.92). The number of taxa recruiting at each location was also not significantly different (U = 32.0, p = 1.00) (Fig. 40).

At Ny-Ålesund, there was a significantly lower number of recruits on plates deployed all year than on plates deployed in the spring-summer (U = 6.00, p = 0.006), but there was a significantly higher number of taxa (U = 6.00, p = 0.005) (Fig. 40). Differences between numbers of recruits and taxa in spring-summer and all-year deployments were not significant at Longyearbyen (N, U = 32.0, p = 1.0; S, U = 21.0, p = 0.233) (Fig. 40). For both locations, high numbers of *Circeis armoricana* were observed on spring-summer and year-long plates, but the barnacle *Semibalanus balanoides* (Fig. 41) also recruited in high numbers, particularly at Longyearbyen. Dense macroalgae, including *Desmarestia aculeata* (spring-summer, 285 ± 44.9; year, 659 ± 74.7 individuals per 225 cm plate, mean ± standard error), *Dermatocelis laminariae* (spring-summer, 2759 ± 343; year, 1366 ± 203 plate^{-1}), and *Chorda* sp. (spring-summer, 134 ± 20.4; year, 85.5 ± 17.9 plate^{-1}), recruited to spring-summer and year-long settlement plates at Ny-Ålesund (Fig. 42).

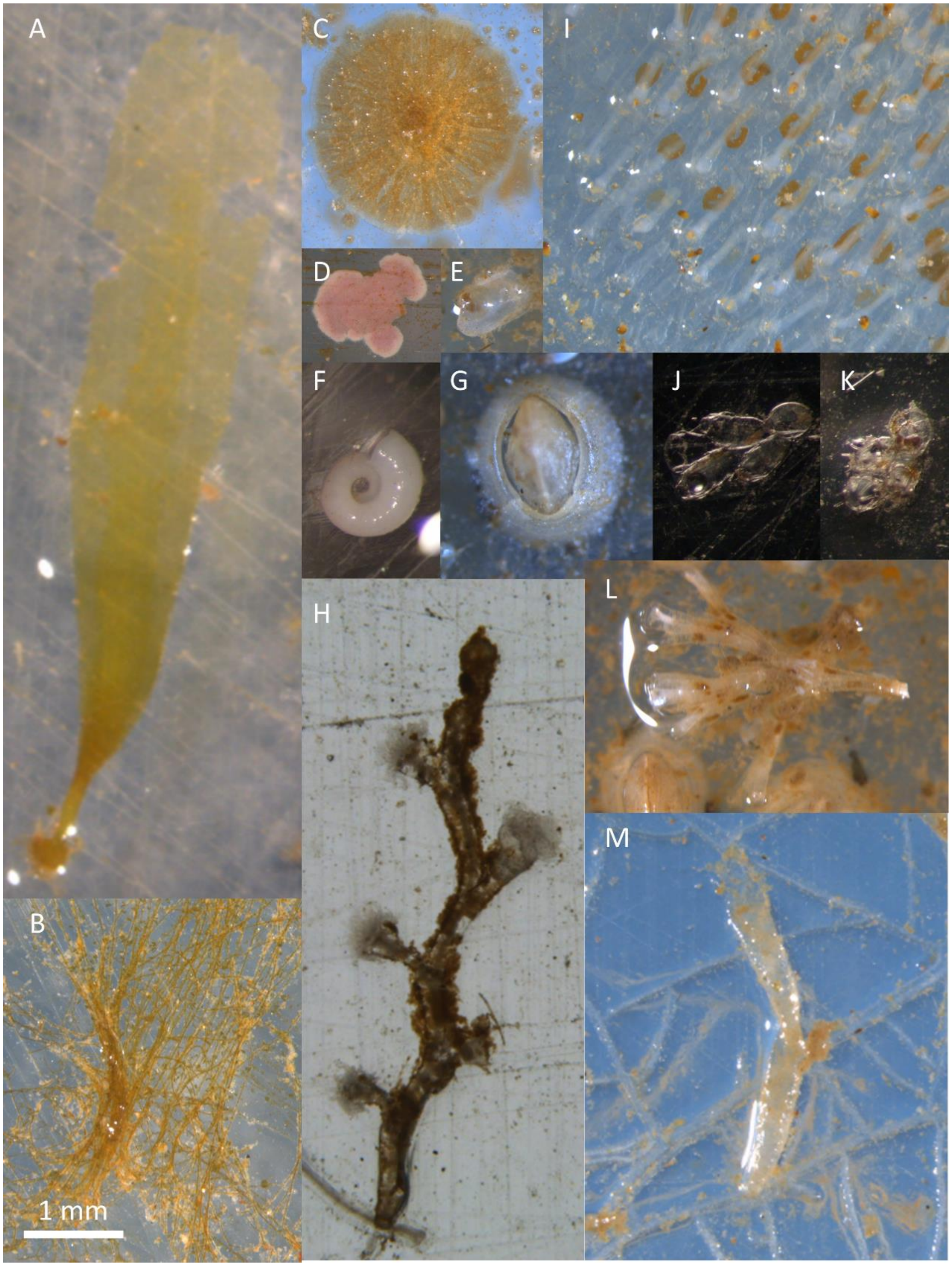

Fig. 41. Common and selected taxa found on settlement plates. A, *Saccharina latissima*; B, *Chorda* sp.; C, *Dermatocelis laminariae*; D, crustose coralline alga; E, *Hiatella arctica*; F, *Circeis armoricana*; G, *Semibalanus balanoides*; H, *Obelia geniculata*; I, *Alcyonidium gelatinosum*; J, *Celleporella hyalina*; K, *Callopora craticula*; L, *Crisiella producta*; M, *Stegopoma plicatile*.

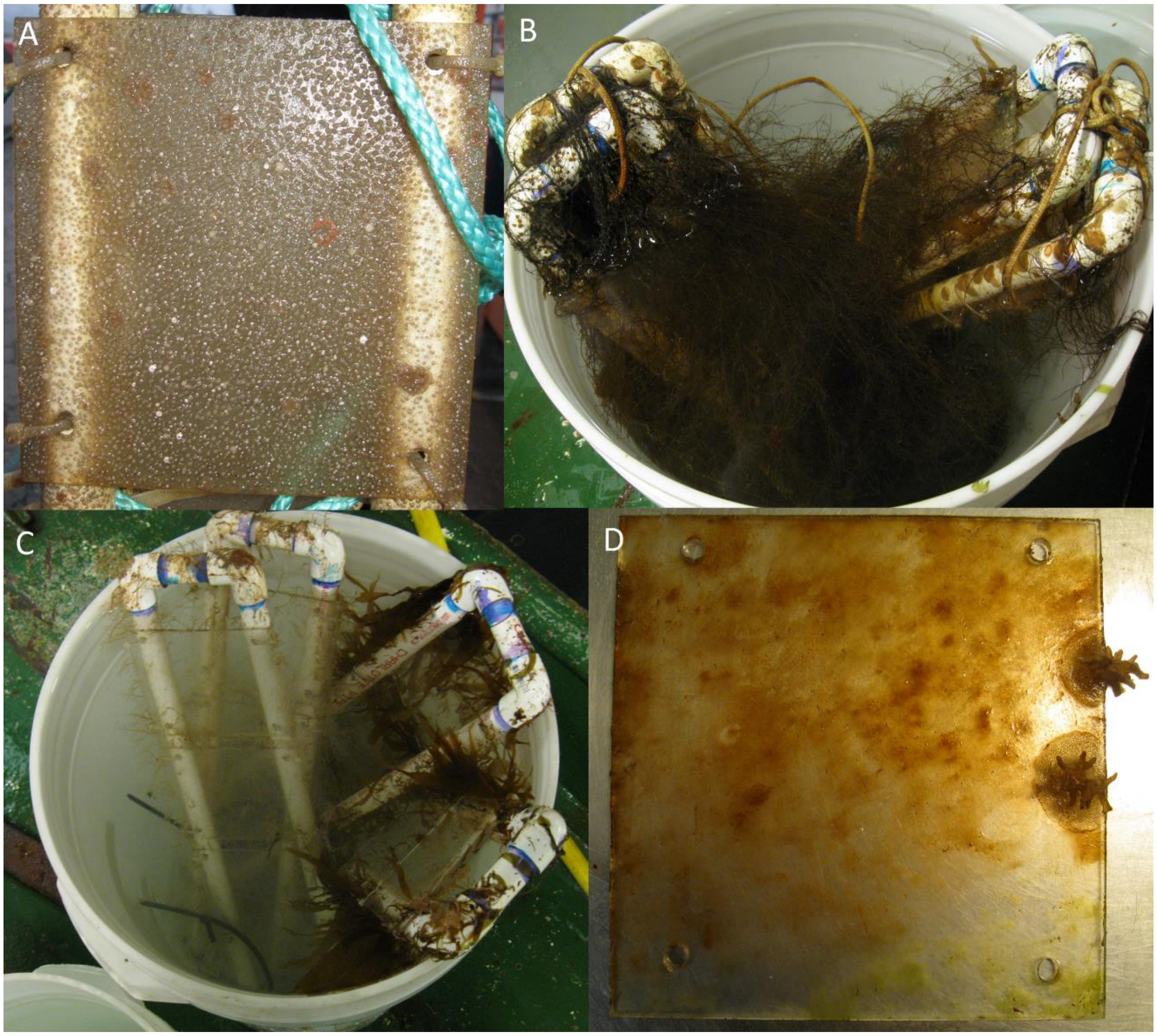

Fig. 42. Macroscopic differences between recruiting communities for selected settlement plates. A, Longyearbyen, year-long deployment, covered in barnacles, spirorbids, and encrusting bryozoans; B, Ny-Ålesund, spring-summer and year-long deployments, dominated by *Desmarestia aculeata*; C, Kongsfjorden mooring deep (215 m) and shallow (30 m) plates, dominated by *Stegopoma plicatile* and *Saccharina latissima*, respectively; D, Rijpfjorden mooring shallow (30 m) plate, with heavy brown sedimentation and two large colonies of *Alcyonidium gelatinosum*. All settlement plates are 15 x 15 cm.

There were significant multi-variate differences among the assemblages of recruits in different seasons (fall-winter, spring-summer, and year) and locations (Longyearbyen and Ny-Ålesund) (two-way crossed ANOSIM; deployment period, R = 0.837, p = 0.001; location, R = 0.905, p = 0.001; Fig. 43). Pairwise differences between

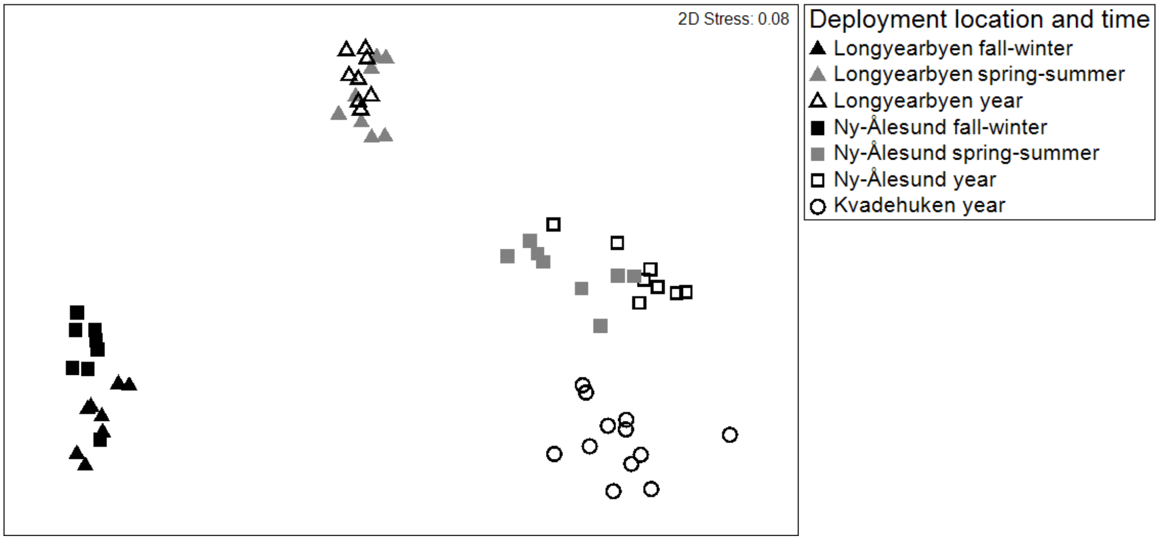

Fig. 43. Non-metric multidimensional scaling (MDS) plot showing differences in communities of recruits in different seasons and at different locations. Only shallow locations shown.

the deployment periods were strong and significant for fall-winter and spring-summer (R = 1, p = 0.001), fall-winter and year (R = 1, p = 0.001); pairwise differences between spring-summer and year-long recruitment were still significant but not as large, as indicated by the much lower R value (R = 0.521, p = 0.001). An MDS plot also shows that points belonging to spring-summer and year-long settlement plates at these locations tend to cluster near one another and far away from the fall-winter plates (Fig. 43).

A small number of species recruited to settlement plates in both fall-winter and spring-summer; these species include the bivalve *Hiatella arctica*, the bryozoans *Celleporella hyalina* and *Crisiella producta*, and the spirorbid *Circeis armoricana* (Fig. 41). The bryozoan *Callopora craticula* (Fig. 41) was abundant on fall-winter plates (Longyearbyen, 5.00 ± 1.15 plate^{-1}; Ny-Ålesund, 47.8 ± 13.3 plate^{-1}) but not observed on spring-summer or year-long settlement plates. All algal taxa recruited exclusively in the spring-summer. Other common taxa recruiting to spring-summer plates but not fall-winter plates included the barnacle *Semibalanus balanoides*, the bryozoans *Lichenopora* sp., *Tegella arctica*, *Harmaria scutulata*, *Electra arctica*, *Alcyonidium* cf. *mytili*, *Cauloramphus intermedius*, the hydroids Campanaluriidae sp. 1 and sp. 2, and the spirorbids *Paradexiospira vitrea* and *Circeis spirillum*.

Differences among shallow locations

There were obvious differences in recruitment at shallow locations, even upon macroscopic examination of the settlement plates (Fig. 42). For example, spring-summer and year-long plates from Ny-Ålesund were densely populated by long strands of *Desmarestia aculeata* (spring-summer, 285 ± 44.9; year, 659 ± 74.7 plate^{-1}), a species that was observed on settlement plates from no other location. Spring-summer and year-long plates from Longyearbyen were characterized by high numbers of encrusting bryozoans, while year-long plates from Kvadehuken were covered by small algal individuals of *Dermatocelis laminariae* (789 ± 86.9 plate^{-1}), *Chorda* sp. (32 ± 12.1 plate^{-1}), and an unidentified crustose coralline alga (61.7 ± 15.8 plate^{-1}) (Fig. 41D).

Assemblages on plates deployed in fall-winter were more similar to one another than to plates deployed at other times, as indicated by their proximity on the MDS plot (Fig. 43). There was still a significant difference, however, between the assemblages of recruits on fall-winter plates deployed at Longyearbyen and Ny-Ålesund (ANOSIM, R = 0.715, p = 0.002). There was also a significant difference between spring-summer plates at these two locations (ANOSIM, R = 1, p = 0.001).

For plates deployed at shallow sites for the entire year (Longyearbyen, Ny-Ålesund, and Kvadehuken), there was a significant difference among the assemblages at different locations (ANOSIM, R = 1, p = 0.001). Pairwise tests showed strong and significant differences between all pairs of locations (R = 1, p = 0.001 for each pair). Points belonging to settlement plates deployed for the full year formed distinct clusters for each shallow location in an MDS plot (Fig. 43).

Recruitment across depth

Significantly different assemblages of organisms recruited to settlement plates on the moorings (30 and 195 – 215 m) compared to year-long settlement plates at shallow locations. When all year-long plates were analyzed together, there were significant differences among the locations (ANOSIM, R = 0.989, p = 0.001), and all pairwise differences were significant (R = 0.931 – 1, p = 0.001 – 0.02). An MDS plot shows that points belonging to year-long plates from different locations form distinct clusters, with plates from the deep sites (195 and 215 m) clustering closest to one another, far away from the shallower sites (7 – 30 m) (Fig. 44). There was also a general gradient of the clusters, with the shallowest sites clustering in the upper right corner of the plot and 30 m mooring sites clustering further to the left (Fig. 44). Among the shallower sites (7 – 30 m), those in Kongsfjorden (Ny-Ålesund, Kvadehuken, the Kongsfjorden mooring shallow plates) clustered closer to one another than to sites in Isfjorden (Longyearbyen) or Rijpfjorden (shallow mooring plates).

Shallow settlement plates (30 m) on the Kongsfjorden mooring were characterized by dense stands of *Saccharina latissima* (237 ± 59.9 plate^{-1}) *Dermatocelis laminariae* (242 ± 51.1 plate^{-1}), and *Chorda* sp. (110 ± 23.8 plate^{-1}) (Fig. 41), while deep (215 m) settlement plates were covered by the hydroid *Stegopoma plicatile* (Fig. 41M).

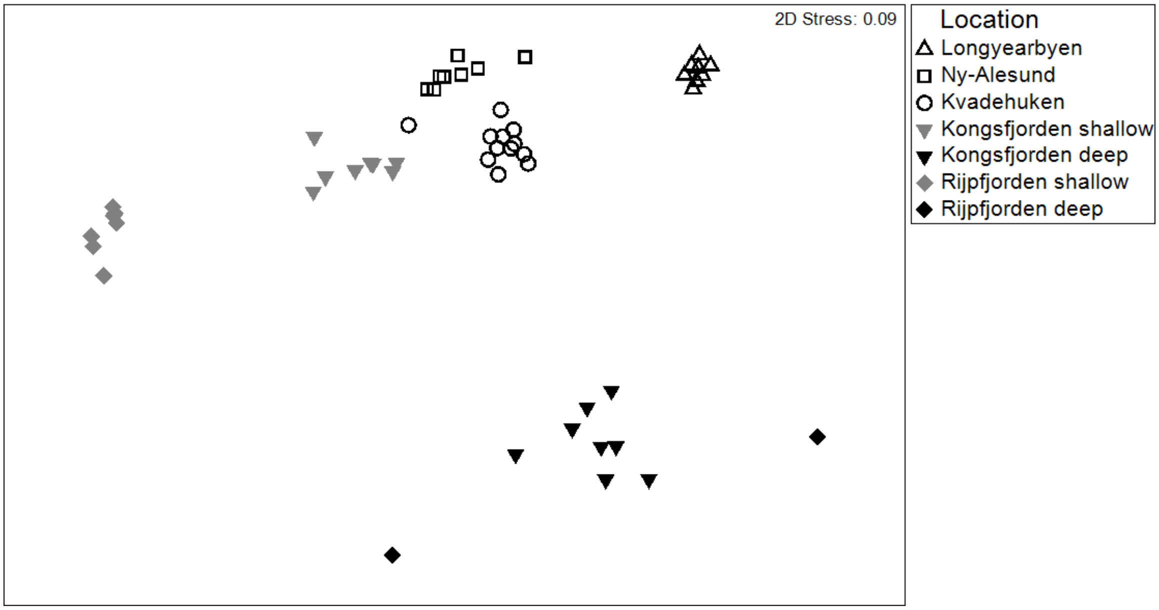

Fig. 44. MDS plot showing differences in communities recruiting to various piers and moorings in Svalbard fjords over a year. “Kongsfjorden” and “Rijpfjorden” locations are moorings.

Shallow settlement plates (30 m) from the Rijpfjorden mooring had high numbers of *Saccharina latissima* (498 ± 167 plate^{-1}) and large colonies of *Alcyonidium gelatinosum* (Fig. 42D), while the deep plates (195 m) were almost uninhabited. Only one individual each of *Circeis armoricana* and *Hiatella arctica* occurred on the 8 settlement plates from this location.

Much lower recruitment was observed at the deep mooring sites, and in fact, there was a negative exponential relationship between the number of recruiting individuals and depth ($R^2 = 0.9916$, Fig. 45A). There was also a negative exponential relationship between the number of recruiting taxa and depth ($R^2 = 0.7648$, Fig. 45B).

Algal species were largely absent from the deeper sites, though single individuals of *Saccharina latissima*, *Dermatocelis laminariae*, and the crustose coralline alga (Fig. 41) were observed on plates from 215 m on the Kongsfjorden mooring. *Saccharina*

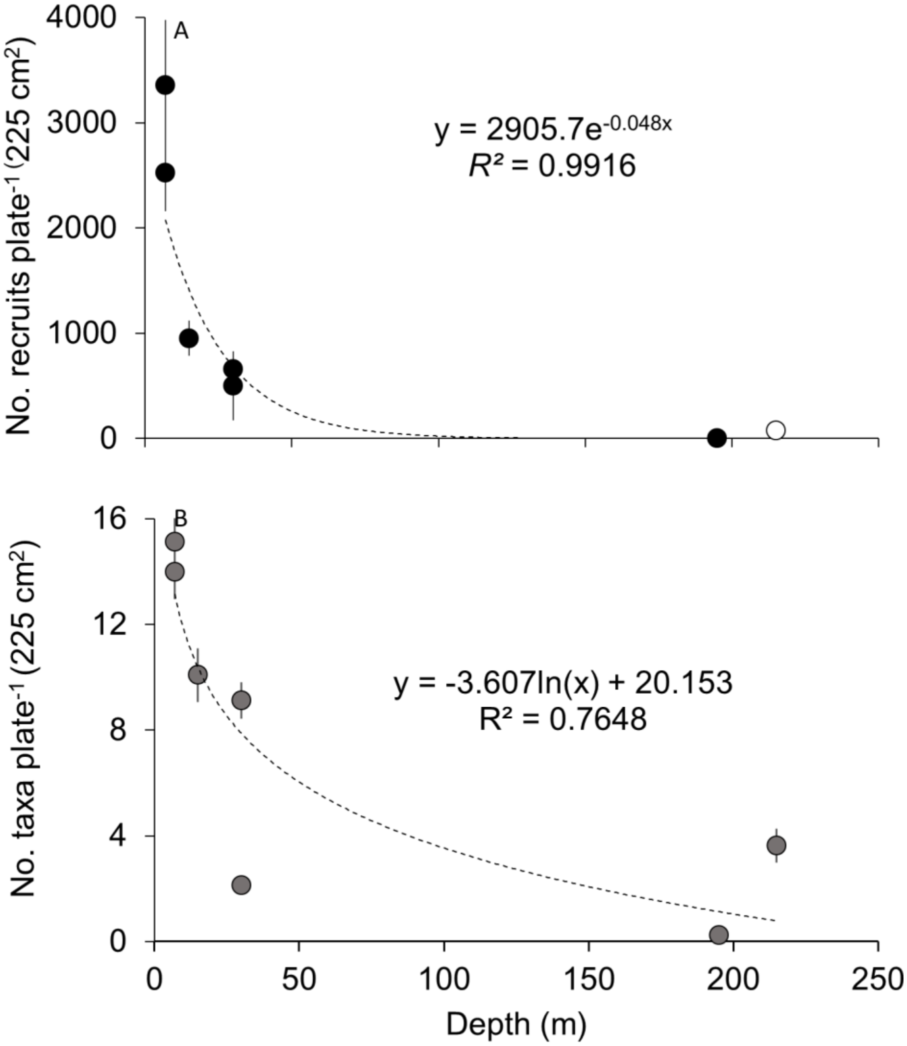

Fig. 45. A, number of individuals; B, number of taxa recruiting to settlement plates over a year-long deployment at various depths in Svalbard fjords. White point indicates settlement plates deployed at 215 m on the Kongsfjorden mooring, which were not included in the exponential trendline. On these plates, upright forms of the hydroid *Stegopoma plicatile* were counted as a relative proxy for recruitment of this species. Error bars show 95% confidence intervals.

latissima recruited in high numbers to the shallow plates (30 m) on both the Kongsfjorden (237 ± 59.9 plate^{-1}) and Rijpfjorden moorings (498 ± 167 plate^{-1}). Other algal species present on the 30 m settlement plates included *Dermatocelis laminariae, Ulothrix implexa*, *Alaria esculenta*, *Halosiphon* sp., and the crustose coralline alga in Kongsfjorden and *Chorda* sp. in both fjords.

Non-random species distribution patterns

Species distribution patterns on pseudoreplicate settlement plates were not significantly different from the distribution generated by a fixed-fixed null model ($C > e$ and $C < e$, $p > 0.05$). Species on settlement plates co-occurred randomly.

DISCUSSION

Seasonality of recruits

The faunal and floral compositions of spring-summer and year-long settlement plates were similar, so the significant differences between the assemblages are due to the relative abundances of species. Recruitment is often patchy both in space and in time (Siegel et al. 2008), so dense recruitment events may have influenced the composition of the recruiting communities. Settlement plates can also be influenced over temporal scales by variation in the amount of biofilm (Keough and Raimondi 1996), facilitation by species already on the plates (Keough 1998), or predation pressure on recruits (Bowden et al. 2006) and larvae (Stanwell-Smith and Barnes 1997). The higher taxonomic richness but lower abundance on year-long plates at Ny-Ålesund compared to spring-summer plates could indicate that some recruits were overgrown or consumed throughout the course of the year. Overgrowth competition was observed on the settlement plates, with *Semibalanus balanoides* being overgrown by several bryozoans (*Tegella arctica*, *Cribrillina annulata*, *Harmeria scutulata*, and *Cauloramphus intermedius*) and *Circeis armoricana* being overgrown by *Umbonula arctica* (Fig. 46). Competitive hierarchies are stronger in polar habitats than at lower latitude (Barnes 2002, Barnes and Kukliński 2003).

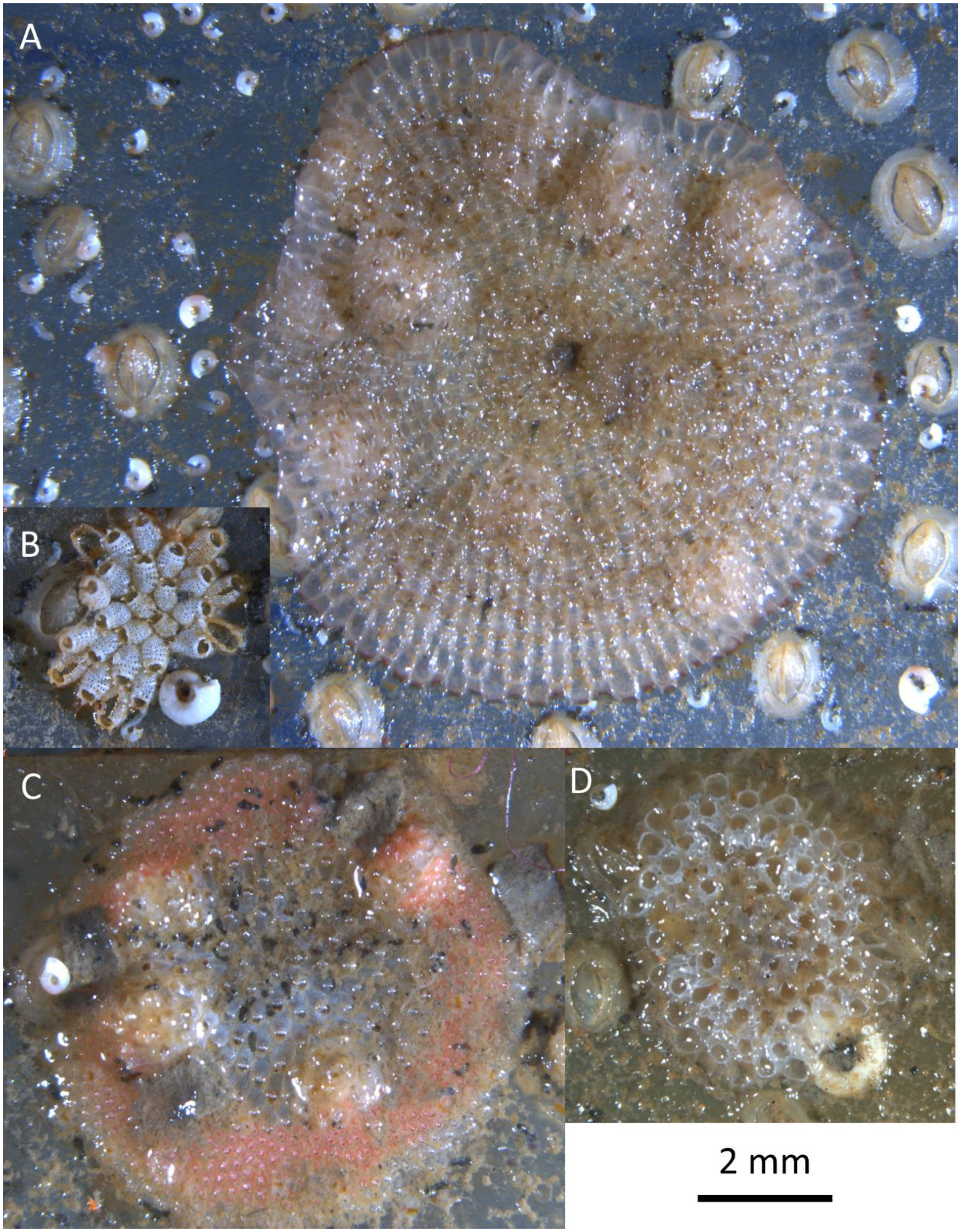

Fig. 46. Examples of *Semibalanus balanoides* and *Circeis armoricana* being overgrown by bryozoans on settlement plates. A, *Tegella arctica*; B, *Cribrilina annulata*; C, *Harmeria scutulata*; D, *Umbonula arctica*.

Callopora craticula recruited in high numbers in fall-winter but not spring-summer and was never found on settlement plates deployed all year. This species' absence from year-long plates indicates it may have been consumed or overgrown by spring-summer recruits. Many more species recruited in spring-summer than in fall-winter, and the fauna and flora on year-long settlement plates were more similar to spring-summer plates, indicating that spring-summer recruitment dominates hard-bottom communities in Svalbard. Kukliński et al. (2013a) hypothesized that species recruiting in the winter did so in order to avoid competition with other recruiting species in the spring. Winter-recruiting polar species may be efficient suspension feeders at low food concentrations and gain nutrition from nanoplankton (Barnes and Clarke 1995, Bowden 2005). This would allow growth when food availability is low, and perhaps increase their ability to compete with later-arriving taxa. However, our results suggest that this advantage may be minimal, as spring settlers were superior competitors when food abundance was higher despite a possible initial disadvantage.

Differences in recruitment among fjords

The communities of recruits at the two shallowest locations, Longyearbyen and Ny-Ålesund, were significantly different for every deployment period (fall-winter, spring-summer, and all-year), despite apparent similarities between the two deployment locations. Both are located in Atlantic-influenced fjords (Isfjorden and Kongsfjorden, respectively) and adjacent to populated areas. Both deployment locations were on underwater structures associated with docks. Water temperatures at the two locations were almost identical over the course of the year-long deployment, but nevertheless, recruiting communities were significantly different. Multiple species of macroalgae, including *Desmarestia aculeata*, *Dermatocelis laminariae*, and *Chorda sp.*, recruited in high densities at Ny-Ålesund, but algal species were never observed on settlement plates from Longyearbyen. The deployment location at Ny- Ålesund is surrounded by dense macroalgae, but no macroalgae is present near the deployment location at Longyearbyen. It is therefore likely that local species composition, larval/spore availability, and local circulation patterns strongly influenced recruitment.

Local species composition likely influenced recruitment at Kvadehuken, as demonstrated by the abundance of crustose coralline algal recruits. This morphotype was found only at Kvadehuken and on the 30 m Kongsfjorden mooring plates. The anemone *Urticina eques,* which is a common species at Kvadehuken, also only recruited to plates at this site (Beuchel and Gulliksen 2008, Laudien and Orchard 2012).

One of the most striking differences between sets of settlement plates was for the 30 m mooring stations in Kongsfjorden and Rijpfjorden. The Rijpfjorden plates were dominated by numerous small recruits of *Saccharina latissima* and large colonies of *Alcyonidium gelatinosum*, whereas the Kongsfjorden 30 m plates had *S. latissima* and *A. gelatinosum,* but also a diverse community of macroalgae and invertebrates. The *S. latissima* blades in the two fjords were of vastly different size: in Kongsfjorden, the algal blades were several centimeters long, whereas the *S. latissima* recruits in Rijpfjorden could only be seen under a dissecting microscope (K. Meyer pers. obs., Fig. 42C,D). It is possible that later ice break-up or lower water temperature in Rijpfjorden meant that *S. latissima* individuals settled later in the year or did not grow as quickly in this fjord.

The low recruitment in Rijpfjorden contrasts starkly with the high diversity of the benthic adults. Underwater photography revealed a diverse soft-bottom community in outer Rijpfjorden, along with occasional stones inhabited by encrusting fauna (Chapter V). Hard-bottom species are clearly able to recruit near the location of the mooring or at least have done so in the past, but nevertheless, only two individuals recruited to a total of eight settlement plates deployed at 195 m in Rijpfjorden. It has been shown that reproductive and recruitment success in polar invertebrates depend on temperature *per se* (Hoegh-Guldberg and Pearse 1995) or on food availability (Vace 1973, Clarke 1982), but unfortunately, these two factors are often correlated and difficult to separate (i.e., Brey and Hain 1992). The plates themselves were also quite clean, without even a noticeable biofilm (K. Meyer, pers. obs.). Perhaps the low temperature and productivity in Rijpfjorden mean that a biofilm takes longer to form than in other fjords. Biofilms are an indicator that a substratum has been underwater for a period of time and is stable; thus they serve as settlement cues for many encrusting organisms (Hadfield 2011). The two individuals that did recruit to deep Rijpfjorden plates, *Circeis armoricana* and *Hiatella arctica*, are both calcareous, typically early-succession species, which do not require a thick biofilm for settlement (Keough and Raimondi 1996).

Glacial sedimentation is much lower in Rijpfjorden than in Atlantic-influenced fjords, so benthic organisms are less likely to be smothered or have their feeding impeded by sedimentation (Włodarska-Kowalczuk et al. 2005, Chapter V). Once hard-bottom fauna have successfully recruited, it may take longer for them to die and create space for other organisms. Our results show lower recruitment in Rijpfjorden than Kongsfjorden, but further studies are required to determine exactly what mechanisms lead to this difference.

Recruitment across depth

Our data revealed an exponential decline in both the number and richness of recruits with increasing depth (Fig. 45). Water temperature was colder at greater depth in the summer months in Kongsfjorden and Rijpfjorden, so this may explain the lower recruitment. Sites at greater depth are also sheltered from wind-driven mixing (Cottier et al. 2010), so there may be less circulation at greater depth (Svendsen et al. 2002). Reduced circulation or slower bottom current at greater depth may mean there is less food supply for suspension feeders (Laudien and Orchard 2012), which many of the recruiting species were.

Deep (215 m) settlement plates deployed in Kongsfjorden were dominated by *Stegopoma plicatile*, which is a common deep-water hydrozoan (Vervoort 1966, Edwards 1973). In fact, it has been found on the west Svalbard continental shelf and slope down to 1300 m in the Fram Strait (Bergmann et al. 2011b, Meyer et al. 2013). Hydrozoans are commonly the first recruits to substrata in deep water. They are poor competitors and are easily overgrown (Ronowicz et al. 2008). The dominance of *S. plicatile* on the 215 m Kongsfjorden settlement plates implies that these plates were at an early stage of succession.

Life-history traits of recruits and their roles in succession

Recruitment is the first step in succession. While succession on hard substrata is poorly understood for the high Arctic, the process is well-described for temperate latitude. According to the tolerance model of succession (Connell and Slatyer 1977), pioneer species are fast-growing, poor-competitive species that quickly senesce or are overgrown by slower-growing superior competitors, the late-succession species. The tolerance model is a good fit for some cases of hard-bottom succession at temperate latitude (Edwards and Stachowicz 2010), though there is also an element of stochasticity in recruitment (Sutherland 1974). We thus hypothesized that the recruits to settlement plates in Svalbard waters would be fast-growing, poor-competitive pioneer species.

The spirorbid polychaete *Circeis armoricana* was ubiquitous, recruiting to settlement plates at all depths and in all seasons. Populations of *C. armoricana* have been observed to undergo continuous reproduction and recruitment, with more individuals reproducing in the spring (Ivin 1997), and our results corroborate this previously-documented pattern. In fact, *C. armoricana* and *Semibalanus balanoides* were dominant recruiting species at all shallow stations during spring-summer and year-long deployments. At temperate latitudes, acorn barnacles and spirorbid polychaetes are often the first recruits to settlement plates, and these taxa characterize the first stage in succession on hard substrata (Osman 1977, Dean and Hurd 1980). The presence of calcareous invertebrates has been shown to facilitate the recruitment of mid- and late-succession taxa, particularly ascidians (Osman and Whitlatch 1995a,b). Calcareous polychaetes (along with bryozoans) were also the dominant recruiting taxon on shortterm settlement plates in the Antarctic (Stanwell-Smith and Barnes 1997, Bowden 2005, Bowden et al. 2006).

The bryozoans *Harmeria scutulata* and *Celleporella hyalina* were present in high abundance on both spring-summer and year-long settlement plates. *Harmeria scutulata* is an opportunistic, annual species, and is one of the fastest-growing Arctic bryozoans (Kukliński and Taylor 2006). It also loses ~70% of its interspecific competitive interactions (Barnes and Kukliński 2003). *Celleporella hyalina* is also a poor competitor, winning < 15% of interspecific interactions (Barnes and Kukliński 2003). In the Spitsbergen intertidal, where ice scour disturbance is common and boulder communities are kept in an almost constant state of primary succession, *H. scutulata* and *S. balanoides* are the most common species (Kukliński and Barnes 2008). Certainly the most common taxa observed on settlement plates – *C. armoricana, S. balanoides, H. scutulata, C. hyalina* – can be characterized as early-succession species.

The bryozoan *Alcyonidium gelatinosum* occurred in large colonies at 30 m on Kongsfjorden and Rijpfjorden moorings, suggesting that this species recruited to the plates relatively early in the deployment period, in the fall or winter. At lower latitude, *A. gelatinosum* has been observed to have low fecundity and large, brooded embryos and to recruit in winter (Ryland and Porter 2003). This species may be a good example of an inferior competitor that recruits in the winter in order to escape competition with species that recruit in spring (Kukliński et al. 2013a). It grows quickly, according to the observed colony sizes in this study, and is highly susceptible to predation, even stimulating feeding by amphipod predators (Lippert et al. 2004). Though the colonies are large enough to be observed without magnification, *A. gelatinosum* was not observed in photographic or suction-sampling surveys on Kongsfjorden hard-bottom habitats (Jørgensen and Gulliksen 2001, Beuchel et al. 2006, Beuchel and Gulliksen 2008, Laudien and Orchard 2012), possibly indicating that any recruiting colonies have been consumed or overgrown in these mature communities. *A. gelatinosum* is most abundant when and where faunal richness is low (and therefore competition and predation are also low), such as the 30 m settlement plates in this study and the heavily-sedimented inner part of Kongsfjorden (Kukliński et al. 2005). As a fast-growing inferior competitor that is readily consumed, *A. gelatinosum* has the characteristics typical of an early-succession species.

One well-known superior competitor, a crustose coralline alga (Fig. 41D; unfortunately, no further identification could be made) also recruited in high abundance to settlement plates at Kvadehuken. However, recruits of this pink encrusting morphotype were very small, often barely visible on the settlement plates, even with magnification (K. Meyer, pers. obs.). Crustose coralline algae are known to grow very slowly and win all interspecific competitive interactions (Kukliński 2009). This morphotype thus has the life history characteristics of a late-successional species according to the tolerance model (Connell and Slatyer 1977, Edwards and Stachowicz 2010), though it recruits to settlement plates in high numbers at both poles (Bowden et al. 2006). The seafloor at Kvadehuken is dominated by crustose coralline algae, so we expect that in time, the recruits to the Kvadehuken settlement plates would similarly outcompete other encrusting species and cover the plates at this station. Coralline algae increased in percent cover over time and was much more prominent on settlement plates exposed for three years at Kvadehuken than on plates exposed for one or two years (Schmiing 2005).

Tegella arctica, another superior competitor, was present on settlement plates deployed in spring-summer and all year at shallow locations (Longyearbyen, Ny-Ålesund, Kvadehuken). However, this species recruited only in small numbers and did not dominate the settlement plates. In a study of bryozoan growth rates, Kukliński et al. (2013b) found that *T. arctica* grew faster than other Arctic bryozoans but that no differences were observed until the second year of growth. Given sufficient time, *T. arctica* may outcompete and outgrow other bryozoans on the settlement plates.

Taxa conspicuously absent from our shallow settlement plates included ascidians and sponges. Encrusting species of both taxa, notably *Didemnum albinum* and *Halichondria* sp., are present at Kvadehuken (Jørgensen and Gulliksen 2001, Beuchel and Gulliksen 2008, Laudien and Orchard 2012), but none recruited to the settlement plates there or at any other station. Both ascidians and sponges are superior competitors in Arctic waters (Barnes and Kukliński 2004, Konar and Iken 2005) and are characteristic late-succession species at temperate latitude (Osman and Whitlatch 1995a, Edwards and Stachowicz 2010). Encrusting sponges and solitary ascidians have recruited to settlement plates in Antarctica (Bowden 2005, Bowden et al. 2006), but at temperate latitude, these species tend to recruit to substrata with already-established fauna (Osman and Whitlatch 1995b). *Urticina eques* and *Hormathia nodosa* are abundant and dominant anemones at the Kvadehuken site, but only a single individual of *U. eques* was observed on a settlement plate at Kvadehuken. This species is known to live over 40 years (Beuchel and Gulliksen 2008) and is well-defended against predators in the field (Lippert et al. 2004), so it is likely a late-succession or climax-community species.

To summarize, the settlement plates deployed for one year in shallow water were dominated by fast-growing, inferior-competitor species. Slower-growing superior competitors were present but not dominant. With time, the superior competitors would likely come to dominate, as is observed at temperate latitude (Edwards and Stachowicz 2010).

Non-random species distribution patterns

Our results showed only random species co-occurrence patterns on the settlement plates. Meyer et al. (Chapter IV) found evidence of non-random co-occurrence of encrusting fauna on dropstones in the Fram Strait, west of Svalbard, but also never observed overgrowth competition among dropstone morphotypes. In this study, by contrast, we found no evidence of non-random co-occurrence of taxa, but overgrowth competition *was* observed on the settlement plates (Fig. 46). Therefore, our results, when combined with those of Meyer et al. (Chapter IV), demonstrate that there is not necessarily a link between interspecific competition and non-random co-occurrence for hard-bottom marine fauna at high latitude, as has been traditionally assumed for terrestrial fauna (Diamond 1975a). If our results can be generalized to other environments, non-random co-occurrence where found may be the result of another factor. Even stochastic faunal distributions can lead to apparently non-random co-occurrence (Ulrich 2004). For dropstones, some taxa were found to co-occur *more* often than expected by chance as a result of epibiontism (Chapter IV).

CONCLUSIONS

Recruitment of hard-bottom fauna in Svalbard fjords is highly site-specific and is significantly different even among sites in the same fjord. Lower recruitment was observed in fall-winter than in spring-summer, and taxa recruiting in fall-winter may do so to gain a competitive advantage over spring recruits. Lower recruitment also occurred in an Arctic-influenced fjord compared to Atlantic-influenced fjords and could be the result of lower temperature and/or productivity. An exponential decline in recruitment with greater depth can be explained by lower temperature, circulation, and/or particulate food supply at these locations. Recruiting taxa were generally early-succession fauna, characterized by fast growth and poor competitive ability. Overgrowth competition was observed, but there recruiting taxa co-occurred randomly, indicating there is not a relationship between these two concepts for the isolated hard substrata in this study. The results presented here are difficult to interpret mechanistically and suggest a need for long-term studies involving microscopic examination of settlement plates in order to better understand community assembly of hard-bottom fauna in the high Arctic.

CHAPTER VII

GENERAL CONCLUSIONS

ISLAND BIOGEOGRAPHY AS A FRAMEWORK

Isolated hard substrata on the seafloor constitute island-like habitats. They are inhabited by hard-bottom fauna not otherwise found on the soft sediment, and in many cases, they have the same species distribution patterns as terrestrial islands. However, while the patterns on terrestrial islands and marine island-like habitats may be similar, the mechanisms leading to these patterns are not necessarily the same.

The five species distribution patterns common on terrestrial islands defined in Chapter II are: (1) a log-linear relationship between species richness and island size, (2) higher species richness on islands closer to a mainland, (3) "incidence functions," or different assemblages of organisms inhabiting islands of different size, (4) nestedness, or ever-smaller or ever-more-isolated islands being inhabited by ever-smaller sub-sets of fauna (Fig. 2A), and (5) non-random co-occurrence, or pairs of species being found together more or less often than expected by random chance.

SUBTIDAL AND DEEP-SEA HABITATS AS ISLANDS

Species-area relationship and island size

A log-linear relationship between species richness and island size was observed for both shipwrecks (Chapter III) and dropstones (Chapter IV). This ubiquitous pattern has been attributed to a variety of mechanisms on terrestrial islands, but for marine island-like substrata, very simple mechanisms may be responsible (Abele and Patton

1976, Schoener and Schoener 1981, Huntington and Lirman 2012). Larger substrata are also exposed to faster bottom current in the benthic boundary layer and may have greater larval supply and particulate food supply for suspension feeders. Larger substrata have more surface area and can be inhabited by more species as that area is filled. This was demonstrated on shipwrecks, because smaller shipwrecks were heavily dominated by one or two species, while larger shipwrecks had more even communities and higher species richness. When left untransformed, the log-linear relationship of species richness to substratum area is asymptotic, indicating that the traditional, ubiquitous relationship may be due to nothing more than the finite nature of the species pool.

Degree of isolation

Higher species richness on islands closer to a mainland was apparent on dropstones, as higher numbers of morphotypes and higher numbers of individuals occurred on stones nearer to a deepwater rocky reef. This pattern may be the result of increased larval supply from the rocky reef. For both dropstones and shipwrecks, substrata closer to one another had more similar communities. Again, larval supply may be the responsible mechanism, because larvae may easily disperse among substrata in close proximity to one another, leading the communities to converge over time. Many hard-bottom species have restricted dispersal (< 1 km), which helps ensure that larvae will find a suitable substratum for settlement (Grantham et al. 2003).

Incidence functions

Incidence functions were not found for shipwrecks or dropstones. There was a greater degree of similarity among the biological communities on shipwrecks of similar size, which could be interpreted as evidence for incidence functions, but there are two more likely explanations. The smallest wrecks were located closest to one another on the seafloor, so the convergence in their communities could be the result of larval dispersal among close wrecks. In addition, the largest wrecks were inhabited by up to two-thirds of the available taxa. Such large sub-sets of the morphotype pool are bound to converge because the majority of available taxa are present.

The lack of evidence for incidence functions on isolated hard substrata in this dissertation is particularly interesting when compared to species distribution patterns on stones at shallower depth. Small stones in the intertidal and shallow subtidal are often overturned by waves. Such frequent disturbance means these stones are only inhabited by opportunistic pioneer species (Sousa 1979). On larger stones, where disturbance is less frequent, opportunistic taxa are overgrown by superior competitors, which dominate the rock surface (Sousa 1979). Shallow subtidal and intertidal stones thus show evidence for incidence functions, with different assemblages of species inhabiting stones of different size. The island-like substrata in this dissertation were located at great enough depth to not experience wave disturbance, and incidence functions were not found.

Nestedness

Nestedness was never found for marine island-like substrata in this dissertation. For terrestrial habitats, nestedness is the result of only opportunistic species being able to live on small islands or in small habitat islands (Diamond 1975b, Tjørve 2010). However, on the marine island-like substrata in this dissertation, small substrata were not inhabited by only opportunistic species. Nestedness could be found for other marine island-like habitats (seamounts, hydrothermal vents) that are currently under consideration for protection. If nested patterns of fauna are found, then the implications for natural reserve design (i.e., larger reserves conserve more species) should be borne in mind.

Non-random co-occurrence

Non-random co-occurrence was observed on one of the island-like substrata in this dissertation (dropstones) but not on shipwrecks or settlement plates in Svalbard fjords. For dropstones, some species pairs had negative non-random co-occurrence, even though interspecific overgrowth competition was not observed. On settlement plates, species co-occurred randomly, even though interspecific overgrowth competition was observed. These results, when considered together, show that there is not necessarily a relationship between interspecific competition and non-random co-occurrence for marine island-like substrata, such as has been traditionally assumed for terrestrial islands (Diamond 1975a).

Rather than interspecific competition, morphotypes on dropstones may non-randomly co-occur because of restricted larval dispersal. Dropstone fauna had a clumped distribution, and if short-duration larvae of dropstone species are only able to disperse within a restricted area, this may prevent morphotypes from having randomly-overlapping distributions.

The main difference between dropstones, on which species co-occurred non-randomly, and shipwrecks, on which species co-occurred randomly, is the size and complexity of the substrata. Dropstones in this dissertation were small enough to be observed in a single benthic photograph (3 – 4 m^2), whereas shipwrecks were much larger substrata (45 – 301 m long, standing 2 – 18 m off of the seafloor). Dropstones were only inhabited by a maximum of 46% of the available morphotypes, while the largest shipwreck had 67% of the available morphotypes. Larger substrata may have only random co-occurrence because they can be inhabited by most of the available species pool. The Senke rocky reef, a large hard-substratum habitat adjacent to the dropstone study sites, also has only random co-occurrence of species.

PROCESSES UNDERLYING THESE PATTERNS

Larval dispersal

The fauna inhabiting shipwrecks (Chapter III) had two modes of larval dispersal. Most encrusting, colonial species had short-duration lecithotrophic larvae but were capable of asexual reproduction by fission as adults, while most solitary or mobile invertebrates had long-duration planktotrophic larvae. Planktotrophic larvae may have dispersed to the shipwrecks from far away. For the encrusting, colonial species, it would be more difficult for a short-duration lecithotrophic larva to reach a shipwreck from far away, but once established on a shipwreck, a small number of individuals could build up a dense population through philopatry (recruitment of larvae back to the natal substratum) and asexual budding as adults.

More research is required to understand the larval dispersal mechanisms and developmental modes of dropstone fauna. However, the overdispersed distribution of dropstone morphotypes and their identity as encrusting, colonial species suggest that dropstone fauna may have short-lived larvae and be capable of asexual budding as adults.

Succession

Recruitment can be considered the first step in succession one of the first steps in community assembly (defined in Chapter II). Recruitment in Svalbard fjords varied significantly among fjords. Fewer recruits were present in fall-winter than in spring-summer, and in cold Rijpfjorden than in warmer Atlantic-influenced fjords (Chapter VI). Rijpfjorden has a diverse megabenthic community, however, including encrusting sponges on isolated stones (Chapter V). Community assembly in this cold, Arctic-influenced fjord may be a slower process. There is lower recruitment, and adult organisms may have greater longevity because they are less likely to be smothered by glacial sedimentation.

There is a well-described shift in the life-history traits of fauna on isolated hard substrata at temperate and tropical latitude, with fast-growing, poor-competitive species dominating the community early in succession but slow-growing superior competitors dominating later in succession (Edwards and Stachowicz 2010; Perkol-Finkel et al. 2005, 2006). Recruits on settlement plates in Svalbard were also generally fast-growing, poor-competitive taxa, such as *Semibalanus balanoides*, *Circeis armoricana*, *Hiatella arctica*, and *Harmeria scutulata* (Chapter VI). Two notable superior competitors were present on the settlement plates, crustose coralline algae and the bryozoan *Tegella arctica*. These taxa may have come to dominate the plates if they were left submerged for longer (i.e., multiple years).

Communities on shipwrecks can be described as being in a stage of mid-succession. The opportunistic calcareous species typical of early succession at temperate latitude (acorn barnacles and spirorbid polychaetes) were not present on the shipwrecks; rather, a diverse community of hydroids, anemones, and sponges (the second stage in temperate-latitude succession, Dean and Hurd 1980) was observed (Chapter III). Shipwrecks at shallower depth were dominated by slow-growing, superior-competitor species and resembled natural reef communities after 100 years underwater (Perkol-Finkel et al. 2005), so the shipwrecks in the present dissertation, underwater for 88 – 91 years, may be undergoing succession at a slower rate than similar shallower substrata. Recruitment is much lower at greater depth (Chapter VI). Slower bottom current may mean there is less particulate food for suspension-feeding species and restricted larval supply at greater depth. Community assembly may be a slower process at greater depth because of these factors.

Competition

The results in Chapters IV and VI of this dissertation show that there is not necessarily a relationship between interspecific competition and non-random co-occurrence for island-like marine hard substrata. Rather, positive non-random co-occurrence on dropstones was the result of epibiontism, as several suspension-feeding species elevated themselves in the benthic boundary layer by settling or resting on top of sponges. It is still an open question how and under what circumstances suspension-feeders may compete for food (Chapter II). A better understanding of facilitative biotic interactions will improve ecological theory (Bruno et al. 2003).

A DIRECTION FORWARD

The analyses presented in this dissertation were largely observational and correlative. A more complete understanding of island-like marine habitats could be gained through experimentation to determine what mechanisms cause the observed species distribution patterns. For example, the higher species richness found on larger dropstones is likely the result of greater particulate food supply higher in the benthic boundary layer but could also be due to a greater number of microhabitats (areas with different current regimes and/or stone textures) on larger stones. Much more information about the life-histories of dropstone species and bottom current regimes in the Fram Strait is needed for a complete understanding of larval dispersal among dropstones and the adjacent rocky reef. Experimental manipulation is also required to understand the mechanisms of succession (tolerance, facilitation, or inhibition, Connell and Slatyer 1977) on isolated hard substrata. This dissertation bridges two parallel traditions – terrestrial and marine ecology – and is an important step in understanding community assembly on island-like marine hard substrata.

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