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Colonization of benthic invertebrates in a submarine canyon in the NW Atlantic

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ABSTRACT: The paucity of data on colonization of benthic invertebrates in the deep sea can severely inhibit our ability to predict the potential for recovery of these vulnerable ecosystems from anthropogenic disturbances, such as deep sea mining and trawling. In this study, we measured abundance and family richness of benthic invertebrate colonists on 2 types of substrates with the same planar area, but different levels of structural complexity, at 3 locations (655, 662 and 883 m depth) in the Middle Canyon of the Northeast Channel Coral Conservation Area, NW Atlantic, over 4 yr. The complex substrate allowed colonization in the third dimension, while the simpler substrate allowed colonization in only 2 dimensions. Anthozoan and bivalve colonists were present at a higher frequency on simple substrates, and maxillopods, nematodes, gastropods and ostracods on complex ones. Abundance of colonists varied among locations, but not consistently for all taxa and substrate types. Family richness of the colonizing assemblages was greater on complex than on simple substrates and also varied among locations in the canyon. Colonization on simple substrates was low and similar to those few values previously recorded in deep-sea, non-chemosynthetic habitats. Colonization on complex substrates was higher, in some cases by an order of magnitude, and similar to other studies that have used complex substrates. Overall, the low rates of colonization in the deep sea indicate the vulnerability of these ecosystems to anthropogenic disturbances.

KEY WORDS: Colonization rate · Family richness · Submarine canyon · Marine benthic invertebrates · Northeast Channel Coral Conservation Area

INTRODUCTION

For sessile marine benthic invertebrates, successful recruitment depends on the combination of larval supply to a population, larval selection of suitable substrate, larval attachment and metamorphosis, and post-settlement survival from predation, competition and food limitation. The processes that regulate recruitment and the important role of patterns of recruitment in shaping adult communities are well understood for shallow temperate marine habitats (Connell 1985, Caley et al. 1996, Pawlik 1992, Olafsson et al. 1994, Hunt & Scheibling 1997). In the deep sea, rates of settlement and recruitment are often impossible to differentiate because of the necessarily long sampling intervals. Additionally, many of the studies have measured recruitment onto newly created habitats (e.g. basalt blocks, trays of azoic sediment) rather than into existing assemblages. For these reasons, the term colonization is often used instead of recruitment in studies on the deep sea; we follow this convention in our study. Much less is known about colonization in the deep sea than in shallow water habitats, and most of our understanding is based on chemosynthetic habitats, such as hydrothermal vents and cold seeps (Metaxas & Kelly 2010).

From the limited studies in non-chemosynthetic environments of the deep sea, measured rates of colonization are slow (on the order of <10 to tens of individuals per 100 cm^2 yr^{-1}), particularly compared to

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shallow water systems (Grassle 1977, Grassle & Morse-Porteous 1987, Smith & Hessler 1987, Mullineaux & Butman 1990, Snelgrove et al. 1994, Levin & DiBacco 1995, Bertram & Cowen, 1999, Beaulieu 2001). However, high colonization rates have been measured in chemosynthetic habitats, such as hydrothermal vents (Mullineaux et al. 1998, 2003, Kelly et al. 2007), cold-seeps (Levin et al. 2006) and organic falls (Smith & Baco 2003). High colonization rates, particularly in relation to the surrounding community, have also been measured on experimentally enriched food patches on soft sediments (Snelgrove et al. 1994). The increased colonization in chemosynthetic ecosystems is thought to be in part related to locally increased carbon production and associated enhanced biomass (Metaxas & Kelly 2010). Low rates imply slow population colonization or recovery and high vulnerability to perturbations (Smith & Hessler 1987). Given the paucity of data on colonization in the deep sea, the factors that regulate it are also poorly known, although some evidence suggests that predation may be important (Grassle & Morse-Porteous 1987, Micheli et al. 2002).

Habitat complexity can enhance rates of colonization by increasing food supply (Hull 1997), providing shelter from predation (Menge et al. 1985), and facilitating colonization of associated species by increasing the surface available for settlement (Eckman, 1987) or enhancing propagule retention (Bologna & Heck 1999). Habitat complexity (or heterogeneity) has also been associated with increased species richness and diversity (Huston 1979, Boström & Bonsdorff 2000, Eriksson et al. 2006, Freestone & Osman 2011). In non-chemosynthetic habitats in the deep sea, enhanced biodiversity has been related to increased habitat heterogeneity, including biogenic structures such as deep-water corals and sponges (Levin et al. 2001, Levin & Dayton 2009, McClain & Barry 2010, Vanreusel et al. 2010). At hydrothermal vents, Kelly & Metaxas (2008) recorded increased diversity of the colonizing assemblages on complex relative to simple artificial substrates.

Submarine canyons occur throughout the world's continental margins (De Leo et al. 2010, Harris & Whiteway 2011). Their presence increases regional topographic heterogeneity and the canyons act as conduits for transport and accumulation of primary production to the deep sea (Levin & Sibuet 2012, Leduc et al. 2014). As a consequence of the increased food supply relative to adjacent slope habitats, enhanced faunal biomass and, in some cases, diversity have been recorded in canyons, particularly in organically enriched regions (Vetter & Dayton 1998, Vetter et al. 2010, Cunha et al. 2011, Leduc et al. 2014). While many studies have suggested that the increased food supply in canyons can lead to increased colonization (e.g. Vetter et al. 2010, Cunha et al. 2011), measures of colonization of benthic invertebrates in deep-water canyons are lacking.

In this study, we measured abundance and family richness of the colonizing assemblage in the Northeast Channel (NEC), a submarine canyon in the NW Atlantic. The NEC harbours the densest known deep-water coral assemblages in Atlantic Canada (Mortensen et al. 2001, Mortensen & Buhl Mortensen 2004, Gass & Willison 2005, Bryan & Metaxas 2006). In 2002, the canyon was partially closed to fishing following designation of the Northeast Channel Coral Conservation Area (NECCCA) by Fisheries and Oceans Canada. Prior to 2002, different fisheries (e.g. groundfish, lobster and crab), including trawling and long lining, had been active in the NEC, and some of these continue in the western- and eastern-most portions of the channel outside the conservation area (Mortensen et al. 2005, ESSIM Planning Office 2006).

Most studies in the NEC to date have focused on deep-water corals and the diversity of associated faunal assemblages. These show, for example, associated epifaunal invertebrates are dominated by crustaceans, while their diversity and abundance are related to coral morphology (Buhl-Mortensen & Mortensen 2005). Metaxas & Giffin (2004) and Metaxas & Davis (2005) described the epibenthic assemblages in the NEC and identified suspension-feeders as the dominant megafauna. A single study measured rates of colonization in the NECCCA, focusing specifically on deep-water corals (Lacharité & Metaxas 2013).

In this study, we measured the abundance and family richness of benthic invertebrate colonists on 2 types of substrate at 3 depths (655, 662 and 883 m) in the Middle Canyon of the NECCCA over a 4-yr period. We compared a complex substrate that allowed colonization in 3 dimensions with a simple substrate that only allowed colonization in 2 dimensions. This study complements Lacharité & Metaxas (2013) which deployed the same experimental units, but focused only on colonization of the deep-water corals *Primnoa reseaformis* and *Paragorgia arborea*. Our study aims to provide new estimates of colonization in the deep sea, which are sorely lacking, particularly for submarine canyons. Estimating colonization in the deep sea is becoming increasingly important in light of impending anthropogenic impacts, particularly those associated with resource extraction (Ramirez-Llodra et al. 2011, Puig et al. 2012). Colonization rates can be used to estimate the

rate and extent of population recovery from disturbances, including anthropogenic ones such as deep-sea mining or trawling. The paucity of such information severely hampers the development of management strategies for the sustainable use of resources in the deep sea.

MATERIALS AND METHODS

Study area

In the Gulf of Maine (NW Atlantic), the NEC is located 175 km from the nearest landmass (southwestern Nova Scotia) (Fig. 1) and separates Georges Bank and Browns Bank. The NEC represents the only deep-sea connection between the Atlantic Ocean and the Gulf of Maine (Ramp et al. 1985). The NEC has a sill that is ~230 m deep and, at the shelf edge where it is 20 to 30 km wide, it drops off sharply into 3 steep-walled canyons to depths of ~1000 m (Ramp et al. 1985, ESSIM Planning Office 2006). An outflow of fast currents on the southwest side of the NEC is balanced by an inflow in the rest of the channel (Ramp et al. 1985). The net carbon production of the overlying community has been estimated at 1.8 to 4 mol C m^{-2} (Shadwick & Thomas 2014). The NEC harbours the highest known densities in Atlantic Canada of 2 species of large gorgonian corals: sea corn coral *Primnoa resedaeformis* and bubblegum coral *Paragorgia arborea* .

We focused on 3 sites in the Middle Canyon in the NECCCA that represent a range of physical (currents) and geological settings, on the north and south walls (North wall: 41° 59′ 15.22″ N, 65° 38′ 51.95″ W; depth 655 m; South wall: 41° 58′ 12.40″ N, 65° 38′ 32.51″ W; depth 662 m; horizontal distance 2 km) and on the floor of the canyon (Floor: 41° 58′ 35.30″ N, 65° 38′ 20.75″ W; depth 863 m) (Fig. 1). The surficial walls of the Middle Canyon are mostly composed of glacial and glaciomarine depositional sediment, i.e. isolated cobbles and boulders in a matrix of coarse sand patches, derived from till tongues (Edinger et al. 2011). On the canyon floor, the substrate is mostly composed of sand and a handful of very large boulders (>1 m diameter).

Colonies of *P. resedaeformis* are present on both walls, with higher densities on the north wall than on the south wall, whereas on the floor of the canyon, a few colonies of *P. arborea* can be observed in the vicinity of our study area (Watanabe et al. 2009, Lacharité & Metaxas 2013). Other common megafaunal species recorded in the Middle Canyon include the anemones *Bolocera tudiae* and *Actinauge verrilli* and the ophiuroid *Ophiacantha abyssicola* (Metaxas & Giffin 2004, Metaxas & Davis 2005).

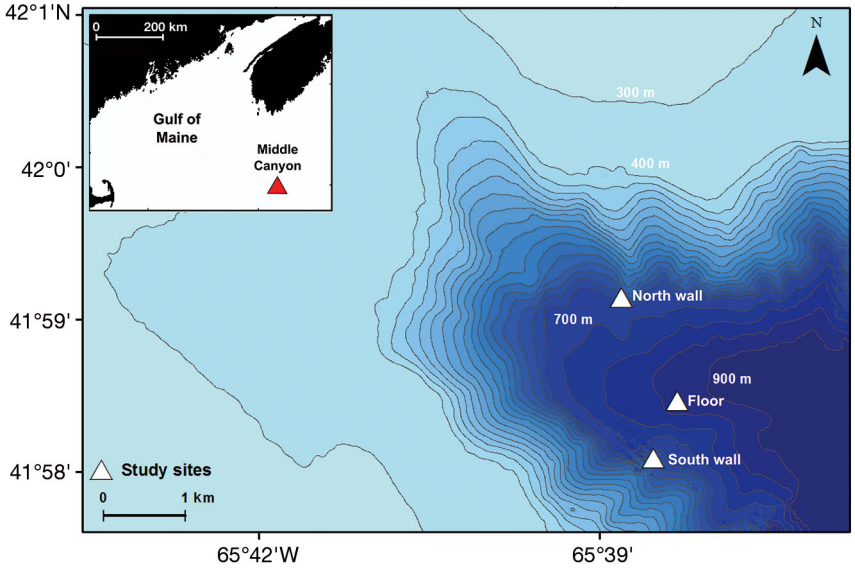

Fig.1. Middle Canyon in Northeast Channel (NEC), showing the location of (white triangle) study sites (North wall, South wall, Floor) where collectors were deployed to measure colonization by benthic invertebrates. Between 400 and 700 m depth, 20 m isobaths are shown. Below 700 m, 50 m isobaths are shown. Bathymetric data were provided by the Canadian Hydrographic Service. Inset: Location of the Middle Canyon in the Gulf of Maine (NW Atlantic)

Field experiment

To measure colonization, we deployed 16 collectors (Kelly & Metaxas 2008, Lacharité & Metaxas 2013) at each of the 3 sites over a period of 4 yr (2006 to 2010). At each site, the collectors were attached to a single galvanized steel frame (45 × 45 cm) for ease of deployment (see Appendix 1). Because deep-sea organisms are known to have slow rates of growth and colonization (see 'Introduction'), a 4-yr deployment period was considered to be necessary to allow quantification of colonization. Moreover, since previous studies report rates of colonization of <50 colonists per collector yr^{-1} (see 'Introduction'), we did not anticipate that space on the substrate would become limiting over this period.

We used 2 types of substrate with different levels of complexity for the

collectors. On each frame we deployed 10 'simple substrate' collectors composed of solid basalt blocks (approximate size 7 × 10 × 2 cm), and 6 'complex substrate' collectors made from Scotch-Brite all-purpose scour pads (approximate size 7.5 × 10 × 1.5 cm, mesh opening ~3.5 mm^2) that allowed colonization in 3 dimensions. The planar surface area was similar, at 70 cm^2 for simple substrates and 75 cm^2 for complex substrates. For complex substrates, the volume available for colonization was 140 cm^3 (Kelly & Metaxas 2008). Each substrate type was held in a plastic container (10.5 × 7.5 × 2.5 cm), 20 cm above the seafloor. Individual collectors were separated by a few centimetres and were not in contact with one another, providing independent replicates when measuring colonization in sessile species or ones with limited motility. These are the same experimental units used by Lacharité & Metaxas (2013). We employed 2 types of collectors with different levels of complexity to enhance the probability of sampling a broad range of colonist types. However, other characteristics may play a role in the effectiveness of the collectors, such as their material.

The arrays of collectors were recovered in a polycarbonate lidded box (approximate size 80 × 60 × 35 cm) by the remotely operated vehicle (ROV) 'ROPOS'. A piece of open cell foam was attached to the underside of the box lid to avoid dislodgement of organisms during the ascent. Digital photographs of the surface of each substrate were taken *in situ* before recovery, using a Nikon D700 (12 megapixels) (f-stop: f/5; exposure time: 1/125 s; focal length: 52 mm) mounted on 'ROPOS'. We enumerated organisms visible on these photographs (>5 mm) and compared those counts to those from physically retrieved samples from the individual collectors to evaluate potential loss during ascent. Of the individuals observed on the pictures taken before recovery, 88% were recovered from the collectors during processing. All collectors were preserved in individual containers in 95% ethanol at sea.

For each collector, we removed all invertebrate specimens manually and by sieving the seawater in the container through a 63-µm sieve, enumerated them, and assigned them to family level based on morphology. Because of the prohibitively long time it takes to process each pad (weeks), we randomly selected 3 of the 6 replicates from each location for processing. Previous analyses have shown sufficient statistical power when ≤6 replicates are used (Kelly & Metaxas 2008, M. Lacharité & N. Kelly unpubl. data). Morphotypes were assigned to families using the World Registry of Marine Species (WoRMS; www.marinespecies.org) database and associated publications referred to in the database. Polychaetes were assigned to family during a training workshop for morphological and molecular identification of deep-sea colonists organized by the International Network for Scientific Investigation of Deep-sea Ecosystems (INDEEP; www.indeep-project.org) in Southampton, UK, in 2012. While certain morphotypes could have been assigned to lower taxonomic levels (e.g. genus or species), we utilized family as the common level of taxonomic resolution that could be assigned to all morphotypes and used for analyses on diversity. Hydroid colonies were quantified using dry biomass (g). We considered specimens found in the foam sections or floating in the sample containers to have been dislodged from their corresponding substrate.

Data analyses

We expressed space available for colonization as surface area (cm^2) for simple substrates and as volume (cm^3) for complex substrates. It was not possible to obtain a measure of 'living space' that was comparable between substrate types. We calculated relative abundance by dividing the abundance of each taxon in a replicate collector by the total abundance of specimens of all taxa in that replicate. Estimates of relative abundance can be used to determine whether the same taxonomic groups colonized the 2 substrate types with the same frequency. Because of the way they were measured (as biomass rather than numerical abundance), we did not include hydroids in the estimate of total abundance. To standardize our measures between substrate types, we calculated abundance of colonists (number of colonists per 100 cm^2) by dividing the number of colonists by the surface area of the collector (70 cm^2 for simple substrates and 75 cm^2 for complex substrates). We considered as colonists all post-metamorphic specimens that presumably had survived a period of post-settlement mortality until retrieval (termed either recruits or colonists in other studies) (as defined in Metaxas & Kelly 2010). These assemblages may include some migrants from neighbouring habitats, although we consider this unlikely since in our study most taxa were either sessile or of limited motility.

For each substrate type, we compared abundance of colonists for the most common taxa (Anthozoa, Bivalvia, Gastropoda, Malacostraca, Maxillopoda, Nematoda, Ostracoda, and Polychaeta) among locations using 1-way ANOVA. We did not include

hydroids in the statistical analysis because of the difficulty in distinguishing families, and we did not include ophiuroids because of our inability to distinguish between colonists and individuals that were migrating over the collectors.

Patterns in diversity were assessed using individual-based rarefaction curves and non-metric multidimensional scaling (nMDS). We computed individual-based rarefaction curves to compare richness among substrate types and sites by pooling all specimens from a given substrate type at each site (i.e. producing a total of 6 curves). Individual-based rarefaction curves compute the expected number of families/morphotypes as a function of the number of individuals, using a re-sampling without replacement approach (Gotelli & Colwell 2001). For nMDS, we used Bray-Curtis similarity coefficients. Relative abundances were fourth-root transformed prior to constructing similarity matrices to avoid biases arising from over-representation of numerically dominant taxa. We tested the similarity of the assemblages of colonists among substrate types and of locations within a substrate type with an analysis of similarities (ANOSIM). We assessed family/morphotype contribution to the dissimilarity between substrate types with an analysis of similarity percentages (SIMPER).

We performed all statistical analyses in the R statistical computing environment version 3.0.0 (R Development Core Team 2008). All tests were considered significant at $\alpha = 0.05$.

RESULTS

We recovered colonists on all 48 collectors. In total, we collected 2636 specimens, representing 14 classes and several families (Tables 1 & 2). Anthozoans, polychaetes, maxillopods, malacostracans, ostracods, bivalves, gastropods and nematodes were the most abundant taxa (Table 1). Most families were present on all collectors, except hexactinellids, which were only recorded at the North wall. A single aplacophoran was retrieved from a collector with complex substrate from the North wall. Among the anthozoans, actinarians were only found on simple substrates, and the deep-water gorgonian coral *Primnoa resedaeformis* was collected on both substrate types.

Mean total abundance was 21 to 67 individuals across an area of 138 cm^2 for simple substrates, and 135 to 341 individuals across a volume of 140 cm^3 for complex substrates, suggesting that space for colonization was not limiting during the deployment, particularly for simple substrates (Fig. 2). Relative abundance varied between substrate types, but the effects were taxon-specific (Fig. 2, Table 1). Anthozoans were the most abundant taxon on simple substrates, whereas the assemblages were more evenly distributed across taxa on complex substrates. The relative abundance of gastropods, maxillopods, nematodes, and ostracods was greater on complex than simple substrates, whereas the opposite was the case for abundance of bivalves, anthozoans, and biomass of hydrozoans (Table 1). Polychaetes were sampled at similar frequencies by the 2 substrate types. The abundance of colonists per unit area varied among locations for 5 and 2 out of 9 taxa on simple and complex substrates, respectively (Fig. 3, Table 3). The strongest effects were for anthozoans, bivalves, malacostracans and polychaetes on simple substrates.

Since none of the rarefaction curves reached an asymptote, any patterns should be viewed with cau-

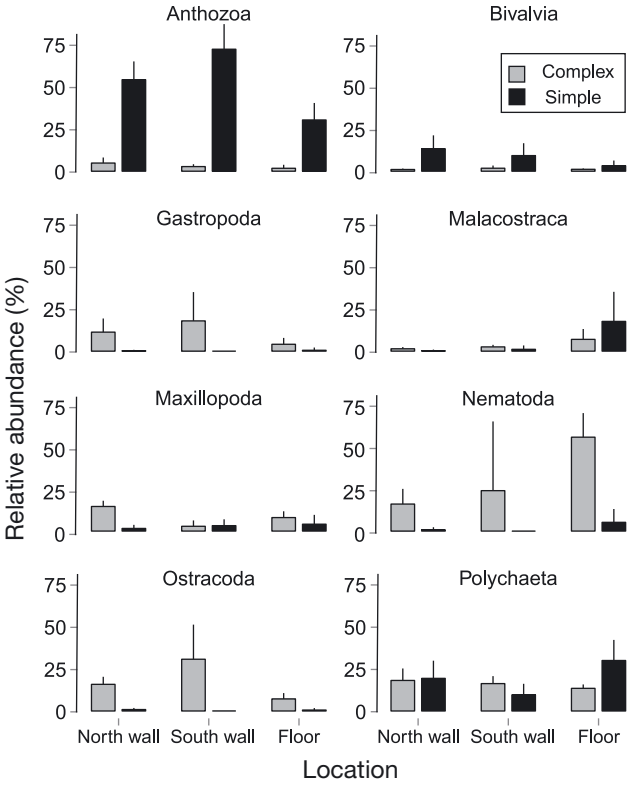

Fig. 2. Mean (+SD) relative abundance of colonists of the most abundant taxa on settlement collectors with simple (n = 10 per location) and complex (n = 3 per location) substrates deployed at the North wall, South wall and Floor of the Middle Canyon in the Northeast Channel Coral Conservation Area (NECCCA). Relative abundance was calculated by dividing the abundance of each taxon in a replicate collector by the total abundance of specimens of all taxa in that replicate

Table 1. Mean (±SD) total abundance per collector(n = 10 for simple substrates and 3 for complex ones) of all invertebrate taxa recovered on the settlement collectors with simple and complex substrates deployed at 3 locations in the Middle Canyon of the Northeast Channel Coral Conservation Area (NECCCA) in the Gulf of Maine (NW Atlantic) from 2006 to 2010. For hydroids, total dry biomass (g) is shown

	North wall		South wall		Floor	
	Simple	Complex	Simple	Complex	Simple	Complex
Anthozoa	36.4 ± 14.0	14.7 ± 6.11	15.5 ± 9.58	3.33 ± 2.31	7.60 ± 2.22	2.33 ± 2.52
Primnoidae						
Primnoa resedaeformis	35.8 ± 13.4	14.7 ± 6.11	15.0 ± 9.61	3.33 ± 2.31	4.80 ± 1.62	2.33 ± 2.52
Actinaria	0.600 ± 1.26	0	0.500 ± 1.41	0	2.80 ± 3.05	0
Hexactinellida	1.50 ± 2.12	0.670 ± 0.577	0	0	0	0
Farreidae	0.300 ± 0.675	0	0	0	0	0
Other	1.20 ± 1.55	0.670 ± 0.577	0	0	0	0
Ophiuroidea						
Ophiacanthidae						
Ophiacantha abyssicola	0.100 ± 0.316	0.670 ± 1.15	0	4.33 ± 3.21	0	1.33 ± 1.15
Maxillopoda	1.10 ± 1.66	47.6 ± 10.8	0.900 ± 1.10	4.33 ± 6.66	3.00 ± 2.62	12.7 ± 7.37
Copepoda						
Harpacticoida	0	44.0 ± 12.2	0.100 ± 1.10	3.67 ± 6.35	0.800 ± 1.32	7.33 ± 2.31
Calanoida	0.400 ± 0.966	0	0	0	0	0
Other Copepoda	0.300 ± 0.675	3.33 ± 2.08	0	0.333 ± 0.577	0.100 ± 0.32	5.33 ± 5.13
Scalpellidae	0.400 ± 0.843	0	0	0	0	0
Thecostraca	0	0.333 ± 0.577	0.800 ± 1.03	0.333 ± 0.577	2.10 ±2.42	0
Ostracoda	0.600 ± 0.699	57.0 ± 32.5	0	41.3 ± 42.2	0.200 ± 0.422	11.3 ± 6.81
Malacostraca	0.200 ± 0.632	4.00 ± 1.73	0.200 ± 0.422	3.00 ± 1.73	6.50 ± 8.57	11.3 ± 11.0
Ampithoidae	0	0	0	0	2.20 ± 3.74	2.00 ± 2.65
Caprellidae	0	0.333 ± 0.577	0	1.00 ± 1.00	2.20 ± 2.74	9.00 ± 11.4
Melitidae	0	0	0	0	1.80 ± 5.69	0
Stenothoidae						
Metopa spp.	0.200 ± 0.632	0	0.100 ± 0.316	0.333 ± 0.577	0	0
Amphipoda	0	1.33 ± 0.577	0.100 ± 0.316	1.33 ± 2.31	0.200 ± 0.422	0.333 ± 0.577
Munnidae	0	1.33 ± 0.577	0	0.333 ± 0.577	0.100 ± 0.316	0
Paramunnidae	0	0.333 ± 0.577	0	0	0	0
Isopoda	0	0.667 ± 0.577	0	0	0	0
Pycnogonida	0	0.330 ± 0.577	0.100 ± 0.316	0.330 ± 0.577	0.200 ± 0.422	0.333 ± 0.577
Bivalvia	7.80 ± 2.15	3.67 ± 2.31	1.80 ± 1.40	2.33 ± 0.577	0.900 ± 0.738	1.67 ± 0.577
Anomiidae	7.20 ±2.49	1.33 ± 1.53	1.60 ± 1.26	0	0.500 ± 0.527	0
Pectinidae						
Delectopecten spp.	0.400 ± 0.700	0	0.100 ± 0.316	2.00 ± 1.00	0	0
Unidentified spp.	0.200 ± 0.422	0.333 ± 0.577	0	0	0.400 ± 0.516	1.00 ± 1.00
Other	0	2.00 ± 1.73	0.100 ± 0.316	0.333 ± 0.577	0	0.667 ± 1.15
Gastropoda	0.20 ± 0.422	41.7 ± 30.9	0	17.3 ± 13.2	0.200 ± 0.632	5.67 ± 4.51
Buccinidae	0	0	0	1.00 ± 1.73	0.100 ± 0.316	0.333 ± 0.577
Other Gastropoda	0.20 ± 0.422	41.7 ± 30.9	0	16.3 ± 13.0	0.100 ± 0.316	5.33 ± 4.51
Aplacophora	0	0.330 ± 0.577	0	0	0	0
Polychaeta	13.1 ± 8.18	56.33 ± 3.21	1.50 ± 1.08	21.3 ± 12.7	7.50 ± 2.55	20.3 ± 3.21
Ampharetidae	3.70 ± 3.40	21.7 ± 8.39	0.800 ± 1.03	11.7 ± 4.04	0.500 ± 0.707	5.67 ± 1.15
Cirratulidae	0	1.33 ± 1.15	0	0.333 ± 0.577	0	0
Dorvilleidae	0	0	0	0	0.100 ± 0.316	1.67 ± 1.53
Hesionidae	0.500 ± 0.850	5.67 ± 1.53	0	0.667 ± 1.15	0.100 ± 0.316	0
Lacydoniidae	0	0	0.300 ± 0.483	0	0	3.33 ± 5.77
Lumbrineridae	0	1.00 ± 1.00	0	0.667 ± 1.15	0	0.667 ± 0.577
Nereididae	0	0.333 ± 0.577	0	0.667 ± 1.15	0	0.333 ± 0.577
Paraonidae	0	0.333 ± 0.577	0	0	0	0
Phyllodocidae	0	1.33 ± 1.15	0	0	0	0
Sabellidae	1.10 ± 2.81	7.00 ± 5.29	0	1.00 ± 1.73	0.200 ± 0.422	2.00 ± 1.73
Serpulidae						
Spirorbis spp.	5.80 ± 4.13	3.33 ± 3.51	0	0.667 ± 1.15	2.90 ± 1.79	1.00 ± 1.00
Other Polychaeta	2.00 ± 3.65	14.33 ± 5.51	0.400 ± 0.516	5.67 ± 4.04	3.70 ± 2.58	5.67 ± 4.73
Nematoda	0.50 ± 1.08	51.3 ± 24.4	0	40.7 ± 69.6	1.60 ± 2.55	85.3 ± 27.5
Hydrozoa	0.051	0.005	0.024	0.003	0.241	0.005

Table 2. Mean (±SD) family richness per collector(n = 10 for simple substrates and 3 for complex ones) of all invertebrate taxa recovered on collectors with simple and complex substrates, deployed at 3 locations in the Middle Canyon of the NECCCA

	North wall		South wall		Floor	
	Simple	Complex	Simple	Complex	Simple	Complex
Anthozoa	1.50 ± 0.972	1.00 ± 0	1.50 ± 0.707	1.00 ± 0	2.70 ± 1.25	0.667 ± 0.577
Octocorallia	1.00 ± 0	1.00 ± 0	1.00 ± 0	1.00 ± 0	1.00 ± 0	0.667 ± 0.577
Actinaria	0.500 ± 0.972	0	0.500 ± 0.707	0	1.70 ± 1.25	0
Hexactinellida	0.900 ± 0.876	0.667 ± 0.577	0	0	0	0
Ophiuroidea	0.100 ± 0.316	0.667 ± 1.15	0	4.33 ± 3.21	0	1.33 ± 1.15
Maxillopoda	0.700 ± 0.949	3.67 ± 1.15	0.600 ± 0.699	1.00 ± 1.00	1.20 ± 0.788	3.67 ± 2.08
Thecostraca	0.200 ± 0.422	0.333 ± 0.577	0.500 ± 0.527	0.333 ± 0.577	0.700 ± 0.483	0
Copepoda	0.500 ± 0.850	2.67 ± 1.15	0.100 ± 0.316	0.667 ± 1.15	0.500 ± 0.527	3.67 ± 2.08
Ostracoda	0.500 ± 0.527	3.33 ± 0.577	0	2.33 ± 0.577	0.200 ± 0.422	3.00 ± 0
Malacostraca	0.100 ± 0.316	3.33 ± 1.53	0.200 ± 0.422	2.00 ± 1.00	1.400 ± 1.17	3.00 ± 0
Amphipoda	0.100 ± 0.316	1.33 ± 0.577	0.200 ± 0.422	1.67 ± 1.15	1.300 ± 1.06	3.00 ± 0
Isopoda	0	2.00 ± 1.00	0	0.333 ± 0.577	0.100 ± 0.316	0
Pycnogonida	0	0.333 ± 0.577	0.100 ± 0.316	0.333 ± 0.577	0.200 ± 0.422	0.333 ± 0.577
Bivalvia	1.40 ± 0.516	2.67 ± 1.53	1.00 ± 0.471	1.33 ± 0.577	0.900 ± 0.738	1.33 ± 0.577
Gastropoda	0.200 ± 0.422	10.7 ± 7.02	0	5.67 ± 4.04	0.200 ± 0.632	3.00 ± 1.73
Aplacophora	0	0.333 ± 0.577	0	0	0	0
Polychaeta	3.30 ± 1.64	14.3 ± 2.52	1.20 ± 0.789	7.67 ± 5.03	3.50 ± 1.43	8.67 ± 2.52

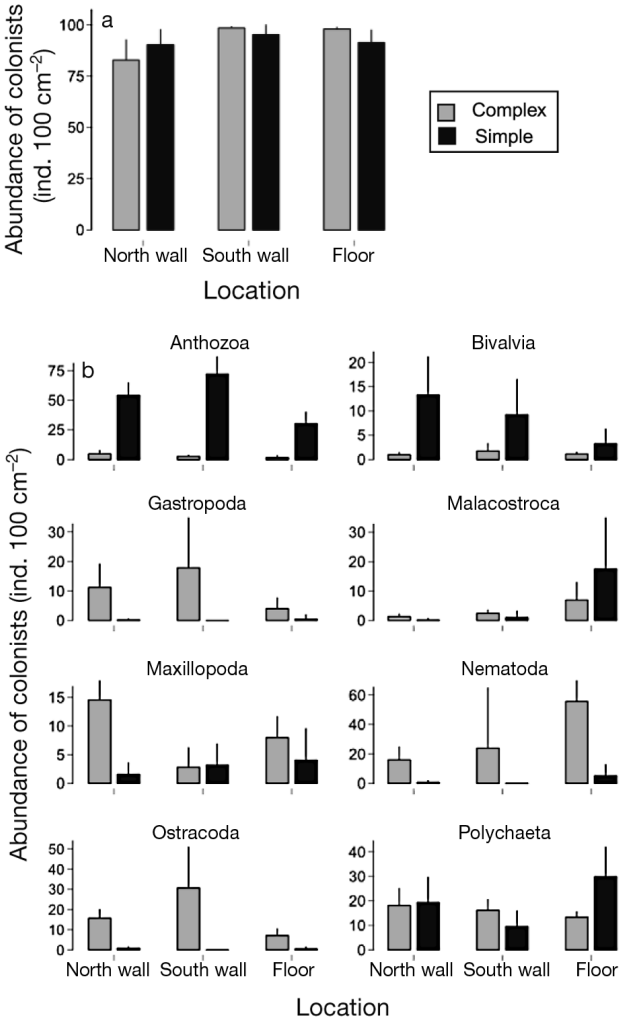

Fig. 3. Mean abundance (± SD) of colonists calculated for the planar area of each substrate type for (a) all taxa combined and (b) for the most abundant taxa on simple (n = 10 per location) and complex (n = 3 per location) substrates on the North wall, South wall and the Floor of the Middle Canyon in the NECCCA

tion. However, the trend of the curves indicated that colonist assemblages were more diverse on complex than simple substrates at all 3 sites (Fig. 4, Table 2). Not enough individuals were collected from the South wall and the Floor to determine statistically whether there was a difference in richness among locations.

Assemblages of colonists clustered by substrate type (Fig. 5) and the 2 groups were significantly different from one another (ANOSIM, R = 0.854, $p < 0.001$). Assemblages on collectors with simple substrates were significantly different between pairs of sites (ANOSIM, $p < 0.01$ in all cases), but assemblages on complex substrates did not differ between any pair of sites (ANOSIM, p = 0.075 to 0.090). The SIMPER analysis showed that all taxa contributed evenly to the dissimilarity between substrate types. The highest contributions to the total dissimilarity were 2 to 4% for each of 7 taxa (primnoids, anomids, 2 families of ostracods, harpacticoid copepods, 1 family of gastropods, and ampharetids), while 79 families/morphotypes contributed <1% to total dissimilarity between substrate types.

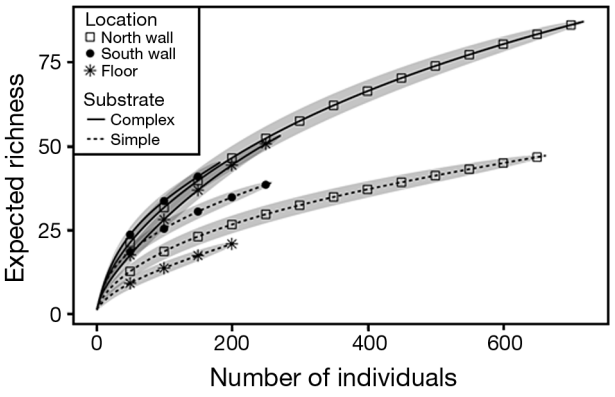

Fig. 4. Individual-based rarefaction curves (±SE) for collectors with both simple (n = 10) and complex substrates (n = 3) deployed on the North wall, South wall and the Floor of the Middle Canyon in the NECCCA. All individuals from a given substrate type were pooled at each location

DISCUSSION

Our collectors were colonized by abundant and diverse assemblages that were dominated by anthozoans (both corals and anemones) and bivalves on simple substrates, and by a combination of polychaetes, gastropods ostracods, nematodes and copepods on complex ones. However, except for anthozoans, no taxon had a relative abundance >30%, a pattern commonly observed in deep-sea ecosystems (Grassle & Maciolek 1992, Henry & Roberts 2007). Although we allowed colonization to proceed for 4 yr, the rarefaction curves still did not reach asymptotes. Since there was still space available on all our collectors upon recovery, the absence of asymptotes could be the result of slow colonization. It is also possible that species replacements may have occurred over the deployment period, as a result of succession, which we would not have been able to detect over a single, integrative sampling event. However, despite the absence of asymptotes, we believe that the differences in richness between collector types are great enough to indicate higher richness in the more complex collectors.

Our study contributes to the sparse measures of colonization available for deep-sea organisms. At all locations, we measured colonization rates for total fauna on simple substrates within the range previously recorded in 3 studies on non-reducing deep-sea habitats (i.e. 10^{-5} to 10^{-4} colonists cm^{-2} d^{-1}) (Grassle 1977, Grassle & Morse-Porteous 1987, Smith &

Table 3. Results of 1-way ANOVAs examining differences among 3 locations (North wall, South wall, Floor) in total colonist abundance (number of colonists per 100 cm^2) and that of the 8 most common taxa on collectors deployed in the Middle Canyon of the NECCCA. Data are untransformed except for Bivalvia and Polychaeta on simple substrates, and Maxillopoda on complex substrates, which were square-root transformed to yield normality (as detected by Shapiro-Wilk's tests). For all analyses, variances were homogeneous (as detected by Levene's tests) except for Malacostraca, Nematoda and Ostracoda on simple substrates. In these cases, untransformed data were used for the analyses since no transformation successfully eliminated heterogeneity. Significant p-values ($p < 0.05$) are shown in **bold** type

Family	Simple substrates MS_{Group}, $F_{2,27}$, p	Complex substrates MS_{Group}, $F_{2,6}$, p
Total recruits	66.7, 1.64, 0.213	236.7, 6.91, **0.028**
Anthozoa	4404, 30.1, **<0.0001**	7.46, 1.31, 0.337
Bivalvia	10.96, 8.14, **0.0017**	0.493, 0.475, 0.643
Gastropoda	0.658, 0.675, 0.518	143.6, 1.17, 0.373
Malacostraca	958.1, 9.22, **0.0009**	26.07, 1.95, 0.223
Maxillopoda	16.30, 0.998, 0.382	4.70, 6.24, **0.034**
Nematoda	78.69, 3.65, **0.039**	1314, 2.01, 0.214
Ostracoda	1.88, 2.45, 0.106	423.4, 2.82, 0.137
Polychaeta	16.37, 11.46, **0.0002**	16.53, 0.660, 0.551

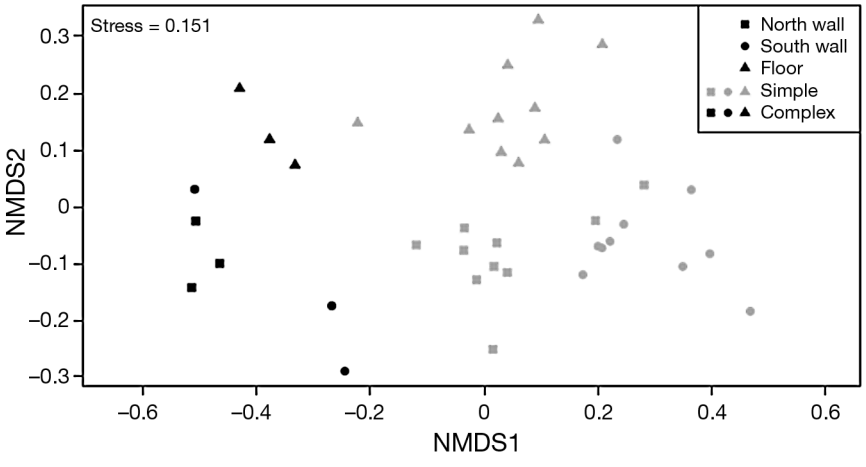

Fig. 5. Non-metric multidimensional scaling (nMDS) of colonist assemblages recovered on collectors with simple (n = 10 per location) and complex (n = 3 per location) substrates on the North wall, South wall, and the Floor of the Middle Canyon in the NECCCA. Distance between assemblages was estimated with Bray-Curtis similarity coefficients

Hessler 1987). On complex substrates, colonization rates were in some cases an order of magnitude greater, and similar to rates obtained in recolonization experiments on artificial sponge stalks at 4100 m (1.6×10^{-3} colonists cm^{-2} d^{-1}; Beaulieu 2001), polycarbonate plates deployed at Cross Seamount at 410 m (2×10^{-4} colonists cm^{-2} d^{-1}; Mullineaux & Butman 1990), mineral coated plates deployed at Cross Seamount at 1985 m (3.3×10^{-3} colonists cm^{-2} d^{-1}; Bertram & Cowen 1999), and sediment trays at Santa Catalina Basin, California, at 1300 m (3.5×10^{-3} colonists cm^{-2} d^{-1}; Levin & Smith 1984), St Croix, US Virgin Islands at 900 m (~1 to 2×10^{-3} colonists cm^{-2} $d^{-}{}_{1}$, Snelgrove et al. 1994) and Fieberling Seamount at 635 m (8×10^{-4} colonists cm^{-2} d^{-1} in short-term experiments; Levin & DiBacco 1995).

The paucity of measures of colonization in the non-chemosynthetic habitats of the deep sea must be addressed particularly in light of the increased interest in resource extraction in these habitats (Clark et al. 2010, Wedding et al. 2013, Mengerink et al. 2014, Hilario et al. 2015). Only a handful of studies have examined colonization in the bathyal deep-sea, at depths of <2000 m, and even fewer have focused on abyssal depths (e.g. Beaulieu 2001, Ingole et al. 2001). The low rates of colonization in the deep sea suggest that these ecosystems may have low resilience to perturbations. Without measures of colonization, the viability of a population cannot be predicted.

Overall, both in ours and in previous studies in the deep sea, colonization rates were low compared to shallow water, intertidal and subtidal habitats (Connell 1985, Grassle 1977, Minchinton & Scheibling 1993, Vermeij & Sandin 2008). In the deep sea, relatively high colonization rates have only been found in chemosynthetic ecosystems such as hydrothermal vents, cold seeps and large organic falls (0.001 to 0.01 colonists cm^{-2} d^{-1}; Metaxas & Kelly 2010). In contrast to non-reducing environments, carbon production in chemosynthetic ecosystems is high, and can support higher biomass including that of recruits. In the few experiments that have examined the role of increased food supply in colonization in the deep sea, the results are equivocal, demonstrating both much higher (Snelgrove et al. 1994) and much lower (Levin & Smith 1984) colonization in food-enriched sediment trays compared to controls. It is possible that the higher rates of colonization that we observed on complex compared to simple substrates were related to particulate organic matter being trapped in interstitial spaces, thus increasing food supply for recruits. The frequency and roles of physical and biological (including predation) disturbance in the deep sea are unknown, making the recovery potential of these ecosystems impossible to estimate based solely on colonization rates.

The background macrofaunal epibenthic assemblages in the NEC have not been described in detail to date. The numerically dominant epibenthic megafauna, previously sampled in Middle Canyon, included many suspension and some deposit feeders, such as the actinarians *Actinuage verrilli* and *Bolocera tudiae*, as well as unidentified anemones and sponges, echinoderms, and the extremely abundant *Ophiacantha abyssicola* (Metaxas & Giffin 2004, Metaxas & Davis 2005). In our study, the assemblages of colonists on simple substrates included early benthic stages of actinarians and sponges, and many ophurioids. The composition of the colonists on complex substrates was also similar to that of faunal assemblages associated with gorgonian corals in the study area, with crustaceans dominating faunal assemblages (Buhl-Mortensen & Mortensen 2004, 2005).

Most invertebrate colonists were suspension-feeders, including sabellids, which were the dominant polychaetes on both substrate types. Strong currents characterize the NEC (Ramp et al. 1985) and, while the local water circulation has not been described in the Middle Canyon, it has been suggested that steep topography increases particle encounter rates and resuspension of particulate organic matter, while reducing sediment deposition in deep-water habitats (Genin et al. 1986). Together, these features form suitable habitat for suspension-feeders, which are commonly found in submarine canyons as part of epibenthic megafaunal assemblages (Vetter et al. 2010, Williams et al. 2010). At the local scale, the elevated position of the collectors at 20 cm above the seafloor may have placed them sufficiently high in the benthic boundary layer to enhance flow and, therefore, delivery of particles to the suspension-feeding colonists, enhancing their survival.

In the present study, faunal family richness was higher on complex than simple substrates at 2 of the sites. Based on relative abundance, the biggest differences between collector types were for anthozoans and polychaetes. Complex substrates can provide shelter from predators or currents, and thus increase survivorship (Menge et al. 1985, Auster et al. 1995, Auster 2005). Interstitial spaces in the scour pads could have enhanced colonization by increasing 'living space' or available surface for larval settlement (Eckman 1987). In the present study, the most abundant colonists on complex substrates were meiofauna and macrofauna typically occuring in soft-bottom habitats, including burrowing species and

many deposit feeders (e.g. nematodes, some ostracods, dorvilleids, hesionids, and paraoinids).

The patterns in abundance of colonists that we observed varied somewhat among the 3 locations in the canyon, but not consistently among taxa. Several characteristics varied among the 3 locations, such as the substratum, hydrodynamics and possibly food supply. The substrate of the floor of the canyon was mainly coarse sand, whereas on the walls it was dominated by coarser cobbles, pebbles and boulders. Differences in currents likely exist as a result of patterns in inflow and outflow of the dominant circulation (Ramp et al. 1985), resulting in differences in the supply of both food particles and propagules. Despite the observed differences in the abundance of colonists among sites, the scale of spatial variation (kilometres among sites versus metres within sites) cannot be inferred given our sampling design, in which within-site variation was measured on scales of tens of centimetres and is likely not adequately represented.

In summary, the present study is one of the few studies that have measured colonization of marine benthic invertebrates in non-chemosynthetic habitats of the deep sea. The time scale over which we measured colonization was longer than in most other studies, in order both to allow for weathering of the artificial substrates and to provide enough time to collect typically slow colonizers (such as anthozoans). We recorded very slow colonization rates, underscoring the potentially great vulnerability of these ecosystems to disturbance. Increased knowledge of colonization to deep-sea habitats is urgently needed, given the increasing pressures from human exploitation that these ecosystems are currently facing.

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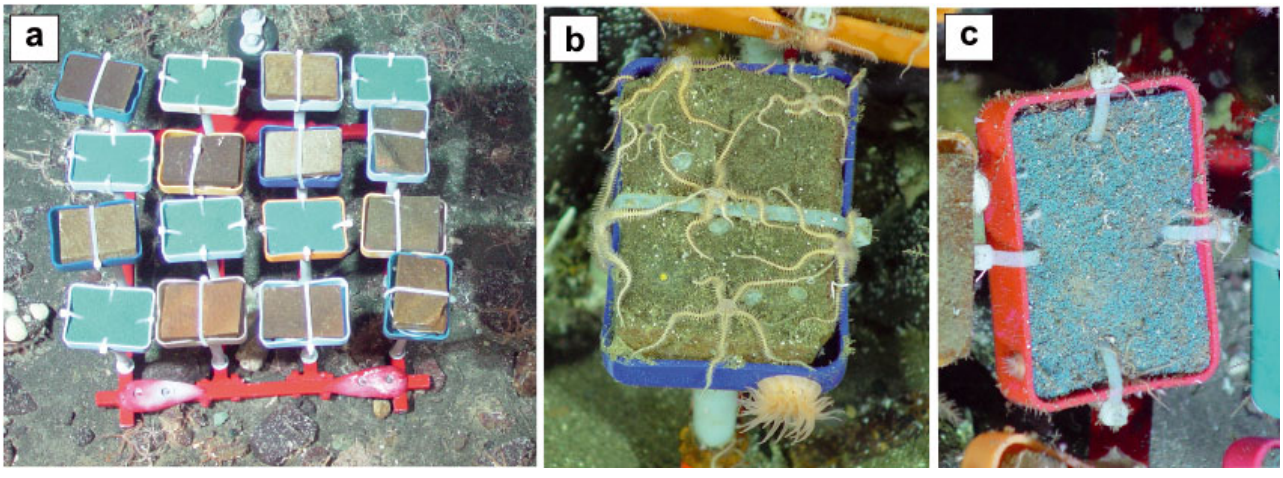
Appendix 1. Arrays of collectors deployed in the Northeast Channel Coral Conservation Area (NECCCA), Gulf of Maine from 2006 to 2010. (A) Array at the south wall at deployment in 2006. (B) Simple substrate (basalt rock) from the array at the north wall at recovery in 2010. (C) Complex substrate (mesh pad) from the array at the north wall at recovery in 2010. (Photographs: Canadian Scientific Submersible Facility)



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