

A high local species richness and biodiversity within high-latitude calcareous aggregates of tube-building polychaetes

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Abstract In general, biodiversity and species richness follow the latitudinal diversity gradient and decrease from the tropics towards the poles. Exceptions have however been recorded, as for deep coldwater coral reefs at high latitudes, which comprise biodiversity hotspots. Here we assess and characterise the high-latitude (69°N) species richness and diversity of a local shallow-water fauna associated with small calcareous aggregations of a serpulid polychaete. A dense and very species rich fauna was recorded within aggregations of *Filograna implexa* Berkeley, 1828. Totally 4663 individuals belonging to 99 species (61 solitary, 38 colonial) were recorded in a total aggregation volume of only 4.4 l covering an area less than 0.05 m² of a wreck situated in a tidal stream in North Norway. The number of species within each aggregation was positively related to its size, indicating that the high species diversity may be due to structural heterogeneity, which increase with aggregation size and probably creates new microhabitats and protect against predation. We present a species list including abundance and biomass, pin-point common species and describe a method for sampling such faunas associated with calcareous structures.

Keywords Diversity · Heterogeneity · Biogenic structure · *Filograna implexa* · Microhabitat

Introduction

It has long been recognised that biodiversity and species richness in general are higher in the tropics and decrease along a latitudinal gradient towards the poles (Fischer 1960; Rosenzweig 1995; Hawkins 2001). Across a range of spatial scales, and for a wide spectre

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of taxonomic groups, it has been documented that average species richness within a sampling area of a given size increase when moving from high to low latitudes (Stevens 1989; Gaston 1996, 2000; Witman et al. 2004). Many hypotheses have been put forward to explain the observed patterns but few causal relationships have been identified (Pianka 1966; Gaston 2000; Hillebrand 2004; Jablonski et al. 2006; Harrison and Cornell 2007; Buckley et al. 2010). These patterns also exist in the marine benthos (Sanders 1968; Roy et al. 1998; Gray 2001; Witman et al. 2004), with diversity culminating on tropical coral reefs. Exceptions are however found within some taxa (Hillebrand 2004; Krug et al. 2007) and at some high latitude biodiversity hotspots like those created by deep coldwater coral reefs (Jensen and Fredriksen 1992; Freiwald et al. 2004).

Generally, structural complexity provides shelter against predation and physical disturbance (Menge et al. 1983; Mattila 1995; Walters and Wethey 1996) and introduces additional habitats and higher species diversity (Menge and Sutherland 1976; Sebens 1991). Encrusting organisms with hard exoskeletons build secondary substrate and may increase substrate complexity with crevices and cavities (Dean 1981; Senn and Glasstetter 1989; Sebens 1991). A species rich and diverse fauna is thus often associated with aggregated calcareous-building species and non-tropical shallow-water examples are found in aggregations of red algae (Sneli 1968; Salas and Hergueta 1986; Sintes 1987; Sintes et al. 1987) and serpulid polychaetes (Haines and Maurer 1980a, b; Kirkwood and Burton 1988; Moore et al. 1998). Especially in canals and tidal inlets with high current velocities, reef-like structures of encrusting animals may develop (Odum et al. 1974).

Serpulid polychaetes cement their tubes to firm substrates and occur throughout the world, often aggregating in unstable environments. Their growth is fast and some species can develop reefs that are several meters thick and kilometres long (ten Hove 1979), which provide habitats, feeding grounds, refuge, and reproduction areas for an abundant and diverse fauna (Moore et al. 1998). The genus *Filograna* is widely distributed, but due to the smallness of the tubes their aggregations are not spectacular (ten Hove 1979). Unlike most other genera, *Filograna* aggregations grow by asexual budding (Faulkner 1930; Kupriyanova and Jirkov 1997), possibly in addition to larval gregariousness, at a pace that on settlement panels can reach 4500 individuals per month (ten Hove 1979).

In this study we assess and characterise a very species rich and diverse fauna found living within aggregations of the polychaete *Filograna implexa* Berkeley, 1828 attached to an old shipwreck in a high-latitude tidal stream (69°N).

Area and substrate description

The tidal stream “Rystraumen” is situated at 69°N in northern Norway (Fig. 1) and has current velocities that exceed four m/s (Sjøkartverk 1957; McClimans 1977). It is only 500 meters wide at the most narrow and has a sill depth of 35 meters. It connects two deep fjords (Balsfjorden and Malangen), which both have high annual primary production and large stocks of zooplankton (Gaarder 1938; Eilertsen and Taasen 1984; Tande 1990). Large volumes of homogenised water flow back and forth each tidal cycle (McClimans 1977; Svendsen 1995) and the exchange of dispersing larva, phyto- and zoo-plankton between the two fjords is probably important all through the productive season from late March through June (Reigstad and Wassmann 1996; Reigstad 2000). Food and recruitment is thus unlimited for benthic animals.

The *M/S Flint* (wrecked 1926) is situated 50 m from land and offers vertical hard substrate from 17 to 36 m depth. Kelp forest extends down to the upper parts (<18 m) and

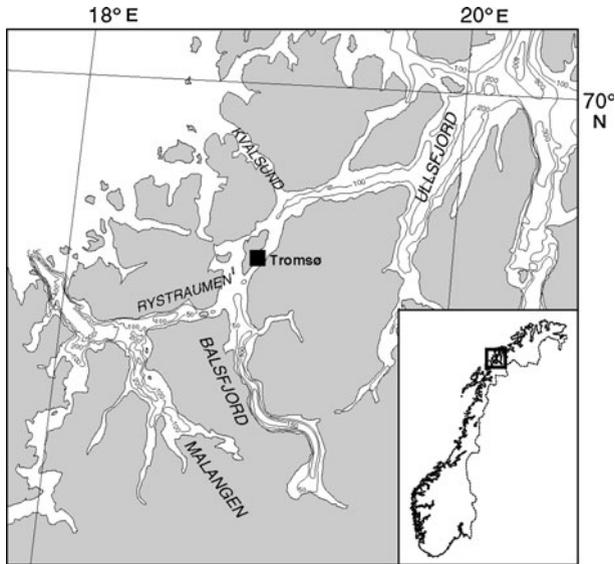


Fig. 1 Map showing the tidal inlet Rystraumen and adjacent waters of Tromsø, northern Norway (redrawn from Reigstad 2000)

a dense sessile fauna covers most of the wreck. The hull is mostly intact and lays in the direction of the stream (W/E) in an upright position. The lack of a deck makes it open to predators. Water currents are much slower along the inside of the hull but *F. implexa* aggregations grow densely on both the inside and outside of vertical surfaces. Aggregations are also found on rocky substrata elsewhere in the Rystraumen and in other local tidal streams (Kvalsund, the entrance of Ullsfjord, Fig. 1) but are less common here compared to on the surface of wreck. The aggregations attain sizes from a few centimetres wide to continuous patches up to a meter long and comprise many levels of structural heterogeneity. The tubes form a lattice (Kupriyanova and Jirkov 1997) and run parallel adhering together to form ridges and protuberances (Knight-Jones and Moyse 1961). Crevices and holes in the lattice range in size from millimetres between single tubes to centimetres between protuberances (Fig. 2), and within the whole scale of structural levels animals are found.

Methods and materials

Eight aggregations of *Filograna implexa* were sampled from verticals beneath the rail on the wreck “*M/S Flint*” within a range of 19–24 m depth in the tidal stream “Rystraumen” during four SCUBA dives in spring. The aggregations were pinched off after two plastic bags had been put around each of them to ensure that none of the associated fauna escaped before or after sampling. After the dive each aggregation (still in plastic bags) was put in a separate plastic container and transported back to the laboratory. The volume of each aggregation was measured in litres (l) from the water expelled at submersion (Jensen and Fredriksen 1992), and animals that escaped through the plastic bags during transport were retained on a sieve with a 1.0 mm mesh.

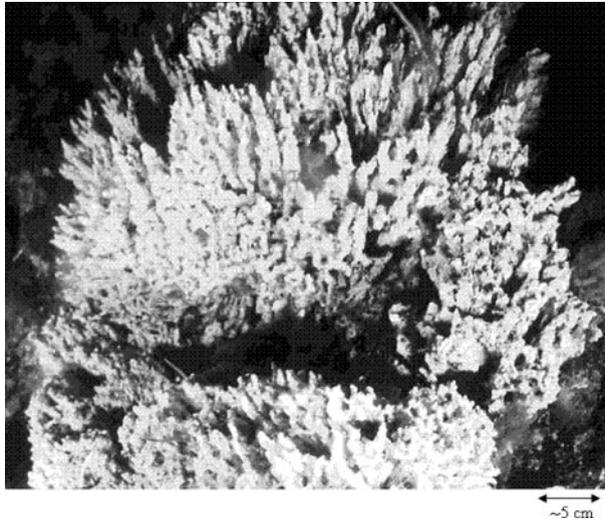


Fig. 2 *Filograna implexa* Berkeley, 1828 aggregate on the wreck of “M/S Flint” in the tidal stream Rysstraumen, North Norway. The picture is approximately 1/3 of natural size. An approximately 5 cm scale is shown on the picture. The aggregate shows two levels of structure scale; (1) millimetres among single tubes entwined into the finger-like projections and (2) centimetres among the finger-like projections

Obtaining the associated fauna of aggregations was problematic as animals were easily destroyed when the brittle aggregations were dismantled. Hydrochloric acid has been used by others to dissolve calcareous aggregations (Haines and Maurer 1980a) but was found to destroy the specimens, making species-identification difficult. We instead initiated an escape of the animals from within the aggregations by creating anoxic conditions in buckets with a lid for 24 to 48 h, following an assumption that O₂ first would be consumed within the aggregate and animals then would follow the O₂ gradient out. Low temperatures (4°C) in darkness gave the best result with most escaped animals compared to with room temperatures when animals died rather than escaping. Animals were retrieved from the bucket water on a sieve with 1.0 mm mesh, and preserved in 96% ethanol. The few animals remaining inside were obtained by dismantling the aggregations tube by tube, using tweezers and a magnifier glass (2x). Cryptic sponges of the class Demospongia were obtained by dissolving the *Filograna* lattice by weak hydrochloric acid. All specimens were afterwards donated to the Zoological Department of Tromsø University Museum.

The aggregations were identified as of the species-complex *Filograna/Salmacina* according to Kupriyanova and Jirkov (1997), but as Faulkner (1930) we observed both operculate and non-operculate specimens. We do not wish to participate in the debate on classification and call the specimens at hand *Filograna implexa* Berkeley, 1828. Specimens of the associated fauna of interest were classified to the lowest possible taxon. In the genera *Musculus* (Mollusca) and *Myxilla* (Porifera), the family Syllidae (Polychaeta), and the phyla Platyhelminthes and Nemertea, specimens were recognised as separate species and numbered. The Syllidae sp. 1 had a varying morphology and may constitute more than just one species. Juvenile specimens were included with adults if identifiable or treated separately, as with *Musculus* spp. (j). In the family Terebellidae (Polychaeta), juveniles were classified as *Thelepus cincinnatus*, which is a very common Terebellid in these waters (Brattegard and Holthe 1997), on the basis of a similar bristle configuration and body

shape. Tube-building serpulids were not recorded quantitatively due to their high similarity to *Filograna* tubes, and were in addition to fragments and decaying specimens omitted from the analyses. All identified specimens were cross-checked with a catalogue of both published and unpublished records in Norwegian waters (Brattegard and Holthe 1997).

Individuals of solitary specimens were counted (anterior parts) and the biomass of all species weighed (wet). Biomass was included to avoid having to estimate the numbers of individuals in colonial species, and for comparison of solitary and colonial species distributions. The fauna was characterised by total species richness, solitary species richness, individual numbers (solitary species) and biomass (all species). Shannon–Wiener diversity indices were calculated from both the biomass composition of all species and from the abundance composition of solitary species using the function $H' = \sum (p_i \times (\log_2 p_i))$ where p_i is the proportion of the i 'th species of the total sample (Krebs 1989).

Relationships of the above parameters with aggregation volume were investigated through regression. Since space often is limiting on hard substrate and new additional space colonised immediately (Jackson 1977), linear trend lines intersecting the origin were used for individual numbers and biomass, which were believed to increase continuously with the additional substrate and cavities provided by larger aggregations. Habitat number is not expected to increase continuously with additional substrate and cavities but rather reach a maximum involving a certain amount of associated species, and geometric trend lines were therefore used for solitary and total species richness regression against aggregation volume.

Results

In totally 4.4 l of *Filograna implexa* aggregations ($n = 8$) we identified 61 solitary species (4663 individuals) and 38 colonial species that weighed 160.3 g together (Table 2). However, many different crustacean specimens were not identified to the species level but rather merged in congregated taxonomic groups (Caprellida, Gammaridea, Isopoda; Table 1, Appendix Table 2), and the total species number was therefore even higher. The *Filograna* aggregations protruded approximately 10 cm from the substrate and covered in total less than 0.05 m². The observed species richness is therefore very high. There were few predominating species. On average, only 16 species were represented by more than three individuals, and eight species with more than 0.5 g of biomass per aggregation. This reflects the very high biodiversity within the small aggregations. Only the congregated taxon Gammaridea spp. was present with more than 100 individuals on average per aggregation (Table 1), but these represented many species. The average *Filograna* aggregate volume was 0.55 l (SE = 0.14), the Shannon–Wiener diversities 2.8 (abundance, SE = 0.29) and 2.7 (biomass, SE = 0.27), the solitary species number 30.4 (SE = 4.0), the total species number 46.9 (SE = 5.6), the individual number 582.9 (SE = 263.1), and the biomass 20.04 g (SE = 5.1) per aggregation. Shannon–Wiener indices varied from low (1.3) to high (3.5), demonstrating from skew to even distributions of species.

The number of individuals (solitary), the biomass, the solitary and total species richness all increased with aggregation volume (Fig. 3). However, the relation of biomass was less linear due to a dominance of the sponge (*Myxilla* sp. 1) in the second largest aggregation and a comparably low biomass in the largest aggregation where animals were of a small size. Interestingly, both the solitary and total species numbers increased geometrically in relation to aggregation volume.

Table 1 Common species in the fauna associated with aggregates ($n = 8$) of *Filograna implexa* Berkeley, 1828, from the wreck of “M/S Flint” in the tidal stream Rysstraumen, northern Norway in spring 1998

(a) Abundance (solitary individuals)		
Species	Mean	SE
Gammaridea spp.	380.0	230.1
Syllidae sp.1	48.88	18.57
Isopoda spp.	17.25	5.31
<i>Ophiopholis aculeata</i>	15.13	3.83
<i>Hiatella arctica</i>	13.25	6.96
Caprellida spp.	11.63	4.13
Nematoda sp.	11.50	6.07
<i>Musculus</i> spp. (juv.)	7.38	2.76
<i>Thelepus cincinnatus</i>	5.75	1.77
<i>Boltenia echinata</i>	5.13	1.90
Syllidae sp.2	4.25	1.92
Terebellomorpha indet.	4.00	1.13
Polynoidae indet	3.25	1.46
Actinaria spp.	3.13	0.93
<i>Eulalia viridis</i>	3.13	1.23
Polydontidae indet.	3.13	1.76
(b) Biomass (grams wet weight)		
Species	Mean	SE
<i>Ophiopholis aculeata</i>	7.46	1.67
<i>Myxilla</i> sp.1	1.77	1.69
<i>Thelepus cincinnatus</i>	1.45	0.45
Halichondria sp.	1.17	0.75
Gammaridea spp.	1.01	0.55
<i>Hyas araneus</i>	0.98	0.62
<i>Lophaster furcifer</i>	0.72	0.48
<i>Hiatella arctica</i>	0.71	0.39

Species regarded as common are those (of the 61 solitary species) occurring with means > 3 individuals per aggregate and/or those (of the totally 99 sp.) with biomass means > 0.5 g biomass per aggregate

Discussion

This study identifies and characterises a very high local species richness and biodiversity at high latitude (69°N). More than 100 species comprising only 160 g of biomass were found within only a 4.4 l volume of *Serpulid polychate* aggregations. In general, average species richness decrease with latitude from the tropics across a range of spatial scales (Stevens 1989; Gaston 1996, 2000). Witman et al. (2004) demonstrated that also local species richness in the marine epibenthos follows this pattern and provided for various latitudes measures of small-scale species richness (0.25 m²). By comparison, the dense and diverse fauna found within *Filograna* aggregations covering less than 0.05 m² represents a local high-latitude biodiversity hotspot that provides an exception to the latitudinal diversity gradient. Other exceptions to the pattern have been reported at various scales by the high-latitude biodiversity hotspots provided by the faunas associated with deep coldwater coral reefs (Jensen and Fredriksen 1992; Freiwald et al. 2004) and other shallow-water Serpulid

polychaete aggregations (Haines and Maurer 1980a, b; Kirkwood and Burton 1988; Moore et al. 1998).

A high fauna density may be sustained in the *Filograna* aggregations by the abundant supply of food particles passing through the tidal inlet from adjacent productive waters each tidal cycle. The increase of fauna density and biomass with aggregation size indicates that colonisation is related to the available surface area provided by aggregation growth (Fig. 3). High benthic densities are also found at high latitudes in tidal inlets in North American waters, but have lower species richness (Odum et al. 1974). The fauna inside the *Filograna* aggregations is very species rich compared to corresponding faunas associated with less heterogeneous biogenic structures. In aggregated clumps of the algae *Lithothamnion* situated in Norwegian waters with similar currents, a medium-dense and less species rich fauna (55 species, 2593 individuals in 1–1.5 m²) has been found (Sneli 1968). The *Filograna* aggregations have a much finer structure with numerous tiny tubes in irregular spatial patterns (Knight-Jones and Moyse 1961; Kupriyanova and Jirkov 1997) and the greater heterogeneity probably offers a higher diversity of microhabitats. Different

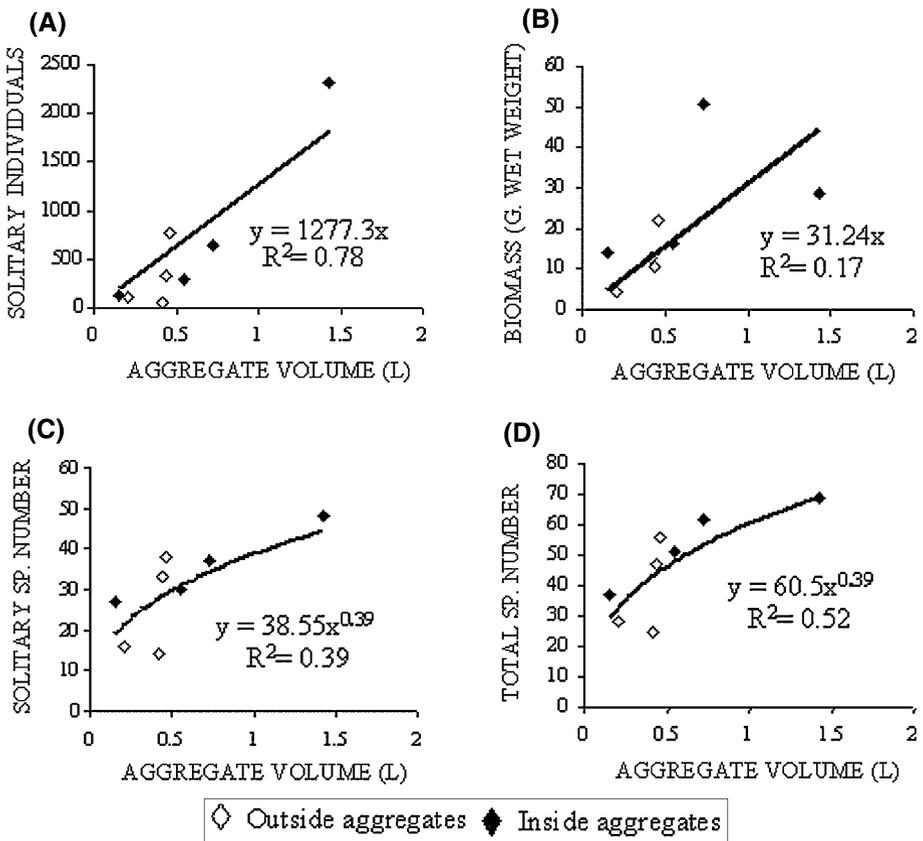


Fig. 3 Relationships between variables of associated faunas and the volume (l) of *Filograna implexa* Berkeley, 1828, aggregates ($n = 8$) from the wreck “M/S Flint” in the tidal stream “Rystraumen” in the northern Norway. Regression equations and coefficients of determination (R^2) are given for the linear trend lines of individual numbers of solitary species (a) and biomass of all species (b), and for the geometric trend lines of solitary species richness (c) and total species richness (d)

species were thus found in variously sized holes and crevices of the *Filograna* aggregations.

Increased microhabitat diversity with increased physical structure is probably the most universal and important of the processes enhancing diversity, especially where biogenic structures or the substratum provide more complexity and attachment sites (Sebens 1991). Structures built by sessile animals increase colonisation of other sessile and motile organisms (Dean 1981; Bros 1987) and aggregated or colonial species decelerate passing water into low, intermediate and strong turbulent flow (Okamura 1984; Sebens et al. 1997) so that microhabitat numbers increase (Sebens 1991). The great heterogeneity of *Filograna* aggregations probably decelerates water into a variety of water velocities suitable for species with different optimal foraging velocities. This may explain the high recorded number of different filter feeders, ranging from quite passive (e.g. poriferans, bryozoans, hydrozoans) to active, pumping water with a muscle apparatus (e.g. bivalves, some ascidians). It is also characteristic that the organism with the highest biomass (the echinoderm *Ophiopholis aculeata*) can live with the central disc protected within the aggregates but with the filter-feeding arms emerging out into the water passing by. The increase of habitat diversity with heterogeneity is supported by the increase of species richness with increasing size of *Filograna* aggregations (Fig. 3), suggesting that new tubes and aggregation growth forming new holes, crevices and ridges involve not just more space for additional individuals but also new microhabitats for new species. Similar increases in species number with the size of biogenic structures are also reported for aggregations of another serpulid at deeper waters (Kaiser et al. 1999) and a deep-water coral (Jensen and Fredriksen 1992). A further increase in microhabitat diversity can be created by species already present, as these may involve the coexistence of several new species (Sebens 1991). Within the *Filograna* aggregations both detritivores, scavengers and carnivores were thus present (Table 1 and see Appendix Table 2).

Another effect that probably increases the diversity of the fauna inside *Filograna* aggregations is their exclusion of predators. Rigid structural complexity above a certain threshold lowers predation rates (Coull and Wells 1983; Walters 1992), and is probably the second most universal process enhancing diversity, especially when predators are large and possibly generalised in their diet (Sebens 1991). *Filograna* aggregations provide refuge against large predators like the sea urchin *Strongylocentrotus droebachiensis*, which is regarded a key species in nearby areas (Gulliksen and Sandnes 1980), adult fish, crabs (*Hyas araneus*), and starfish (e.g. *Asterias rubens*). However, micro-predators like gammarids, caprellids, and certain polychaetes (e.g. *Syllidae* spp., *Eulalia viridis*, *Nereis pelagica*) were found inside aggregations and may limit the aggregation fauna diversity.

Wrecks also provide structural complexity and function as artificial reefs (Bohnsack 1991; Bohnsack et al. 1997; Bortone 1998) and their attached fauna is reported to increase in density and diversity with current exposure and lowered sedimentation (Baynes and Szmant 1989). However, these factors together with the slope of the substrate are more important than substrate type in distinguishing wreck faunas from natural substrata (Gabbrielle et al. 1999) and succession on wrecks seems to follow a classical pattern (Warner 1985; Dipper 1991).

We conclude that also at high latitudes, heterogeneity introduced by biogenic structures may increase species richness and biodiversity. The observed species richness and biodiversity was very high compared to the high latitude and small sample sizes, and represent local biodiversity hotspots that provide exceptions to the latitudinal diversity gradient. Comparison with other studies and the relationship between species number and aggregation size in this study suggest that spatial heterogeneity is the main reason for the

elevated diversity at such biodiversity hotspots associated with biogenic structures. Such structures should therefore be mapped and conserved for an optimal management.

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Appendix

Table 2 The species of the fauna associated with aggregates of *Filograna implexa* Berkeley, 1828, sampled from the wreck of “M/S Flint” in the tidal stream Ryastraumen, North Norway the spring of 1998

Species	Abundance (solitary individuals)		Biomass (grams wet weight)	
	Mean	SE	Mean	SE
Porifera				
<i>Chladrina coriacea</i> (Montagu, 1812)			0.01	0.01
<i>Leucosolenia</i> sp.			0.01	0.01
<i>Grantia compressa</i> (Fabricius, 1780)			0.15	0.09
<i>Scypha ciliata</i> (Fabricius, 1780)			0.11	0.05
Adociidae indet.			0.04	0.04
<i>Halichondria</i> sp.			1.17	0.75
Haleciidae indet.			0.01	0.01
<i>Hymedesmia</i> sp.			0.32	0.16
<i>Mycale</i> sp.			0.29	0.16
<i>Myxilla</i> sp.1			1.77	1.69
<i>Myxilla</i> sp.2			0.01	0.01
Cnidaria				
Actinaria spp. (j)	3.13	0.93	0.11	0.06
<i>Calycella syringa</i> (L., 1767)			0.01	0.01
<i>Eudendrium ramosum</i> (L., 1758)			0.01	0.01
<i>Lafoea dumosa</i> (Fleming, 1828)			0.01	0.01
<i>Serturella polyzonias</i> (L., 1758)			0.06	0.05
<i>Tubularia larynx</i> Ellis & Solander, 1786			0.19	0.19
Hydroida indet.			0.01	0.01
Platyhelminthes				
Platyhelminthes sp.1	2.13	0.67	0.01	0.01
Platyhelminthes sp.2	0.38	0.26	0.05	0.03
Nematoda				
Nematoda sp.	11.50	6.07	0.01	0.01

Table 2 continued

Species	Abundance (solitary individuals)		Biomass (grams wet weight)	
	Mean	SE	Mean	SE
Nemertea				
Nemertea sp.1	1.38	0.86	0.01	0.01
<i>Lineus ruber</i> (O.F.Müller, 1774)	1.38	0.52	0.14	0.06
Mollusca				
Ophistobranchia indet.	0.38	0.18	0.01	0.01
<i>Colus gracilis</i> (da Costa, 1778) (j)	2.88	2.20	0.08	0.05
<i>Heteranomia squamula</i> (L., 1758) (j)	1.50	0.76	0.05	0.02
<i>Modiolus modiolus</i> (L., 1758) (j)	1.50	0.96	0.03	0.03
<i>Musculus</i> sp.1 (*)	1.38	0.84	0.28	0.21
<i>Musculus</i> sp.2	0.50	0.38	0.02	0.01
<i>Musculus</i> spp. (j)	7.38	2.76	0.01	0.01
<i>Chlamys islandica</i> (Müller, 1776) (j)	0.75	0.75	0.01	0.01
<i>Hiatella arctica</i> (L., 1758) (j)	13.25	6.96	0.71	0.39
Annelida				
Polychaeta indet.	0.5	0.27	0.01	0.01
Terebellomorpha indet. (j)	4	1.13	0.05	0.03
<i>Cirratulus cirratulus</i> (O.F.Müller, 1776)	0.5	0.5	0.01	0.01
Nereididae indet.	0.25	0.25	0.01	0.01
<i>Nereis pelagica</i> (L., 1758)	1.75	0.90	0.21	0.12
<i>Eulalia viridis</i> (L., 1767)	3.13	1.23	0.03	0.01
Polydontidae spp.	3.13	1.76	0.02	0.01
Polynoidae spp.	3.25	1.46	0.28	0.11
<i>Myxicola infundibulum</i> (Renier, 1804)	0.63	0.63	0.01	0.01
<i>Pseudopotamilla</i> sp.	2.75	1.37	0.02	0.01
Sabellidae indet.	0.38	0.26	0.01	0.01
<i>Sabella penicillus</i> (L., 1767)	0.13	0.13	0.03	0.03
Serpulidae indet.	0.13	0.13	0.01	0.01
<i>Chitinopoma</i> sp.	0.75	0.49	0.01	0.01
<i>Filograna implexa</i> Berkeley, 1828	Not recorded			
<i>Hydroides norvegica</i> Gunnerus, 1768	0.88	0.44	0.03	0.02
<i>Pomatoceros triqueter</i> (L., 1767)	2.75	1.16	0.06	0.03
Sigalionidae sp.	0.38	0.26	0.01	0.01
<i>Jugaria granulata</i> (L., 1767)	2.25	1.37	0.01	0.01
Syllidae indet.	0.38	0.38	0.01	0.01
Syllidae sp.1 (*)	48.88	18.57	0.12	0.05
Syllidae sp.2 (*)	4.25	1.92	0.02	0.01
Syllidae sp.3 (*)	0.38	0.18	0.01	0.01
<i>Proceraea</i> sp.	0.5	0.38	0.01	0.01
<i>Polycirrus</i> sp.	0.13	0.13	0.01	0.01
<i>Thelepus cincinnatus</i> (O.Fabricius, 1780) (*)	5.75	1.77	1.46	0.45

Table 2 continued

Species	Abundance (solitary individuals)		Biomass (grams wet weight)	
	Mean	SE	Mean	SE
Crustacea				
<i>Chirona hammeri</i> (Ascanius, 1767) (j)	2	1.12	0.19	0.11
<i>Verrucia stroemi</i> (O.F.Müller, 1776) (*)	0.88	0.52	0.01	0.01
Caprellida spp.	11.63	4.13	0.08	0.03
Gammaridea spp.	380	230.1	1.01	0.55
<i>Hyas araneus</i> (L., 1758) (j)	0.63	0.18	0.98	0.62
<i>Thorulus chranchii</i> (Leach, 1817)	0.13	0.13	0.01	0.01
Isopoda spp.	17.25	5.31	0.05	0.02
Pycnogonida				
Pycnogonida sp.1	1.88	1.19	0.01	0.01
Bryozoa				
<i>Crisella producta</i> (Smitt, 1865)			0.01	0.01
<i>Crisia eburnea</i> (L., 1758)			0.01	0.01
<i>Crisia</i> sp.			0.01	0.01
<i>Crisia klugei</i> Ryland, 1967			0.01	0.01
<i>Filicrisia</i> sp.			0.01	0.01
<i>Diplosolen obelia</i> (Johnston, 1838)			0.02	0.01
<i>Lichenopora verrucia</i> (O.Fabricius, 1780)			0.01	0.01
Lichenoporidae indet.			0.01	0.01
<i>Oncousoecia</i> sp.			0.02	0.02
<i>Idmidronea atlantica</i> (Forbes, in Johnston, 1847)			0.01	0.01
<i>Tubulipora lillicea</i> (Pallas, 1776)			0.01	0.01
<i>Tubulipora penincillata</i> (O.Fabricius, 1780)			0.06	0.04
Tubuliporidae indet.			0.01	0.01
Cheilostomata indet.			0.01	0.01
<i>Tricellaria ternata</i> (Ellis & Solander, 1786)			0.34	0.20
Echinodermata				
<i>Lophaster furcifer</i> (Düben & Koren, 1846)(j)	1.5	0.38	0.72	0.48
<i>Strongylocentrotus droebachiensis</i> (O.F.Müller, 1776) (j)	0.13	0.13	0.01	0.01
<i>Cucumaria frondosa</i> (Gunnerus, 1770) (j)	0.75	0.31	0.34	0.25
<i>Psolus</i> sp. (*)	1.88	0.90	0.01	0.01
<i>Ekmania barthi</i> (Troschel, 1846) (*)	0.38	0.26	0.01	0.01
<i>Ophiopholis aculeata</i> (L., 1767) (*)	15.13	3.83	7.46	1.67
<i>Ophiotrix fragilis</i> (Abildgaard, 1789)	0.38	0.26	0.09	0.09
Chordata				
Asciacea indet. (*)	0.38	0.26	0.01	0.01
<i>Ascidia</i> sp. (j)	1.88	0.95	0.01	0.01
<i>Ascidia callosa</i> Stimpson, 1852 (*)	1.25	0.45	0.06	0.02
<i>Ascidia obliqua</i> Alder, 1863 (*)	0.88	0.48	0.01	0.01
<i>Didemnum</i> sp.			0.10	0.06
<i>Molgula</i> sp. (*)	1.75	0.82	0.02	0.01

Table 2 continued

Species	Abundance (solitary individuals)		Biomass (grams wet weight)	
	Mean	SE	Mean	SE
<i>Aplidium glabrum</i> (Verrill, 1871) (*)			0.24	0.20
<i>Aplidium</i> sp. (*)			0.01	0.01
<i>Aplidium pallium</i> (Verrill, 1871) (*)			0.02	0.02
<i>Synoicum</i> sp. (j)			0.01	0.01
<i>Boltenia echinata</i> (L., 1767) (j)	5.13	1.90	0.16	0.11
Plant kingdom				
<i>Fucus</i> eggs			0.01	0.01

Species classified by phyla, class or order, and family, and aggregate means and standard errors of abundance (*solitary species*) and biomass (*wet weight*) are presented non-standardised. Weights less than 0.01 g are denoted 0.01 because alcohol wet weight not gave precise measures. Not present species are presented as blanks, as are abundance data of colonial species

(*) Taxa represented also by juveniles

(j) Taxa represented mostly by juveniles

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