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Do bioturbation and consumption affect coastal Arctic marine soft-bottom communities?

Sina Petrowski · Markus Molis · Katrin Schachtl · Christian Buschbaum

Abstract Biotic factors such as bioturbation and predation affect abundance and species composition of marine soft-bottom communities from tropical to temperate regions, but their impact has been rarely investigated in Arctic coastal systems. By conducting a factorial manipulative field experiment, we excluded the bioturbating lugworm *Arenicola marina* and predacious consumers from a sedimentary nearshore area in Kongsfjorden (Spitsbergen) for 70 days to explore their role in structuring the benthic community. The removal of *A. marina* caused an increase in average species number by 25 %, a doubling increase in the average number of individuals and an increase in dry mass of benthic organisms by, on average, 73 % in comparison with untreated areas. Additionally, community composition was significantly modified by lugworm exclusion resulting in higher average densities of the cumacean *Lamprops fuscatus* (4.2-fold), the polychaete worms *Euchone analis* (3.7-fold) and *Pygospio cf. elegans* (1.5-fold), the bivalve *Crenella decussata* (2.8-fold) and the amphipod *Crassicorophium crassicorne* (1.2-fold), which primarily contribute to the observed differences. Consumer exclusion, by contrast, showed no effects on the response variables. This result was independent from bioturbation due to missing interaction between both biotic factors. We conclude that present levels of bioturbation may considerably affect Arctic coastal soft-bottom communities. In contrast, predation by macro-epibenthic consumers currently seems to be of minor importance. This might change in a predicted warmer Arctic with assumed higher predator abundances and a northward expansion of boreal consumers.

Keywords Bioturbation · Predation · Soft-bottom benthos · Arctic shallow water · Field experiment

Introduction

The identification of general mechanisms controlling structure and dynamics of coastal species assemblages is a major goal of marine community ecology. Besides competition, especially predation and bioturbation are considered to be important biotic factors determining the species composition of marine soft-bottom communities from temperate to tropical systems (e.g. Wilson 1991; Woodin 1999; Berkenbusch et al. 2000; Cadée 2001; Reise 2002; Flach 2003; Meysman et al. 2006; Volkenborn and Reise 2007; Pillay and Branch 2011; Passarelli et al. 2014). While the consumption by predators affects directly prey population dynamics, bioturbation by burrowing organisms such as polychaetes, holothurians and crustaceans can cause substantial sediment disturbances and, thus, sediment-mediated indirect species interactions (Wilson 1991; Reise 2002; González-Ortiz et al. 2014). Sediment-

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reworking polychaetes such as the lugworm *Arenicola marina* or callianassid shrimps, for example, preempt the habitat by high rates of sediment turnover with inhibitive but also facilitative effects for other organisms (Riisgard and Banta 1998; Reise 2002; Volkenborn and Reise 2006).

To explore the effects of species interactions on community structure and population dynamics in soft-bottom environments, descriptive investigations may reveal general patterns (Rabaut et al. 2007), but they are not suitable for identifying the underlying processes (Volkenborn and Reise 2006). Thus, manipulative experiments are crucial to specify the linkage from species interactions to community patterns. One appropriate approach is the intentional removal or addition of key organisms in field experiments (Paine 1980; Wilson 1991; Reise 2002). This approach has been, for instance, successfully used in eliciting predation and bioturbation as important drivers of species diversity and dynamics in marine soft-sediment communities of lower latitudes (e.g. Reise 1985; Flach 1992; Passarelli et al. 2014 and references therein). However, as far as we know such manipulative field experiments have rarely been performed in polar marine environments (but see Konar 2007, 2013; Beuchel and Gulliksen 2008), with no information available on the effects of consumption and bioturbation on Arctic soft-bottom communities. Thus, most information on species occurrence, interactions and population dynamics in benthic Arctic coastal systems relies on observational studies (Hop et al. 2002).

The objective of this high-latitude study was to investigate the effects of consumption and bioturbation on an Arctic marine soft-sediment species assemblage by conducting a combined bioturbator and predator exclusion field experiment. Our study was performed in Kongsfjorden (West Spitsbergen), an intensively studied area for which the physical conditions and biota are well documented (Hop et al. 2002; Svendsen et al. 2002; Wlodarska-Kowalczuk and Pearson 2004; Kaczmarek et al. 2005; Kedra et al. 2010; Voronkov et al. 2013 and references therein). For the intertidal and shallow subtidal soft-bottom area in Kongsfjorden, it is generally assumed that occurrence and dynamics of species assemblages are predominantly triggered by abiotic factors such as ice scouring, meltwater discharge and a high sedimentation rate provoking the colonization of these areas with opportunistic, small macrofauna organisms (Ambrose and Leinaas 1988; Gutt 2001; Bick and Arlt 2005; Wlodarska-Kowalczuk et al. 2005; Laudien et al. 2007; Veit-Köhler et al. 2008). These species are well adapted to natural disturbances, and their high reproduction rates enable them to quickly re-colonize disturbed areas (Bick and Arlt 2005; Conlan and Kvitek 2005; Kuklinski et al. 2013). Thus, it can be assumed that biotic factors are of minor importance, and accordingly, we tested the null-hypothesis that consumption and bioturbation by larger organisms such as predatory crabs and burrowing lugworms have no influence on the abundance, diversity and species composition

of a soft-bottom species assemblage. But, if the null-hypothesis has to be rejected, our field experiment reveals strong evidence that also biotic factors can affect coastal sedimentary marine Arctic communities.

The importance of biotic effects for shaping Arctic benthic assemblages will presumably increase when global warming and rising seawater temperature reduce the physical stress for shallow water communities at higher latitudes, due to a shorter ice-season, reduced ice coverage, lower ice thickness and less frequent iceberg scour. At the same time, higher temperature should increase the activity level of consumers and bioturbators. This may lead to an increase in the frequency of species interactions and, thus, in a higher importance of biotic control mechanisms affecting Arctic coastal communities (Weslawski et al. 2011). Therefore, our study focuses on biotic factors, which have rarely been so far considered in polar regions and which may constitute fundamental processes in a forthcoming warmer Arctic marine ecosystem.

Materials and methods

Study site

All experimental field work was conducted at Brandal (N 78°56.869′, E 011°51.177′), a shallow water, soft-sediment site located at the border between the middle and transitional zone on the southern shore of Kongsfjorden, West Spitsbergen. The fjord is influenced by warmer Atlantic and colder Arctic water masses and harbours a mixture of cold temperate and Arctic flora and fauna (Hop et al. 2002). While oceanographic conditions influence the outer fjord, the inner part is strongly affected by large glaciers (Svendsen et al. 2002). Icebergs and floating ice are particularly frequent during summer months (Dowdeswell and Forsberg 1992; Wlodarska-Kowalczuk and Pearson 2004). These glaciers form steep physical gradients in the water body of the fjord, especially in sedimentation rate and freshwater input (Svendsen et al. 2002; Hop et al. 2002). Thus, changes in benthic community composition and abundance from the inner to the outer fjord can be observed (Hop et al. 2002). Semidiurnal tides with a range of about 2 m generate tidal currents of moderate strength (Ito and Kudoh 1997). The seafloor at the study area gently slopes from the shore to a water depth of about 11 m before it drops to a depth of >100 m (pers. comm. M. Schwanitz). Sediment type ranges from fine sand to coarse silt, and in terms of species number, the soft-bottom community at Brandal is dominated by polychaetes, molluscs and crustaceans (Folk and Ward 1957; Herrmann 2006). Close to the seafloor, mean water temperature was 5.4 °C (pers. measurements, min = 3.4 °C, max = 7.0 °C, HOBO®Data Logger) during the experimental period from June to

August 2012. A surface water salinity of 32 (Svendsen et al. 2002) indicates that Brandal is a fully marine site.

Experimental design and set-up

Using a factorial experiment with a nested design, the separate and combined effects of bioturbation and consumption on the diversity and species composition of benthic infauna communities were assessed.

The complete experimental set-up was installed at an average water depth of 7 m in a 9 m × 12 m area on 19 June 2012, i.e. the day when the experiment started. The experiment was terminated on 28 August 2012. Here, a total of 15 plots (1.2 m × 1.2 m) were arranged in five rows, with each row containing three plots, each plot with a different bioturbation treatment (Fig. 1). Within rows, the three bioturbation treatments were randomly distributed. One bioturbation treatment excluded bioturbators by burying a black polyethylene mesh (mesh size 0.4 cm × 0.4 cm) at least 5 cm deep into the sediment. The mesh was fixed at its corners with 40-cm iron rods and prevents the occurrence of large bioturbators such as the lugworm *Arenicola marina* as shown in previous studies (Volkenborn et al. 2007). The second bioturbation treatment was used to test for possible artefacts caused by the mesh burial procedure (=procedural controls). In these procedural control plots, the top 5 cm of sediment was removed like in the first bioturbation treatment, but no mesh was added before the sediment was returned. The location of plots designated for the third bioturbation treatment, i.e. unmanipulated controls, was marked with 40-cm iron rods that were pushed into the sediment at each corner of a plot. The efficacy of treatments to exclude bioturbating organisms, such as the lugworm *A. marina*, was controlled biweekly by counting the number of mounds that were generated by these animals in all 15 plots. To manipulate consumer occurrence (mainly the spider crab *Hyas araneus* and the dogwhelk *Buccinum* sp.), cylindrical cages of 35 cm height and 25 cm in diameter were fixed with three 40-cm iron rods to the sea-floor (Fig. 2). For exclusion of macrobenthic consumers, complete cages were used. These were constructed with two PVC rings (25 cm in diameter) that were 35 cm apart. A polyethylene mesh (mesh size 0.5 cm × 0.5 cm) was wrapped around both rings and permanently fixed with cable ties. The cage top was also covered with the polyethylene mesh, while the bottom side, which was facing in the set-up to the seafloor, remained open. For a second treatment, open cages were constructed to test for cage artefacts. The top of open cages was not covered by a mesh, and three holes (10 cm × 10 cm) were cut into the mesh near the bottom ring to allow consumers to enter and exit cages. As a third treatment areas without cages were used as controls; i.e. no experimental manipulation of consumer densities. Each of the three consumer treatments [(1)

closed cages, (2) open cages and (3) no cages] was twofold replicated on each plot (total of 90 experimental units, Fig. 1). The minimum distance between areas designated for consumer treatments was 30 cm to each other and 10 cm to plot margins to minimize margin effects (Fig. 1).

The presence of the crab *H. araneus* was confirmed from regular catches with unbaited fish traps and direct observations in the field. However, a quantification of its density was not feasible, because of the patchy and irregular occurrence of *H. araneus*.
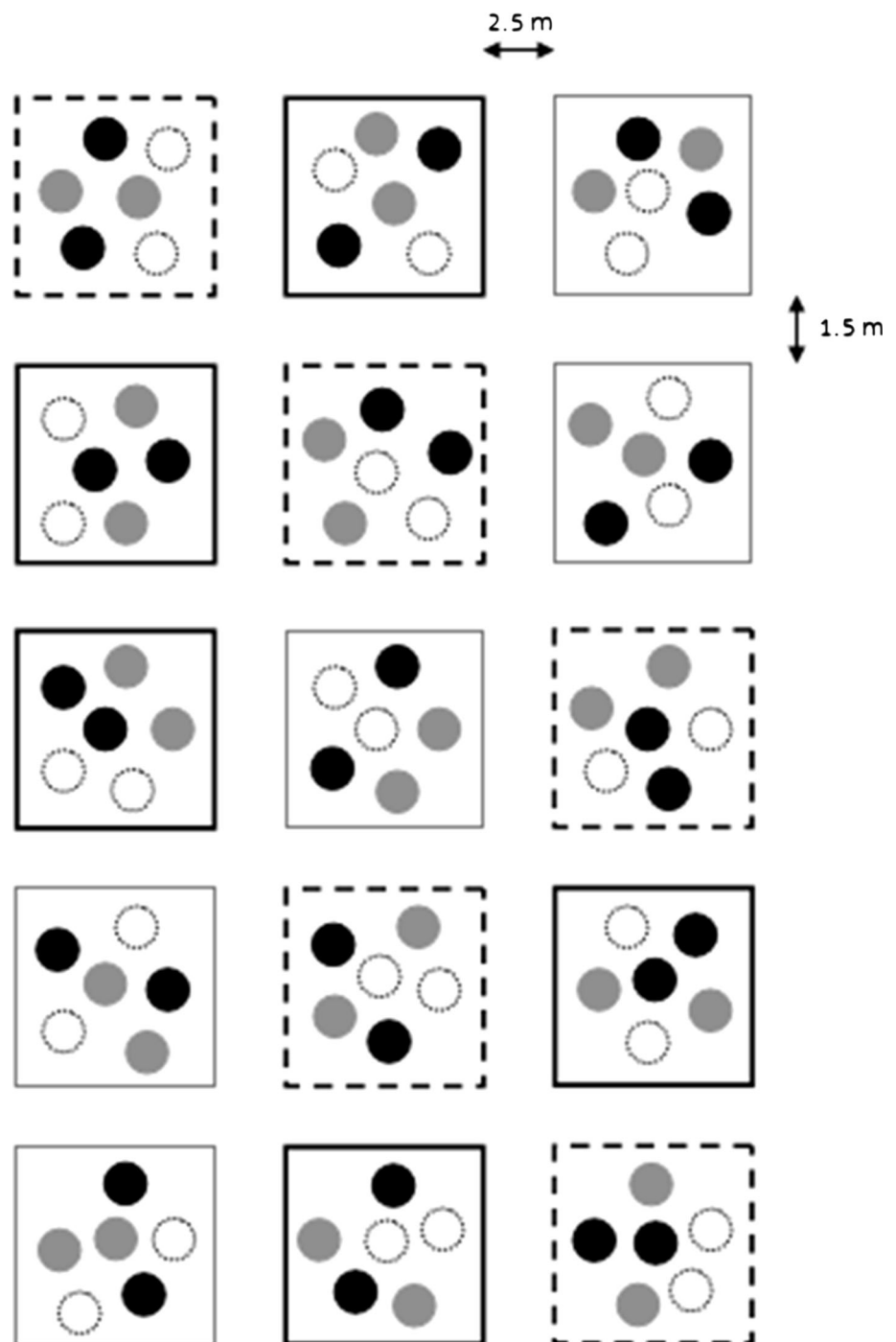
To get an estimate on the density of the lugworm *A. marina* as the largest bioturbating species at the study site, the mounds that were generated by *A. marina* were counted per square metre ($n = 6$) in randomly chosen plots near the experimental set-up on 10, 18 and 31 July 2012. Furthermore, the number of individuals of the second largest bioturbating species, the sea cucumber *Chirodota laevis*, was quantified from 50 cm × 50 cm quadrats after sieving the top 5 cm of airlifted sediment on 2 and 16 August 2012 ($n = 6$). All work at the set-up and measurements were conducted by SCUBA diving.

Determination of sample size and depth

A pilot study was conducted to determine the minimum sample size needed to sample a representative number of species of the prevailing benthic community at Brandal. For this purpose, 12 samples were taken with each of two different corer sizes, i.e. 3.2 and 5.2 cm in diameter that were pushed 10 cm deep into the sediment. All corer samples were transported within 1 h after sampling to the marine laboratory at Ny-Ålesund. Here, all specimens were identified, and cumulative species numbers were calculated for each corer type separately using all 12 samples. Species accumulation curves were plotted for each corer size based on a random order of chosen cores. Both plots show asymptotic curvatures and indicate that, on average, 38 % more species were collected with the larger than with the smaller corer type (Fig. 3). No species additions were recorded after eight or nine cores, which were sampled with the larger and smaller corer type, respectively. This suggests that eight large corers may be sufficient to generate a representative sample of the species inventory that was present at the study site.

We also determined the critical depth of sediment cores by taking corer samples of 10 cm depth at Brandal ($n = 5$), which were divided into two parts (upper and lower 5 cm). Afterwards, the number of species and number of individuals were recorded from both parts. This study showed that 96 % of all species and 98 % of all individuals occurred in the upper 5 cm of the sediment. Consequently, all samples in this study were taken with the larger sediment corer of 5.2 cm diameter (sampled surface area of 21 cm^2) that was pushed 5 cm deep into the sediment.

Fig. 1 Schematic spatial arrangement of bioturbation and consumer treatments. *Quadrates* indicate plot margins: *thick solid lines* represent plots with mesh (i.e. with mat, exclusion of bioturbators), *dashed lines mark* procedural controls (i.e. without mat, burial disturbance), and *thin solid lines* indicate un-manipulated controls. *Circles mark* consumer treatments with closed cages (*grey*), open cages (*black*) and no cages (*white*). Note that scheme is not to scale

Sampling of species assemblage

Two dates for sampling of the community were scheduled. First, samples were taken 7 days after the manipulation started (26 June 2012), to test whether diversity and species composition of infauna communities were still affected from mesh burial activities. Therefore, one core was taken from uncaged areas of each plot where the sediment was disturbed (procedural control of bioturbation treatment)

and from each un-manipulated plot ($n = 5$). Plots with a buried mesh were not sampled.

Second, at the end of the 70-day experimental period (28 August 2012), one core was taken from each experimental unit, i.e. a total of two cores of each consumer treatment of each plot ($n = 90$). The cores were transported ≤2 h to the Marine Laboratory of Ny-Ålesund and stored for <4 days in a cooler at 5 °C until they were analysed. Before the analysis, samples were rinsed with filtered seawater over a

Fig. 2 Picture from the underwater set-up showing one bioturbation plot with two closed and two open cages
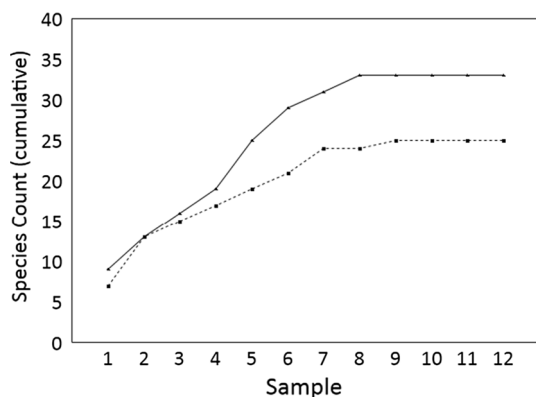

Fig. 3 Species-sample curves for benthic infauna at Brandal using two different corer sizes. The *dashed line* represents a corer size of 3.2 cm, and the *solid line marks* a corer size of 5.2 cm in diameter

0.5-mm sieve and retained organisms were separated from the sediment. All living animals were counted and identified to the lowest possible taxonomic level using a stereomicroscope. The number of species and number of individuals were used to deduce species richness (S), i.e. the total number of taxa, and to calculate Pielou's evenness ($J = H'/\log S$), where H' is the Shannon index, to describe how evenly individuals are distributed across taxa and samples. Dry mass of all organisms of each sediment core was determined on a laboratory balance to the nearest 0.001 g after drying the organisms in an oven at 60 °C to constant weight.

Statistical analysis

Data from the first sampling date were used to test for the effects of mesh burial activity (2 levels, fixed) on diversity and structure of infauna assemblages with Student's t tests and one-way PERMANOVA, respectively ($n = 5$). Data

on species richness, evenness, abundance and dry mass from the second sampling date were analysed using a three-way nested ANOVA, and data on species composition were analysed with a three-way nested PERMANOVA. In all these analyses, factors were bioturbation (three levels, fixed), consumers (three levels, fixed) and plot (fifteen levels, random). Herein, complete or sequential removal of random sources of variance from the ANOVA and PERMANOVA models, recalculation of residuals and selection of appropriate denominators were done when random sources of variance were non-significant at $\alpha \geq 0.25$ (Quinn and Keough 2002, p. 260). Prior to the analysis of data with Student's t tests, normality was confirmed with a Kolmogorov–Smirnov test. For Student's t tests and ANOVAs, homogeneity of variances was confirmed with Levine's and Cochran's test, respectively, and, if necessary, data (i.e. number of individuals and dry mass) were square-root-transformed to meet the assumptions. Data with heterogeneous variances after transformation (i.e. number of *A. marina* mounds) were analysed with Kruskal–Wallis test. Following the recommendation by Clarke and Warwick (2001), data used in PERMANOVAs were routinely square-root-transformed prior to the calculation of Bray–Curtis similarity indices to account for contribution of rarer species to similarity. The Monte Carlo p value was added for PERMANOVAs using less than the selected number of 9,999 permutations. MDS plots were generated to illustrate PERMANOVA results, and a SIMPER analysis was used to determine the contribution of taxa to significant differences in species composition among treatments.

Results

Species occurrence

In total, 73 invertebrate taxa were identified at Brandal during this study in summer 2012. Four of those species have not been reported from Svalbard so far, i.e. the brittlestar *Ophiura albida*, the hermit crab *Anapagurus chiroacanthus* and the polychaete worms *Clymenura tricirrata* and *Ophelia rathkei*. Six additional species are known from Svalbard, but have not been reported from Kongsfjorden, namely the gastropods *Onoba mighelsii* and *Retusa obtusa*, the bivalve *Mya arenaria*, the crustacean *Caprella linearis* as well as the polychaete worms *Arenicola marina* and *Pygospio* cf. *elegans* (Table 1). The community at Brandal was dominated by polychaetes (26 species), followed by crustaceans (14 species) and bivalves (14 species) representing together 77 % of the total species number. The five most abundant species in unmanipulated experimental units during the final sampling at the end of August were

Table 1 List of taxa identified in samples collected in summer 2012 at Brandal

Platyhelminthes
  Platyhelminthes indet.
Nematoda
  Nematoda indet.
Nemertea
  Nemertea indet. 1
  Nemertea indet. 2
Cephalorhynchus
  Priapulida
    Priapulus caudatus (Lamarck, 1816)
Cnidaria
  Anthozoa
    Edwardsia fusca (Danielssen, 1890)
Echinodermata
  Holothuroidea
    Chiridota laevis (O. Fabricius, 1780)
  Ophiuroidea
    Ophiura albida (Forbes, 1839)[a]
Mollusca
  Bivalvia
    Astarte sulcata (da Costa, 1778)
    Axinopsida orbiculata (G. O. Sars, 1878)
    Crenella decussata (Montagu, 1808)
    Cyrtodaria siliqua (Spengler, 1793)
    Hiatella arctica (Linnaeus, 1767)
    Bivalvia indet
    Liocyma fluctuosa (Gould, 1841)
    Macoma sp.
    Montacuta spitzbergensis (Knipowitsch, 1901)
    Mya arenaria (Linnaeus, 1758)[b]
    Mya truncata (Linnaeus, 1758)
    Pandora glacialis (Leach in Ross, 1819)
    Serripes groenlandicus (Mohr, 1786)
    Thracia sp.
  Gastropoda
    Buccinum sp.
    Cylichna sp.
    Lunatia pallida (Broderip & Sowerby I, 1829)
    Margarites sp.
    Naticidae sp.
    Onoba mighelsii (Stimpson, 1851)[b]
    Retusa obtusa (Montagu, 1803)[b]
    Skenea sp.
Arthropoda
  Arachnida
    Acarina indet.
  Crustacea, Malacostraca
    Anapagurus chiroacanthus (Lilljeborg, 1856)[a]
    Caprella linearis (Linnaeus, 1767)[b]

Table 1 continued

    Crassicorophium crassicorne (Bruzelius, 1859)
    Eualus gaimardi gaimardii (Edwards, 1837)
Gammarus sp.
    Hyas araneus (Linnaeus, 1758)
    Lamprops fuscatus (Sars, 1865)
    Monoculodes packardi (Boeck, 1871)
    Orchomenella minuta (Krøyer, 1846)
    Pleustes panoplus (Krøyer, 1838)
    Priscillina herrmanni (d'Udekemd'Acoz, 2006)
    Synidotea nodulosa (Krøyer, 1846)
    Thysanoessa inermis (Krøyer, 1846)
  Crustacea, Maxillopoda
    Copepoda indet.
  Crustacea, Ostracoda
    Ostracoda indet.
Annelida
  Polychaeta
    Arenicola marina (Linnaeus, 1758)[b]
    Capitella capitata (Fabricius, 1780)
    Chaetozone setosa (Malmgren, 1867)
    Clymenella sp.
    Clymenura tricirrata (Arwidsson, 1906)[a]
    Clymenura sp.
    Dipolydora quadrilobata (Jacobi, 1883)
    Euchone analis (Krøyer, 1865)
    Glycera sp.
    Maldanidae indet. 1
    Maldanidae indet. 2
    Maldanidae indet. 3
    Maldanidae indet. 4
    Marenzelleria wireni (Augener, 1913)
    Nephtys sp.
    Ophelia rathkei (McIntosh, 1908)[a]
    Ophelina sp.
    Owenia fusiformis (Delle Chiaje, 1844)
    Pholoe assimilis (Oersted, 1845)
    Phyllodoce groenlandica (Oersted, 1842)
    Praxillella sp.
    Pygospio cf. elegans (Claparède, 1863)[b]
    Scalibregma sp.
    Spio armata (Thulin, 1957)
    Terebellidae juv.
    Travisia forbesii (Johnston, 1840)
Hemichordata
  Enteropneusta
    Enteropneusta indet.

[a] Taxon not reported for Svalbard

[b] Taxon not reported for Kongsfjorden, but for Svalbard, according to Gulliksen et al. 1999; Kaczmarek et al. 2005; Laudien et al. 2007; Włodarska-Kowalczuk 2007; Voronkov et al. 2013

Table 2 Three-way nested ANOVAs analysing the effects of bioturbation on species richness, number of infauna individuals, evenness and dry mass between different consumer treatments

Source	Species richness				# Individuals			
	df_{pooled}	F	p	MQ_{den}	df	F	p	MQ_{den}
Bioturbation, B	2	4.55	**0.034**	Plot(B)	2	20.34	>**0.001**	Plot(B)
Consumption, C	2	0.40	0.672	Pooled	2	1.50	0.234	C × plot(B)
B × C	4	1.62	0.179	Pooled	4	1.14	0.350	C × plot(B)
Plot(B)	12	2.26	**0.018**	Pooled	12	1.77	0.084	Residual
C × plot(B)		0.96	0.537	Residual	24	1.60	0.087	Residual
Residual	45				45			
Pooled	69				No pooling			

Source	Evenness				Dry mass			
	df_{pooled}	F	p	MQ_{den}	df_{pooled}	F	p	MQ_{den}
Bioturbation, B	2	1.46	0.238	Pooled	2	4.95	**0.009**	Pooled
Consumption, C	2	1.62	0.205	Pooled	2	2.70	0.074	Pooled
B × C	4	0.80	0.542	Pooled	4	0.33	0.860	Pooled
Plot(B)		1.014	0.446	Pooled		1.28	0.293	Pooled
C × plot(B)		0.98	0.512	Residual		0.47	0.976	Residual
Residual	45				45			
Pooled	81				81			

Elimination of random factors and recalculation of residuals were done after verifying that the variance of random factor(s) = 0, i.e. not significant at $\alpha \geq 0.25$, where used denominator mean square (MQ_{den}) is shown for each source of variation in columns MQ_{den}. Pooled term = random factor(s) + Residual, df_{pooled} = degrees of freedom after elimination of random factor(s), significant results at $\alpha \leq 0.05$ in bold, $n = 5$

the cumacean *Lamprops fuscatus* (5,510 ind. m^{-2}), the crustacean *Crassicorophium crassicorne* (8,700 ind. m^{-2}), the polychaetes *Pygospio cf. elegans* (4,524 ind. m^{-2}) and *Euchone analis* (2,033 ind. m^{-2}) and the bivalve *Crenella decussata* (2,666 ind. m^{-2}).

The density of *A. marina* mounds as well as of the sea cucumber *C. laevis* was not significantly different between sampling dates (*A. marina* mounds: one-way ANOVA, $F_{2,15} = 0.98$, $p = 0.397$; *C. laevis* density: t test: $t_{10} = 0.70$, $p = 0.498$). The average density of *A. marina* mounds per 0.25 m^{-2} was 2.9 (± 2.1 SD), while the number of individual *C. laevis* was, on average, 18.1 (± 6.5 SD) per 0.25 m^{-2}.

Bioturbation and consumption effects

The number of individuals, species richness and dry mass, but not evenness was significantly different between bioturbation treatments (Table 2). There were significantly more species (on average 25 %), two times, on average, more individuals, and a higher dry mass (on average 73 %) recorded from plots with mats than from un-manipulated plots. Yet, neither species richness, nor the number of individuals, evenness and dry mass were significantly different between un-manipulated plots (no mat) and burial controls (Fig. 4). Furthermore, species richness and the number of individuals, but not dry mass were significantly

higher by, on average, 28 and 85 %, respectively, in plots with mats than in burial controls. A significant plot effect for species richness indicates that the number of species was different across the experimental area. For the interpretation of treatment effects, it is, however, important that this patchiness neither obscured the effects of bioturbation on species richness nor was the "consumer × plot (bioturbation)" interaction significant (Table 2), indicating consistency in consumer manipulations on species richness across the experimental set-up.

Consumer treatments were without effect on any of the four response variables tested, and this result was independent of bioturbation treatments, as indicated by a non-significant consumer × bioturbation interaction (Table 2; Fig. 4).

Species composition was significantly affected by bioturbation but not by consumers (Table 3). The composition of the benthic assemblages from un-manipulated plots and procedural controls was not significantly different from each other, but both were significantly different in their composition of encountered species to plots with mats (Fig. 5). Species were generally negatively affected by bioturbation (Table 4). The cumacean *L. fuscatus,* the amphipod *C. crassicorne*, the polychaetes *P. cf. elegans* and *E. analis,* and the bivalve *C. decussata* contributed strongest to the observed differences in species composition between bioturbation treatments (Table 4).

Fig. 4 Mean (+SEM, standard error of the mean) species richness (**a**), number of individuals (**b**), evenness (**c**) and dry weight (**d**) of infauna assemblages for different combinations of bioturbation and consumer treatments (per 21 cm^2 sampled surface area). *White*, *black* and *grey bars* indicate consumer treatments without cages (no cage), open cages (pc, i.e. procedural control) and closed cages (cage), respectively. Bioturbation treatments are un-manipulated plots (no mat), no mat but burial activity (burial control) and bioturbator exclusion (with mat). Statistically significant differences in bioturbation treatments are marked by *different letters*
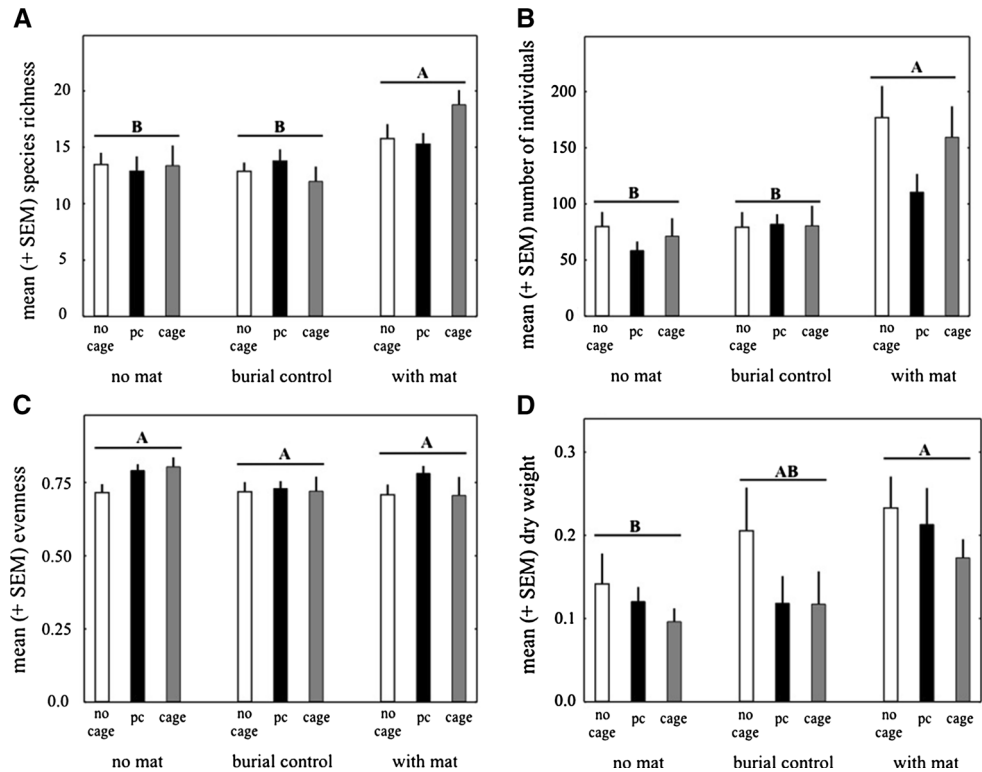

Table 3 Results of three-way nested PERMANOVA analysing the effects of bioturbation and consumer treatments on species composition

Source	df_{pooled}	MQ	*Pseudo-F*	*p*	Permutations	*p*(MC)	MQ$_{den}$
Bioturbation, B	2	4,273.6	2.88	**0.005**	9,514	**<0.001**	Plot(B)
Consumption, C	2	1,408.2	1.49	0.056	9,900	0.072	Pooled
B × C	4	1,035.8	1.10	0.306	9,859	0.312	Pooled
Plot(B)	12	1,482.1	1.57	**<0.001**	9,758	**<0.001**	Pooled
C × plot(B)		947.8	1.00	0.477	9,726	0.474	Residual
Residual	45	943.7					
Pooled	69						

Elimination of random source(s) of variance and recalculation of residuals were done after verifying that the variance of random source(s) of variance = 0, i.e. not significant at $\alpha \geq 0.25$, where used denominator mean square (MQ$_{den}$) is shown for each source of variation in columns MQ$_{den}$. Pooled term = random source(s) of variance + Residual, df_{pooled} = degrees of freedom after elimination of random source(s). Permutations = number of possible permutations, *p*(MC) = probability value obtained from Monte Carlo analysis, significant results at $\alpha \leq 0.05$ in bold, $n = 5$

Control of experimental treatments

Mesh burial activity

Seven days after experimental manipulations started, significantly fewer individuals were found in procedural controls than in un-manipulated plots (Table 5). In contrast, evenness was significantly higher in procedural controls than in un-manipulated plots (Table 5). However, significant differences between both treatments were neither found for species richness (Table 5) nor for the composition of species (one-way PERMANOVA with 126 unique permutations:

$pseudo\text{-}F_{1,8} = 1.68$, $p = 0.076$; $p(MC) = 0.157$), indicating that mesh burial at the beginning of the experiment was followed by a rapid re-colonization.

Effectiveness of buried mesh

The average number of mounds occurring in the different bioturbation treatments was not significantly different between procedural controls (4 ± 1.2 mounds; min = 2, max = 7) and un-manipulated plots (6 ± 3.6 mounds, min = 2, max = 15). In both treatments, however, significantly more mounds were found than on exclusion
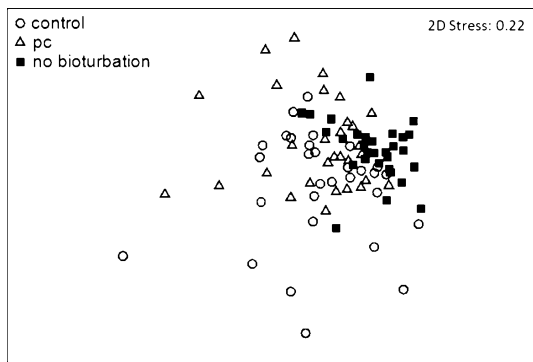
Fig. 5 MDS plot illustrating levels of similarity of infauna assemblages between bioturbation treatments. *Circles* = control, un-manipulated controls; *triangles* = pc, procedural controls; *squares* = no bioturbation, with mat

plots, where no mounds could be detected (Kruskal–Wallis test; H_2: 9.63, $p = 0.008$). Thus, the buried mesh completely excluded larger bioturbating organisms such as the lugworm *A. marina* from experimental plots, while the activities associated with the burial of a mesh did not affect the biotubators.

Discussion

The burial of a mesh significantly reduced the activity of burrowing organisms as indicated by the lower number of mounds in plots with than without mesh. These mounds were caused by the lugworm *A. marina*, which we encountered as the largest bioturbating species at the study site. This reduction in bioturbation activity caused an increase in

Table 5 Mean (±SEM) values of response variables and results from *t* tests for different bioturbation treatments recorded 7 days after the manipulation started ($n = 5$)

	Burial disturbance				
	Control	PC	*df*	*t*	*p*
Richness	13.00 (±0.8)	11.6 (±0.8)	8	1.20	0.264
# Individuals	78.00 (±13.3)	36.60 (±4.7)	8	2.94	**0.019**
Evenness	0.73 (±0.04)	0.86 (±0.02)	8	−2.69	**0.028**
Wet weight	n.a.	n.a.			

Significant results in bold font. n.a. = not applicable, PC = procedural control of burial activity

the number of individuals, species richness and dry weight of the benthic community in plots where a mesh was present. Additionally, bioturbator exclusion significantly changed the species composition of the soft-bottom community. In contrast, species diversity or composition of the soft-bottom community was not significantly different between areas with and without cages, indicating missing consumer effects of epibenthic predators, which were also independent of bioturbation treatments. Neither the activities associated with the burial of a mesh, nor the presence of cages seems to affect community responses permanently.

Effects and occurrence of bioturbators

Placing a mesh into the bottom to inhibit bioturbation in soft-bottom habitats was also applied in different studies conducted in tropical and temperate regions. This method was especially successful to prevent the sediment-

Table 4 Mean (±SD) number of individuals of species constituting >80 % to total density in samples (21 cm^2) of the three bioturbation treatments (burial = procedural control of mat burial, control = unmanipulated plots, mat = plots with a buried mat to exclude the bioturbator *Arenicola marina*)

Species	Burial	Control	Mat	Procedural effect	Bioturbation effect	%
Lamprops fuscatus	22.6 (±16.4)	11.6 (±10.6)	48.9 (±74.2)	no	–	25.7
Crassicorophium crassicorne	16.8 (±12.7)	18.3 (±12.6)	22.0 (±11.5)	no	–	12.3
Euchone analis	2.9 (±2.9)	4.3 (±5.4)	16.1 (±11.8)	no	–	11.3
Pygospio cf. elegans	14.2 (±24.2)	9.5 (±16.8)	14.7 (±13.1)	no	–	10.7
Crenella decussata	4.4 (±4.3)	5.6 (±4.7)	15.7 (±13.0)	no	–	10.6
Ostracods	5.6 (±4.5)	6.6 (±6.7)	7.1 (±5.9)	no	–	5.7
Copepods	1.2 (±1.3)	2.1 (±2.9)	4.1 (±4.1)	no	–	3.2
Nemertini spec.	2.6 (±3.0)	1.8 (±1.5)	3.1 (±2.3)	no	–	2.3
Ophelina spec.	0.7 (±1.2)	0.6 (±1.0)	2.6 (±2.0)	no	–	2.2
Ophiura albida	1.4 (±1.4)	1.0 (±1.5)	2.5 (±2.4)	no	–	2.1
Nematods	1.6 (±2.2)	1.3 (±1.6)	2.0 (±1.8)	no	–	1.6
Gammarus sp.	0.5 (±0.8)	0.6 (±1.2)	1.2 (±1.8)	no	–	1.2

The direction of effects (procedural effect = burial vs. control; bioturbation effect = mat vs. control) is given as − = negative and no = no contribution. % indicates the percent contribution of a species to the detected significant bioturbation effect on species composition ($n = 5$)

reworking activity of larger bio-engineering organisms such as burrowing crabs and lugworms without causing experimental artefacts on smaller organisms occurring in higher sediment layers above the mat (e.g. Dittmann 1996; Volkenborn and Reise 2006, 2007; González-Ortiz et al. 2014).

At our study site, the mean density of the lugworm *A. marina* was about five individuals per m^2 (quantified by counting the faecal casts on the experimental plots without a mesh). This is considerably lower than known from most intertidal flats in the Wadden Sea (Beukema 1976; Volkenborn and Reise 2006, 2007), but similar to densities found on offshore flood delta shoals near the island of Sylt in the south-eastern North Sea (Lackschewitz and Reise 1998) and in the western Baltic Sea (Brey 1991). The latter studies reveal that already a low lugworm density may structure benthic assemblages, because their feeding pits and faecal mounds represent unstable structures avoided by many infauna organisms. On the other hand, they may promote the aggregation of specific species such as copepods, platyhelminths, nemertines and polychaete worms (Reise 2002). Lugworm activity does not only cause sediment instability, but may also change sediment properties such as particle composition, content of organic matter, sulphide concentrations and sediment permeability (Volkenborn and Reise 2006; Volkenborn et al. 2007; Wendelboe et al. 2013). Thus, sediment-mediated indirect effects may have similar importance for benthic species assemblages as the direct physical disturbance caused by *A. marina*. For example, Woodin (1986) and Woodin et al. (1995) show that alterations in sediment properties may affect settlement behaviour of polychaetes and bivalves.

Surprisingly, to our knowledge the lugworm *A. marina* was not detected in other studies conducted at our site and was generally rarely found in Kongsfjorden (e.g. Laudien et al. 2007; Wlodarska-Kowalczuk pers. communication). This is presumably due to methodical constrains. Large-sized lugworms can dig their burrows as deep as 50 cm (Lackschewitz and Reise 1998). Therefore, it is difficult to collect them with traditional sampling gear like a Van Veen grab or an airlift system, which do not penetrate deep enough into the sediment. Instead, live *A. marina* were collected in this study by divers digging with their hands deep into the sediment. We found only comparatively large-sized individuals of about 20 cm in length at our study site but no small or juvenile lugworms. The absence of juvenile lugworms in areas with their adult conspecifics is known from temperate regions, too. There, it is assumed that juvenile *A. marina* suffer from physical disturbances and sediment property changes caused by their adult conspecifics resulting in different spatial usage of the habitat by juvenile and adult lugworms (Reise 1985; Lackschewitz and Reise 1998). The adult *A. marina* at our study site may

have immigrated from nursery grounds outside the study area. Such active migration behaviour by lugworms increasing in size to sites dominated by adults is assumed for the Wadden Sea (Lackschewitz and Reise 1998). In Kongsfjorden, however, small-sized *A. marina* were also rarely detected outside our study site despite their lesser deep burrows that allows sampling with, e.g. a box corer. Thus, it remains unclear whether the absence of juvenile lugworms was due to unknown breeding areas or to sporadic recruitment events, which may not occur every year. High inter-annual variations in recruitment success are generally observed in multiyear-living soft-bottom invertebrates of higher latitudes (Varfolomeeva and Naumov 2013). Although the reason for this variability is often unknown, especially post-settlement factors such as winter mortality of juveniles seem to play a major role (Maximovich and Guerassimova 2003; Strasser et al. 2003; Yakovis et al. 2013).

In our experiment, the tube-building polychaete worms *E. analis* and *P.* cf. *elegans*, the cumacea *Lamprops fuscatus*, the amphipod *C. crassicorne*, and the bivalve *C. decussata* contributed strongest to the community structure differences between areas with and without *A. marina*. On average, all five species showed higher abundances on plots with a buried mesh. This strongly suggests that they benefit from the lugworm exclusion resulting in less disturbance, higher sediment stability and increased availability of organic material (Volkenborn and Reise 2007; Volkenborn et al. 2009). Similar patterns were found in lugworm exclusion experiments conducted in temperate regions. There, the spionid polychaete *P. elegans*, for example, showed higher densities at exclusion sites (Wilson 1991; Flach 1992; Volkenborn and Reise 2006). These small-sized polychaete worms are often opportunistic species with high reproduction and recruitment rates (Beukema et al. 1999; Bick and Arlt 2005), and their life strategy may explain the fast and dense colonization of our experimental plots where *A. marina* was absent. Already after only 70 days, the results of this colonization were obvious.

Effects and occurrence of consumers

Predation is a key factor affecting species occurrence and population dynamics in many marine shallow soft-bottom ecosystems (e.g. Ambrose 1984; Reise 1985; Wilson 1991; Olafsson et al. 1994; Strasser 2002; Quijon and Snelgrove 2005). Only few exceptions are known in which consumption seems to be of minor importance (e.g. Hall et al. 1990). Therefore, it was surprising that the exclusion of epibenthic consumers showed no effect on the species community in our cage experiment performed in an Arctic fjord. It might be that generally, the abundance of

consumers was too low to cause significant effects on the prey densities outside the cages. Indeed, despite regular detections of crabs and predatory gastropods at the study site, consumer densities showed high spatial and temporal variability (own observations), which impeded an accurate quantification of predator density. An estimation of the activity of the spider crab *H. araneus* during the experimental period indicates that crab abundance is far less than one individual per square metre. This is much lower than crab density in sedimentary environments where predation causes strong effects on the benthic community (e.g. Reise 1985; Beukema 1991). We have no information on the density of other highly mobile epibenthic predator species, such as shrimps and fish, but according to our results their effects on the soft-bottom species community seem to be negligible.

Many invertebrate benthic consumers are not obligate predators, but have an opportunistic and omnivorous feeding behaviour. The shore crab *Carcinus maenas*, for example, is an important and widespread predator on Atlantic shorelines, which affects many invertebrate prey populations, but also feeds on carrion and algae (Baeta et al. 2006; Pickering and Quijón 2011). Likewise, necrophagous feeding is also known for the spider crab *H. araneus* (Legezynska et al. 2000; Guijarro Garcia et al. 2006; Markowska et al. 2008). Another example is the gastropod *Buccinum undatum,* which only feeds on living blue mussels after a starvation period of several weeks, because whelks prefer consuming injured or recently died mussels (Thompson 2002). At our study site, mean total abundance of all macrobenthic invertebrate species was about 45,000 ind. m^{-2}. This is quite high compared to many other shallow soft-bottom ecosystems from tropical to boreal regions, where mean density ranges from 1000 to 20,000 ind. m^{-2} (Lackschewitz and Reise 1998; Dittmann and Vargas 2001; Michaelis and Wolff 2001; Varfolomeeva and Naumov 2013). In our investigation, the high abundance of short-living organisms in the upper sediment layer area implies a high natural mortality rate leading to plentiful carcasses of relatively small organisms at the bottom (Legezynska et al. 2000). The potential high availability of dead invertebrates may explain the missing predatory effects in our field experiment. It is very likely that many omnivorous consumers prefer this easy accessible food source, such as the scavenging whelk *Buccinum* sp., which we observed regularly at the study site.

Conclusions

Physical disturbance by, e.g. ice scouring is an important factor affecting species occurrence and community dynamics in Arctic shallow soft-bottom systems. Our results reveal that biotic factors such as bioturbation by the sediment-reworking lugworm *A. marina* may also play an important role in structuring benthic species assemblages, although investigations on the large-scale spatial distribution of invertebrate bioturbators are very rare in Arctic marine soft-bottom communities. Unexpectedly, our experiment indicates that predatory effects seem to be negligible. However, it is assumed that biotic interactions including predation will become of higher importance in the Arctic due to climate change. Rising temperatures cause a decrease in physical disturbance by ice and a northward expansion and higher abundances of many boreal species (Weslawski et al. 2011 and references therein). For example, benthic predatory crabs such as *Cancer pagurus* and *H. araneus* show increasing densities at the Norwegian and western Svalbard coast, respectively (Woll et al. 2006; Berge et al. 2009; Fagerli et al. 2014). Due to higher consumer occurrence, we expect that new predator–prey interactions will develop in the future. They may alter existing structures and dynamics of benthic communities in the Arctic. To unravel the underlying processes of these changes, a manipulative experimental approach, as used in this study, represents an appropriate and important tool, which should be applied more often in Arctic marine soft-bottom research.

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