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Disturbance effects of kelp thalli on structure and diversity of a coastal Arctic marine soft-bottom assemblage

Sina Petrowski[1] · Markus Molis[1] · Anke Bender[2] · Christian Buschbaum[3]

Abstract The effects of biotic disturbances, like seaweed whiplash, on the diversity of benthic communities are well documented for temperate coastal systems, yet missing for Arctic benthos. In Arctic soft-bottom habitats, kelp thalli occur either continuously (e.g. trapped by sediment) or sporadically (by drifting on the sediment) after detachment from rocky shores. To explore whether a kelp thallus can disturb the structure and diversity of a coastal Arctic soft-bottom assemblage, we continuously fixed a single thallus of the kelp *Saccharina latissima* to or sporadically (i.e. biweekly) moved it on the sediment and compared treatment effects to unmanipulated plots (=controls). On 6 September 2013 (i.e. after 73 days of manipulation), one sediment core was taken from each of the 30 plots ($n = 10$), from which the number of individuals of each of the 45 encountered animal taxa was recorded. The continuous presence of an experimentally fixed kelp thallus significantly reduced the number of individuals on average by 27 %. This disturbance effect was even stronger, on average 49 %, where a kelp thallus was biweekly moved on the sediment. Likewise, taxon richness was lowered by an average of 19 and 36 % where a *S. latissima* thallus was continuously or sporadically present, respectively. While the composition of taxa was also significantly different among all treatment groups, evenness and biomass were unaffected by kelp treatments. We conclude that the presence and already movements of a single kelp thallus can promote small-scale patchiness in near-shore soft-bottom assemblage structure and diversity and exemplify a significant connection between rocky and sedimentary coastal habitats.

Keywords Benthos · Community · Disturbance · Habitat connectivity · Kelp · Macroalgae · Patchiness · Soft-bottom · Svalbard

✉ Markus Molis
markus.molis@awi.de

1   Section Functional Ecology, Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Am Handelshafen 12, 27570 Bremerhaven, Germany

2   Institute of Biosciences, University of Rostock, Albert-Einstein-Straße 3, 18059 Rostock, Germany

3   Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Wadden Sea Station Sylt, Hafenstraße 43, 25992 List/Sylt, Germany

Introduction

According to the model by Menge and Sutherland (1987), disturbance affects community regulation across all trophic levels. Empirical evidence corroborates disturbance as a driver of species diversity and community structure on the rocky and sedimentary shores of the temperate zone (e.g. Mackey and Currie 2001). Several studies were conducted at higher latitudes, demonstrating disturbance effects on polar benthic communities, as could be inferred from theory, which suggests a relatively high importance of disturbance effects under harsh environmental conditions (Menge and Sutherland 1987). The reported evidence about the ecological effects of disturbance in polar ecosystems comes, however, mainly from mensurative studies and is to our knowledge exclusively based on the role of physical factors like ice scour (e.g. Conlan and Kvitek 2005; reviewed in Gutt 2001; Laudien et al. 2007) and boulder movements (Konar 2013). From rocky shores in the

temperate zone, it is known that seaweeds are a biological source of disturbance, affecting recruitment and growth of understory organisms directly through thallus movements (Velimirov and Griffiths 1979; Beermann et al. 2013) or indirectly through enhanced consumer impact (Bertness et al. 1999). In sedimentary habitats, seaweeds find to a lower extent also suitable substrata, e.g. on scattered drop stones (pers. observation C Buschbaum), where thallus sweeping can affect the circumjacent substratum (Fig. 1). Detached kelp may also persevere in and affect the fauna of coastal sedimentary habitats through partial thallus burial or increased drag from holdfast-attached rocks (Krumhansl and Scheibling 2012). Besides the continuous effects of stationary thalli, drifting seaweeds can also affect the ecology of sedimentary habitats in coastal areas (Krumhansl and Scheibling 2012). Soft-bottom benthos may benefit from storm-induced kelp debris as external food (Filbee-Dexter and Scheibling 2012) or through an increase in habitat complexity (Norkko and Bonsdorff 1996b). Coverage by kelp, however, can disturb suspension feeding infauna through a reduction in the supply of food and oxygen (Hull 1987; Krumhansl and Scheibling 2012).

The ecology of Arctic habitats may be considerably modified during upcoming decades, because environmental change is expected to be strongest in polar regions (IPCC 2013). The intensity and frequency of storms and ultimately wave action, for instance, are predicted to increase at higher latitude (e.g. Young et al. 2011), which may alter disturbance regimes and affect ecosystem properties (Hooper et al. 2005). In particular, large sessile benthos like kelp will be affected by storms, provoking defoliation and export of kelp detritus to neighbouring and distant habitats (Filbee-Dexter and Scheibling 2012; Krumhansl and Scheibling 2012). The effects of waves on Arctic

Fig. 1 Naturally attached *Saccharina latissima* thallus in arctic Kongsfjorden. *Ripple marks* indicate that ambient forces (e.g. tidal currents) are sufficient in moving a stationary thallus effectively on the substrate. Courtesy of M Schwanitz

coastal ecosystems will amplify with the melt-down of protective sea ice. The observed significant decline in sea ice cover has already influenced productivity and species interactions in Arctic coastal systems (Post et al. 2013). Moreover, warming-induced loss in sea ice earlier to summer solstice has the potential to cause extensive ecological regime shifts due to light-driven tipping points, which may alter dark-adapted communities into those dominated by primary producers (Clark et al. 2013). Indeed, increased kelp production and extension of kelp beds to greater depth have been reported where the period of sea ice cover has shortened (Kortsch et al. 2012; Krause-Jensen et al. 2012; Krause-Jensen and Duarte 2014). Thus, besides more storm effects there will be also more kelp biomass exposed to waves, suggesting an increase in the relevance of disturbance from stationary and drifting kelp, particularly in the coastal areas of a warmer Arctic.

Manipulative field studies on disturbance effects are scarce in Arctic benthic habitats (Konar 2013), though the factors which drive the abundance and distribution of species need to be identified and a mechanistic understanding on how these patterns are generated needs to be developed. Experiments assessing the role of biotic sources of disturbance, in particular those that will most likely increase in their importance in a future Arctic, are, to our knowledge, missing. To fill this gap, we assessed the effects of the presence of kelp on coastal soft-bottom communities in a factorial field experiment. We predict that the continuous presence of a kelp thallus will affect structure and diversity of a coastal Arctic soft-bottom assemblage. The residence time of drifting kelp specimens in soft-bottom habitats will be shorter at any given location than that of stationary conspecifics. Therefore, we further hypothesise that the sporadic presence of a drifting kelp thallus will affect structure and diversity of the underlying benthic assemblage differently than a continuously residing kelp thallus.

Materials and methods

Study site

All experimental work was conducted at Brandal (N 78°56.863, E 011°51.177), a sedimentary area with fine sand to coarse silt (mean ± SD grain size: 67.8 ± 25.0 μm) on the southern shore in the centre of the 20-km-long Kongsfjorden, Svalbard (Norway). The nearest kelp bed, i.e. at Stuphallet, is ca. 1 km westward of Brandal (pers. com. M Schwanitz). The seafloor at Brandal gently slopes to a water depth of about 11 m before it drops to a depth of >100 m. In August and September 2013, mean temperature at a water depth of 8 m was 5.7 °C (min = 3.9 °C, max = 6.9 °C, HOBO® data logger) at the

study site and salinity ranged here from 34 to 36 ‰. The average tidal amplitude in Kongsfjorden is 1.8 m (Svendsen et al. 2002). The soft-bottom community of the study site is dominated by polychaetes, molluscs and crustaceans (Laudien et al. 2007). Stones (≤ 0.3 m in diameter) covered mainly with kelp (primarily *Saccharina latissima* (L.) C.E.Lane, C.Mayes, Druehl and G.W.Saunders, but also with *Alaria esculenta* (L.) Greville and *Desmarestia sp.*) are scattered over the study site (pers. observation C Buschbaum). In addition, single and accumulations of detached thalli of the same species are present in this and in other soft-bottom areas in Kongsfjorden (pers. com. M Schwanitz). Quantification of the abundance of detached seaweeds in four 10×10 m areas near the experimental set-up between June and September ($n = 3$) revealed an average cover of 11 % (ranging from 5 to 20 %). Therefore, *S. latissima* with an average stipe length of 35 cm (ranging from 6 to 110 cm) and average blade area of 2343 cm^2 (ranging from 169 to 8855 cm^2) was the most abundant detached seaweed species.

Experimental design and set-up

A factorial experiment with complete randomised blocks was designed to assess the effects of kelp thallus presence on the diversity and species composition of the soft-bottom fauna at Brandal. Here, the experiment was set up at a water depth of 8 m on 15 June and conducted until 6 September 2013. In total, five blocks (3.5×3.5 m) were arranged with a minimum distance of 7 m between adjacent blocks. Each block contained six plots (0.5×0.5 m,

minimum distance of 1 m between adjacent plots), in which three seaweed treatments were each replicated twice (Fig. 2) and randomly assigned to plots. Each corner of a plot was marked by an iron rod. The first seaweed treatment simulated the effects of kelp naturally growing on scattered stones or being trapped in the sediment by fixing a *S. latissima* thallus (mean $\pm$ SD length 114.14 ± 23.07 cm) in the centre of a plot (=continuous kelp presence). *S. latissima* was selected because it was the most abundant seaweed species encountered at the study site. To fix a *S. latissima* thallus to the seafloor, its basal end was bent and fixed with a cable tie back to the stipe, forming a permanent loop. Two iron rods (40 cm) were put through the loop and completely pushed into the sediment to anchor a *S. latissima* thallus in such a way to the seafloor that it was freely moved by water currents across the plot affecting the immediate vicinity. Ripple marks resulting from thallus movements were visible in the entire plot area, although thallus movements did not affect the entire plot at all times. The second seaweed treatment simulated the effects of drifting seaweeds by biweekly moving a *S. latissima* thallus for ca. 20 s on a plot (=sporadic kelp presence). Each time when this manipulation was performed, a diver took a different detached *S. latissima* thallus haphazardly from the seafloor close to the experimental set-up. Plots designated for the third treatment were not manipulated (=control). Comparisons between controls of this experiment and samples taken at the same time but some 50 m away from the experimental set-up revealed no significant difference for all response variables (all $p > 0.159$), i.e. strongly suggesting independence of
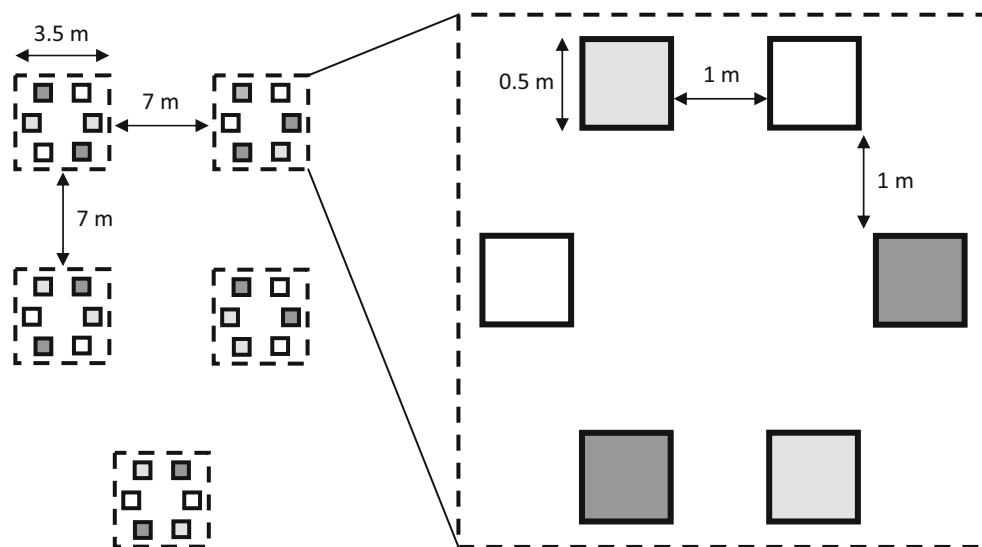
Fig. 2 Scheme (not to scale) of experimental set-up showing on the *left side* five blocks (*dashed lines*) and on the *right side* the allocation of seaweed treatment to six plots (*solid lines*) within one block. Seaweed treatments were either the continuous presence of a

Saccharina latissima thallus (*dark grey*), the sporadic presence of a *S. latissima* thallus (*light grey*), or unmanipulated plots (*white*). *Arrows* with *numbers mark* dimensions of and distances between different experimental units (i.e. blocks and plots)

adjacent plots in the set-up of this study. The set-up was visited biweekly to then immediately (1) replace *S. latissima* individuals that were lost on rare occasions and (2) remove naturally occurring detached seaweeds scarcely residing on plots. It is highly unlikely that drifting seaweed thalli would have only affected manipulated plots (and herein those of one disturbance treatment more than those of the other treatment), given the random allocation of treatments to plots and the blocked design of the study. All installations, maintenance and sampling were conducted by SCUBA-diving. To control for potential artifacts caused by the presence of a diver, divers visited all plots each time when manipulations and maintenance of the experimental set-up were performed.

Sampling

One sample was taken from each plot on 6 September 2013, i.e. at the end of the experiment ($n = 10$). Samples taken from unmanipulated plots in 2012 revealed that diversity and biomass measures did not change significantly between mid-June and the end of August (data not shown), suggesting that treatment effects were not confounded by successional processes. To avoid edge effects, each sample was taken at a minimum distance of 10 cm from plot margins by pushing a sediment corer of 5.2 cm diameter five centimetres deep into the sediment. This method (adopted from Petrowski et al. 2015) was shown to generate representative samples of the soft-bottom fauna at the study site and produced a comparable taxon list to that compiled by Laudien et al. (2007) who used larger corers (20 cm ø) that were pushed deeper (20 cm) into the sediment than in this study. Samples were transported within 2 h to the Marine Laboratory in Ny-Ålesund and stored in a cooler at 5 °C. Within 48 h after sampling, each core was rinsed with filtered sea water over a 0.5-mm sieve to separate retained organisms from the sediment. All living animals were counted and identified to the lowest possible taxonomic level, usually to species level, using a stereomicroscope. For each sample, the number of individuals as well as of taxa was recorded, and Pielou's evenness calculated. After drying the organisms at 60 °C to constant weight, dry mass was quantified with a laboratory balance to the nearest 0.001 g.

Data analysis

The effects of seaweed treatment (three levels, fixed) and block (five levels, random) on taxon richness, number of individuals, Pielou's evenness, and dry mass were analysed in separate mixed model two-way ANOVAs. Complete or sequential removal of random sources of variance (block and the interaction of seaweed treatment * block) from the

ANOVA model, recalculation of residuals, and selection of appropriate denominators was done when random sources of variation were non-significant at $\alpha \geq 0.25$ (Quinn and Keough 2002). Newman–Keuls test was used as a post hoc test. Homogeneity of variances was confirmed with Cochran's test. To assess the effects of seaweed treatments and blocks on soft-bottom taxon composition, the abundance of all taxa encountered in samples was analysed with a mixed model two-way PERMANOVA. Abundance data were log $(x + 1)$ transformed prior to the calculation of Bray–Curtis similarity indices to account for contribution of rarer species to similarity. For PERMANOVAs, the maximum number of permutations was set to 9999. Post hoc results of the PERMANOVA were illustrated through a canonical analysis of principal coordinates, using the CAP-routine of the PERMANOVA + for PRIMER software (Anderson et al. 2008). Finally, a SIMPER analysis determined the contribution of taxa to significant differences in taxon composition among treatments as well as magnitude and direction of the effect of continuous and sporadic kelp presence on separate taxa. Vector overlays, based on a Pearson correlation, illustrate SIMPER results in the CAP plot.

Results

Species occurrence

A total of 45 animal taxa were found in the samples (Table 1). The soft-bottom fauna was dominated by polychaetes and molluscs (15 taxa each) and crustaceans (9 taxa), which represent together 87 % of total taxon richness. The crustaceans *Crassicorophium crassicorne* and *Lamprops fuscatus*, the polychaetes *Pygospio* cf. *elegans* and *Euchone analis*, and the bivalve *Crenella decussata* were the five most abundant taxa at the end of the experiment (Table 1).

Seaweed treatments

The number of individuals and taxon richness were both significantly affected by seaweed treatments, while evenness and dry mass showed no effect (Table 2; Fig. 3). There were significantly less individuals, on average 49 and 27 %, in plots with sporadic and continuous kelp presence, respectively, than in control plots (Fig. 3A). Furthermore, plots with continuous kelp presence accommodated significantly more individuals, on average 30 %, than plots with sporadic kelp presence (Fig. 3A). Likewise, compared to control plots taxon richness was significantly lower, on average 36 and 19 %, in plots with sporadic and continuous kelp presence, respectively (Fig. 3B). There

Table 1 Mean ± SEM number of individuals of each taxon encountered in corer samples (21 cm^2 surface area) taken from plots with different seaweed treatments at the end of the experiment

Class	Taxon	Unmanipulated		Continuous presence		Sporadic presence	
		Mean ± SEM	%	Mean ± SEM	%	Mean ± SEM	%
Plathelminthes	Platyhelminthes *indet.*	0.3 ± 0.21	0.25				
Nematodes	Nematoda *indet.*	1.4 ± 0.70	1.18	0.8 ± 0.51	0.93	0.2 ± 0.13	0.33
Nemerteans	Nemertea *indet.*	2.2 ± 0.47	1.58	2.3 ± 0.56	2.67	1.1 ± 0.35	1.81
Priapulids	*Priapulus caudatus* (Lamark, 1816)	0.3 ± 0.21	0.25				
Holothurids	*Chirodota laevis* (O. Fabricius, 1780)	0.8 ± 0.25	0.67	0.4 ± 0.22	0.46	0.6 ± 0.22	0.99
Ophiurids	*Ophiura albida* (Forbes, 1839)	0.9 ± 0.23	0.76	1.3 ± 0.26	1.51	0.2 ± 0.13	0.33
Bivalves	*Astarte sulcata* (da Costa, 1778)	0.6 ± 0.22	0.51	0.6 ± 0.22	0.70	0.4 ± 0.22	0.66
	Axinopsida orbiculata (G. O. Sars, 1878)	0.2 ± 0.20	0.17	0.1 ± 0.10	0.12	0.1 ± 0.10	0.16
	Crenella decussata (Montagu, 1808)	7.6 ± 1.70	6.40	5.2 ± 0.99	6.03	1.0 ± 0.33	1.64
	Bivalvia *indet.* 1	0.3 ± 0.21	0.25	0.2 ± 0.13	0.23	0.3 ± 0.21	0.49
	Bivalvia *indet.* 2	0.1 ± 0.10	0.08				
	Liocyma fluctuosa (Gould, 1841)	0.2 ± 0.13	0.17	0.1 ± 0.10	0.12		
	Macoma sp.	0.1 ± 0.10	0.08				
	Montacuta spitzbergensis (Knipowitsch, 1901)	0.8 ± 0.29	0.67	0.6 ± 0.34	0.70	0.2 ± 0.20	0.33
	Mya arenaria (Linnaeus, 1758)	0.1 ± 0.10	0.08			0.1 ± 0.10	0.16
	Mya truncata (Linnaeus, 1758)	0.3 ± 0.21	0.25				
	Serripes groenlandicus (Mohr, 1786)	0.2 ± 0.20	0.17				
Gastropods	*Cylichna sp.*	0.2 ± 0.20	0.17	0.2 ± 0.20	0.23	0.1 ± 0.10	0.16
	Onoba mighelsii (Stimpson, 1851)					0.1 ± 0.10	0.16
	Retusa obtusa (Montagu, 1803)			0.1 ± 0.10	0.12		
	Skenea sp.	0.3 ± 0.21	0.25	0.1 ± 0.10	0.12		
Crustaceans	Amphipoda *indet.*	5.5 ± 1.43	4.63	1.4 ± 0.40	1.62	0.4 ± 0.22	0.66
	Copepoda *indet.*	2.9 ± 0.48	2.44	1.3 ± 0.30	1.51	1.0 ± 0.37	1.48
	Crassicorophium crassicorne (Bruzelius, 1859)	39.4 ± 5.93	33.19	26.5 ± 2.42	30.71	16.1 ± 1.33	26.48
	Lamprops fuscatus (Sars, 1865)	22.3 ± 6.35	18.79	27.3 ± 7.46	31.63	3.3 ± 0.76	5.43
	Monoculodes packardi (Boeck, 1871)	0.2 ± 0.13	0.17	0.1 ± 0.10	0.12		
	Orchomenella minuta (Krøyer, 1846)	0.1 ± 0.10	0.08			0.1 ± 0.10	0.16
	Ostracoda *indet.*	2.9 ± 0.84	2.44	3.3 ± 0.60	3.82	5.5 ± 1.18	9.05
	Priscillina herrmanni (d'Udekem d'Acoz, 2006)	1.2 ± 0.39	1.01	0.3 ± 0.21	0.35	0.2 ± 0.13	0.33
	Sclerocrangon boreas (Phipps, 1774)	0.1 ± 0.10	0.08				
Polychaetes	*Capitella capitata* (Fabricius, 1780)	2.1 ± 1.99	1.77	0.2 ± 0.13	0.23		
	Chaetozone setosa (Malmgren, 1867)	0.2 ± 0.13	0.17			0.1 ± 0.10	0.16
	Dipolydora quadrilobata (Jacobi, 1883)	0.1 ± 0.10	0.08	0.1 ± 0.10	0.12	0.1 ± 0.10	0.16
	Euchone analis (Krøyer, 1865)	7.3 ± 1.49	6.15	3.1 ± 0.89	3.59	9.5 ± 2.41	15.63
	Maldanidae *indet.*	0.6 ± 0.34	0.51	0.3 ± 0.15	0.35	0.4 ± 0.16	0.66
	Marenzelleria wireni (Augener, 1913)	0.2 ± 0.13	0.17			0.1 ± 0.10	0.16
	Ophelia rathkei (McIntosh, 1908)					0.1 ± 0.10	0.12
	Ophelina sp.	0.5 ± 0.22	0.42	0.8 ± 0.29	0.93	0.1 ± 0.10	0.16
	Pholoe assimilis (Oersted, 1845)	0.15 ± 0.10	0.08	0.2 ± 0.13	0.23		
	Polychaeta *indet.* 1	0.20 ± 0.13	0.17	0.2 ± 0.13	0.23		
	Polychaeta *indet.* 2	0.20 ± 0.20	0.17				
	Polychaeta *indet.* 3	0.10 ± 0.10	0.08	0.1 ± 0.10	0.12		
	Pygospio cf. elegans (Claparède, 1863)	11.6 ± 3.68	9.77	6.2 ± 2.91	7.81	15.2 ± 4.61	25.00
	Spio armata (Thulin, 1957)	4.0 ± 1.10	3.37	2.6 ± 1.25	3.01	4.2 ± 0.98	6.91
	Travisia forbesii (Johnston, 1840)			0.2 ± 0.13	0.23	0.2 ± 0.20	0.33

Empty cells indicate absence of organisms. " %" = proportion of individuals of a taxon to the total number of individuals encountered in all replicate corer samples of this seaweed treatment, $n = 10$, "unmanipulated" (=absence of a *Saccharina latissima* thallus), "Continuous presence" (=continuous presence of a *S. latissima* thallus), and "Sporadic presence" (=*S. latissima* thallus biweekly moved on the sediment), bold font marks the five overall most abundant taxa

Table 2 Effects of disturbance on taxon richness, number of individuals, evenness, and dry mass after 73 days, i.e. at the end of the experiment

Source of variance	df	MS	F	p	MS$_{den}$	df	MS	F	p	MS$_{den}$
		Taxon richness					Number of individuals			
Seaweed (S)	2	93.10	13.20	**<0.001**	Second pooling	2	8420.7	6.78	**0.019**	S × B
Block (B)	4	7.38	1.06	0.401	First pooling	4	763.50	0.62	0.664	S × B
S × B	8	3.81	0.44	0.880	Residual	8	1242.08	2.25	0.073	Residual
Residual	15	8.70				15	529.00			
First pooling	23	7.00								
Second pooling	27	7.06								
		Evenness					Dry mass			
Seaweed (S)	2	0.0087	1.22	0.310	Second pooling	2	0.0135	1.14	0.336	Second pooling
Block (B)	4	0.0023	0.29	0.885	First pooling	4	0.0106	0.88	0.491	First pooling
S × B	8	0.0058	0.64	0.737	Residual	8	0.0094	0.69	0.692	Residual
Residual	15	0.0091				15	0.0135			
First pooling	23	0.0079				23	0.0121			
Second pooling	27	0.0071				27	0.0119			

Pooling: recalculation of residuals for random source(s) of variance for p values at α ≥ 0.25, with first pooling = S × B + residual and second pooling = S × B + Block + residual; df = degrees of freedom; MS$_{den}$ = mean square denominator shown for every source of variance; significant p values at α ≤ 0.05 are marked in bold. n = 10

were significantly more taxa, on average 21 %, in plots with continuous than with sporadic kelp presence (Fig. 3B). Neither "block" nor the "block × seaweed treatment" interaction was significant for any of the tested responses, indicating that the effects of seaweed treatments, i.e. for the hypotheses of interest, were independent of the location where manipulations were performed at the study site.

Assemblage structure

Taxon composition of the benthic assemblage was also significantly affected by seaweed treatments (Table 3). Taxon composition was significantly different between control plots and plots with sporadic kelp presence (=effect of thallus movement, Fig. 4) as well as between control plots and plots with continuous kelp presence (=combined effects of thallus presence and movements). Taxon composition was also significantly different between plots where a *S. latissima* thallus was sporadically and continuously present (=effect of thallus presence). Thallus movements reduced and thallus presence increased, on average by 54 and 92 %, respectively, the abundance in seven of the eleven taxa contributing strongest to differences in taxon composition (Table 4). Only the abundance of *P. cf. elegans*, *S. armata*, *E. analis*, and ostracods showed opposite trends, being favoured through thallus movements (on average by 28 %) and suppressed through thallus presence (on average by 35 %). The combined effects of thallus presence and movements (=continuous thallus presence) were beneficial for *L. fuscatus* and ostracods

(average increase of 15 % in the number of individuals), but detrimental (average decrease of 31 %) for the remaining nine taxa contributing strongest to differences in taxon composition (Table 4). A significant block effect suggests spatial differences in taxon composition (Table 3). Yet, the non-significant "block × seaweed treatment" interaction (Table 3) infers that this patchiness does not influence the interpretation of the effects of seaweed treatments.

Discussion

After 73 days of manipulation, benthic taxon composition was different between areas where a *S. latissima* thallus was absent or continuously present, i.e. fixed to the sediment. Extended periods during which a kelp thallus occurs at the same position in a soft-bottom habitat are possible, because some kelp specimens recruit and grow on far-scattered stones at the study site (pers. observation C Buschbaum). Alternatively, dislodged kelp can get trapped in sedimentary habitats (Krumhansl and Scheibling 2012), which is common at Brandal (pers. observation C Buschbaum). The detected thallus-mediated change in benthic taxon composition could be due to several, not mutually exclusive factors. First, the presence of a seaweed thallus may represent an additional source of food supply for at least some benthic species (reviewed in Krumhansl and Scheibling 2012), especially if food quality is enriched by bacterial degradation (Norderhaug et al. 2003). Nevertheless, the abundance of most taxa (ca. 80 %) declined in

Fig. 3 Mean number of individuals per corer sample (21 cm^2 surface area) (**A**), taxon richness (**B**), evenness (**C**, note disrupted ordinate), and dry mass (**D**) of the benthic fauna at Brandal in plots without manipulation (*white boxes*), with sporadic (*light grey boxes*), and continuous (*dark grey boxes*) presence of a *Saccharina latissima* thallus. *Boxes* and *whiskers* mark ± SEM and 95 % confidence intervals, respectively. Treatments sharing a *letter* were statistically not significantly different
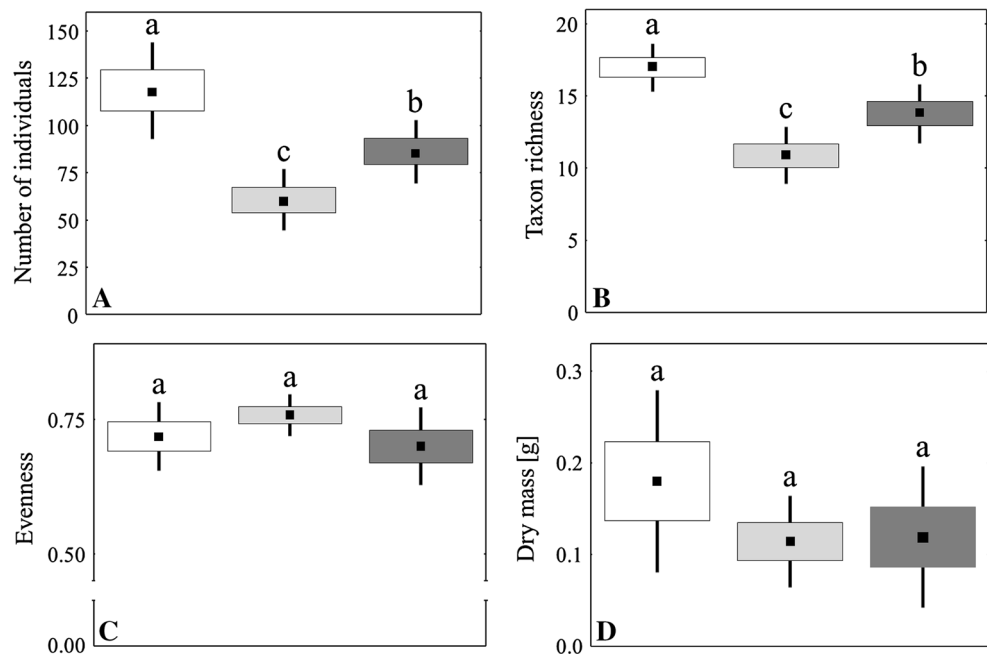
Table 3 Summary of mixed model two-way PERMANOVA based on log(x + 1) transformed Bray–Curtis similarities; permutations = number of realized unique permutations, *p(MC)* = p value based on Monte-Carlo analysis; MS_{den} = mean square denominator shown for every source of variance; Recalculation of residuals for random source(s) of variance with a *p* value at α ≥ 0.25, pooled = random source(s) of variance + residual; significant *p* values at α ≤ 0.05 are marked in bold

| Source of variance	df	MS	Pseudo-F	p	permutations	p(MC)	MS_{den}
Seaweed (S)	2	2809	4.49	**<0.001**	9918	**<0.001**	pooled
Block (B)	4	1072	1.71	**0.010**	9866	**0.018**	pooled
S × B	8	476	0.68	0.973	9867	0.943	residual
Residual	15	705					
Pooled	23	626					

n = 10

areas with continuous kelp presence compared to control areas. Taxa with increasing abundance in plots with continuous kelp presence either contributed little to community structure or were filter feeders, suggesting that the presence of a *S. latissima* thallus attracted few, if any of the potential kelp consumers.

Second, a decline in the number of benthic taxa and total individuals by continuous kelp presence could have been caused by oxygen depletion in the sediment. Oxygen deficiency has been documented, for example, in Baltic Sea sediments that were covered by large quantities of drifting algal mats (Norkko and Bonsdorff 1996a). Signs of oxygen depletion, like blackened sediments, were, however, not visible in sediment cores, suggesting sufficient ventilation of plots. The stronger decline in the number of benthic taxa and total individuals in areas with sporadic thallus presence (i.e. biweekly manually moved) compared to continuous presence of a *S. latissima* thallus further indicates that

changes in community composition were not caused by oxygen deficiencies.

Third, a decline in the number of taxa and total individuals under drifting algal mats has been shown to result from an increase in predation pressure by epibenthic consumers (Arroyo et al. 2012). Thallus size of kelp at the study site ranged from 169 to 8855 cm^2, which seems sufficiently large to provide structural protection for a predator like *H. araneus* (< 10 cm maximum carapace width), particularly in spatially homogeneous areas like at our study site. Yet, taxon number and the abundance of most benthic taxa, including known prey species of *H. araneus* like *C. decussata* (Bender 2014), declined strongest in plots with sporadic presence of a *S. latissima* thallus. This suggests either that detached kelp attract predators other than *H. araneus* in soft-bottom habitats or that predator attraction by kelp, if any, was not important in the present experiment.
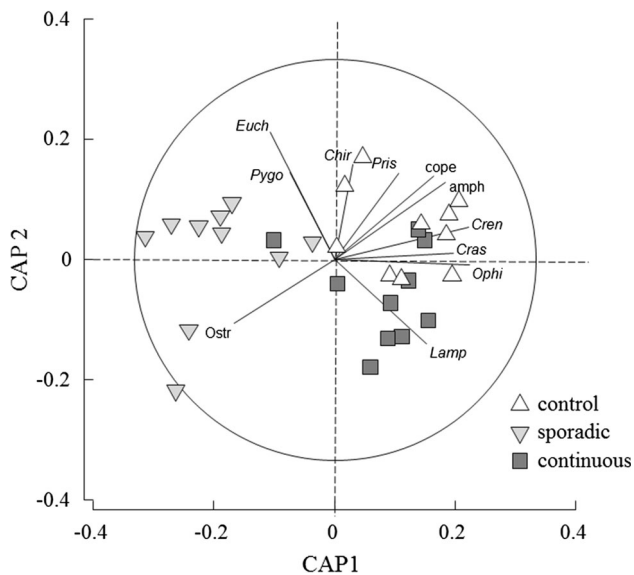
Fig. 4 Canonical analysis of principal coordinates ordination based on Bray–Curtis similarity index computed from log(x + 1) transformed numbers of individuals contained in corer samples taken from plots exposed to the continuous presence of a *Saccharina latissima* thallus (*dark grey quadrats*), sporadic presence of a *S. latissima* thallus (*light grey*, inverted triangles), and without manipulation (*white triangles*). *Circle* (radius = 1.0) scales length of vectors. *Vector length* and *direction* indicate magnitude and sign, respectively, of Pearson correlation between each taxon and CAP axes. The number of *Lamprops fuscatus* individuals, for instance, increased in plots where a *Saccharina latissima* thallus was continuously present. n = 10, Euch = *Euchone analis*, Pygo = *Pygospio cf. elegans*, Chir = *Chirodota laevis*, Pris = *Priscillina herrmanni*, cope = copepods, amph = *Amphipoda indet.*, Cren = *Crenella decussata*, Cras = *Crassicorophium crassicorne*, Ophi = *Ophiura albida*, Lamp = *Lamprops fuscatus*, Ostr = ostracods

The most likely process by which the continuous presence of a *S. latissima* thallus affected taxon composition of the benthic assemblage was through direct disturbance of its movements (sensu White and Pickett 1985). A significant decline in community structure and diversity in plots with sporadic kelp presence relative to undisturbed plots corroborates the paramount role of thallus movements as a source of disturbance. Opposite to our expectations, the sporadic presence of a *S. latissima* thallus had a stronger detrimental effect on most tested community responses as well as on the abundance of the majority of taxa than the effects of a thallus that was continuously present. Several explanations for the lower impact of a continuously present thallus seem plausible. Firstly, the intensity of the disturbance of a manually moved thallus may have been higher than of naturally, current-induced movements of a continuously present thallus, despite similarity in thallus dimensions. Perhaps, the manually moved thallus generated more force onto the sediment. However, resulting ripple patterns were similar to those observed in plots where a thallus was permanently present, suggesting similar disturbance intensity between both treatments. Secondly, timing of manual thallus movements was less regular than that of thalli moved by tidal currents. Irregularly applied disturbances were reported to affect benthic community traits differently than regularly applied disturbances of identical overall intensity (Bertocci et al. 2005; Wollgast et al. 2008). Thirdly, benthic species may benefit moderately from the continuous presence of a thallus. Strong and positive thallus effects were, for instance, apparent in most of the taxa contributing strongest to treatment effects in community structure, while a few,

Table 4 SIMPER analysis

Taxon	Control	Continuous	Sporadic	Thallus	%	Movement	%	Both	%
Lamprops fuscatus	2.70 (±0.38)	2.92 (±0.34)	1.28 (±0.21)	[+128 %]	11.6	[−53 %]	9.5	[+8 %]	15.1
Pygospio cf. elegans	2.09 (±0.35)	1.40 (±0.34)	2.19 (±0.42)	[−36 %]	9.8	[+5 %]	7.7	[−33 %]	8.0
Crenella decussata	1.87 (±0.29)	1.70 (±0.17)	0.57 (±0.17)	[+200 %]	7.9	[−70 %]	7.9	[−9 %]	5.0
Spio armata	1.38 (±0.24)	0.85 (±0.29)	1.44 (±0.23)	[−41 %]	7.1	[+4 %]	4.5	[−38 %]	6.1
Euchone analis	1.96 (±0.19)	1.23 (±0.19)	2.06 (±0.28)	[−40 %]	7.0	[+5 %]	4.8	[−37 %]	5.3
Ostracods	1.11 (±0.25)	1.34 (±0.18)	1.73 (±0.18)	[−23 %]	4.5	[+56 %]	5.2	[+21 %]	4.8
Copepods	1.29 (±0.13)	0.75 (±0.15)	0.50 (±0.18)	[+50 %]	4.0	[−61 %]	4.9	[−42 %]	3.7
Nemerteans	1.07 (±0.14)	1.03 (±0.21)	0.62 (±0.16)	[+65 %]	4.8	[−42 %]	3.2	[−4 %]	3.7
Crassicorophium crassicorne	3.58 (±0.18)	3.27 (±0.10)	2.81 (±0.09)	[+17 %]	3.6	[−21 %]	4.7	[−8 %]	3.4
Nematods	0.60 (±0.23)	0.36 (±0.20)	0.14 (±0.09)	[+158 %]	2.9	[−77 %]	3.1	[−40 %]	3.9
Priscillina herrmanni	0.64 (±0.19)	0.18 (±0.12)	0.14 (±0.09)	[+29 %]	1.7	[−78 %]	3.4	[−72 %]	3.7

Mean (±SEM = 67 % confidence interval) number of individuals (log + 1 transformed) of taxa constituting >85 % to total number of individuals in samples of the three seaweed (*Saccharina latissima*) treatments ("Control" = unmanipulated), "Continuous" = continuous kelp presence, and "Sporadic" = biweekly kelp movements for 20 s). The direction of the effect is given as either "−"= negative or "+" = positive and the magnitude of the average effect is given as per cent in squared brackets. The column headed with " %" indicates per cent contribution of a taxon to the detected significant thallus effect (=sporadic vs. continuous kelp presence), movement effect (=control vs. sporadic kelp presence), or the combination of both effects (=control vs. continuous kelp presence) on taxa composition (n = 10)

relatively weak movement effects were measured (Table 4). Thus, thallus presence partly compensated the negative effects of thallus movements. We speculate that positive effects of a thallus could result from altered hydrodynamics that may increase sedimentation rate of detritus and facilitate food capture of deposit and filter feeders.

Disturbance effects on community composition and reduction in the number of individuals may be partly due to the migration of specimens of relatively more mobile taxa like the cumacean *L. fuscatus*. Missing disturbance effects on evenness indicate, however, that disturbance did not affect the relatively more mobile taxa disproportionately stronger than the less mobile taxa. Thus, less mobile individuals must have been also negatively affected by thallus movements. Such direct, fatal treatment effects should strike small-sized, soft-bodied individuals disproportionately more than larger (e.g. *O. albida* or *C. laevis*) and/or shelled individuals (e.g. ostracods). The lack of treatment effects on biomass also suggests that disturbance predominately affected small-sized individuals, although missing treatment effects on biomass may have been obscured by low test power (23 %).

Patterns observed in this study principally confirm the density and diversity reducing effects of detached seaweeds reported from the temperate zone (Norkko and Bonsdorff 1996a; Arroyo et al. 2012). The present experiment indicates that already a single kelp thallus may alter the structure and diversity of benthic assemblages in Arctic sedimentary coastal areas. This is perhaps the most intriguing result of this study, because it indicates that soft-bottom habitats may be quite sensitive to subtle, temporal disturbances. The processes that generate thallus effects may, however, be different from those that generate mat effects. The latter seem to be mainly driven by the indirect effects of thallus presence, e.g. oxygen deficiency (reviewed in Krumhansl and Scheibling 2012), while the former appear more related to a direct effect of thallus movements (this study). As a consequence of kelp thallus disturbance, soft-bottom community structure may change at the scale of centimetres to metres, mirroring results on disturbance-induced patchiness in structure and diversity of rocky shore communities (e.g. Connell and Keough 1985; Sousa 1985).

This study is, to our knowledge, the second experimental report about a biotic source of disturbance affecting Arctic benthos. Sedimentary habitats adjacent to rocky shore kelp beds that regularly receive detached kelp or provide scattered habitat for successful kelp growth may be strongest affected by kelp movement-induced disturbance. This suggests that detached kelp arriving onto sedimentary areas are one vector by which rocky and sedimentary habitats are connected. Any factor that will alter the efficacy of storm-induced kelp removal from rocky shores may, therefore, also affect benthic assemblages in adjacent soft-bottom habitats. This will very likely apply to a future Arctic, because non-calcified seaweeds are predicted to find improved growth conditions in a more acidic and warmer ocean, especially where herbivorous fish are scarce (Harley et al. 2012). The observed increase in the abundance of erect red and brown seaweeds in Kongsfjord during the last two decades of warming seawater corroborates this prediction (Kortsch et al. 2012). A warmer Arctic will also result in a reduced extent of protective sea ice, which may cause high algal detachment rates especially from winter storms (see references in Renaud et al. 2008). A climate change induced increase in seaweed abundance (Kortsch et al. 2012) in combination with higher rates of wave-induced kelp detachment will likely become challenging drivers of growing importance of seaweed-mediated disturbance of Arctic soft-bottom community structure and diversity, with yet unknown effects on the functionality in these communities.

References

Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth

Arroyo NL, Aarnio K, Maensivu M, Bonsdorff E (2012) Drifting filamentous algal mats disturb sediment fauna: impacts on macro–meiofaunal interactions. J Exp Mar Biol Ecol 420:77–90

Beermann JA, Ellrich AJ, Molis M, Scrosati RA (2013) Effects of seaweed canopies and adult barnacles on barnacle recruitment: the interplay of positive and negative influences. J Exp Mar Biol Ecol 448:162–170

Bender A (2014) Dichteabhängige Effekte und Nahrungspräferenzen von Konsumenten auf arktische Weichbodengemeinschaften. Master Thesis, University of Rostock

Bertness MD, Leonard GH, Levine JM, Schmidt PR, Ingraham AO (1999) Testing the relative contribution of positive and negative interactions in rocky intertidal communities. Ecology 80:2711–2726

Bertocci I, Maggi E, Vaselli S, Benedetti-Cecchi L (2005) Contrasting effects of mean intensity and temporal variation of disturbance on a rocky seashore. Ecology 86:2061–2067

Clark GF, Stark JS, Johnston EL, Runcie JW, Goldsworthy PM, Raymond B, Riddle MJ (2013) Light-driven tipping points in polar ecosystems. Glob Change Biol 19:3749–3761

Conlan KE, Kvitek RG (2005) Recolonization of soft-sediment ice scours on an exposed Arctic coast. Mar Ecol Prog Ser 286:21–42

Connell JH, Keough MJ (1985) Disturbance and patch dynamics of subtidal marine animals on hard substrata. In: Pickett STA, White PS (eds) The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, pp 125–151

Filbee-Dexter K, Scheibling RE (2012) Hurricane-mediated defoliation of kelp beds and pulsed delivery of kelp detritus to offshore sedimentary habitats. Mar Ecol Prog Ser 455:51–64

Gutt J (2001) On the direct impact of ice on marine benthic communities, a review. Polar Biol 24:553–564

Harley CDG, Anderson KM, Demes KW, Jorve JP, Kordas RL, Coyle TA, Graham MH (2012) Effects of climate change on global seaweed communities. J Phycol 48:1064–1078

Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setala H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol Monogr 75:3–35

Hull SC (1987) Macroalgal mats and species abundance—a field experiment. Estuar Coast Shelf Sci 25:519–532

IPCC (2013) Summary for policymakers. Climate change 2013: the physical science basis contribution of working group I to the fifth assessment report of the Intergovernmental Panel on climate change

Konar B (2013) Lack of recovery from disturbance in high-arctic boulder communities. Polar Biol 36:1205–1214

Kortsch S, Primicerio R, Beuchel F, Renaud PE, Rodrigues J, Lonne OJ, Gulliksen B (2012) Climate-driven regime shifts in Arctic marine benthos. Proc Nat Am Soc 109:14052–14057

Krause-Jensen D, Duarte CM (2014) Expansion of vegetated coastal ecosystems in the future Arctic. Front Mar Sci 1:1–10

Krause-Jensen D, Marba N, Olesen B, Sejr MK, Christensen P, Rodrigues J, Renaud PE, Balsby TJS, Rysgaard S (2012) Seasonal sea ice cover as principal driver of spatial and temporal variation in depth extension and annual production of kelp in Greenland. Glob Change Biol 18:2981–2994

Krumhansl KA, Scheibling RE (2012) Production and fate of kelp detritus. Mar Ecol Prog Ser 467:281–302

Laudien J, Herrmann M, Arntz WE (2007) Soft bottom species richness and diversity as a function of depth and iceberg scour in Arctic glacial Kongsfjorden (Svalbard). Polar Biol 30:1035–1046

Mackey RL, Currie DJ (2001) The diversity–disturbance relationship: Is it generally strong and peaked? Ecology 82:3479–3492

Menge BA, Sutherland JP (1987) Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. Am Nat 130:730–757

Norderhaug KM, Fredriksen S, Nygaard K (2003) Trophic importance of *Laminaria hyperborea* to kelp forest consumers and the importance of bacterial degradation to food quality. Mar Ecol Prog Ser 255:135–144

Norkko A, Bonsdorff E (1996a) Altered benthic prey-availability due to episodic oxygen deficiency caused by drifting algal mats. Mar Ecol 17:355–372

Norkko A, Bonsdorff E (1996b) Rapid zoobenthic community responses to accumulations of drifting algae. Mar Ecol Prog Ser 131:143–157

Petrowski S, Molis M, Schachtl K, Buschbaum C (2015) Do bioturbation and consumption affect coastal Arctic marine soft-bottom communities? Pol Biol. doi: 10.1007/s00300-015-1654-7

Post E, Bhatt US, Bitz CM, Brodie JF, Fulton TL, Hebblewhite M, Kerby J, Kutz SJ, Stirling I, Walker DA (2013) Ecological consequences of sea-ice decline. Science 341:519–524

Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. University Press, Cambridge

Renaud PE, Carroll ML, Ambrose Jr WG (2008) Effects of global warming on Arctic sea-floor communities and its consequences for higher trophic levels. In: Duarte CM (ed) Impacts of global warming on polar ecosystems. FBBVA Press, Bilbao, pp 139–177

Sousa WP (1985) Disturbance and patch dynamics on rocky intertidal shores. In: Pickett STA, White PS (eds) The ecology of natural disturbance and patch dynamics. Academic Press Inc., Orlando, pp 101–124

Svendsen H, Beszczynska-Møller A, Hagen JO, Lefauconnier B, Tverberg V, Gerland S, Ørbæk JB, Bischof K, Papucci C, Zajaczkowski M, Azzolini R, Bruland O, Wiencke C, Winther J-G, Dallmann W (2002) The physical environment of Kongsfjorden–Krossfjorden an Arctic fjord system in Svalbard. Polar Res 21:167–208

Velimirov V, Griffiths CL (1979) Wave-induced kelp movements and its importance for community structure. Bot Mar 22:169–172

White PS, Pickett STA (1985) Natural disturbance and patch dynamics: an introduction. In: Pickett STA, White PS (eds) The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, pp 3–11

Wollgast S, Lenz M, Wahl M, Molis M (2008) Effects of regular and irregular temporal patterns of disturbance on biomass accrual and species composition of a subtidal hard-bottom assemblage. Helgol Mar Res 62:309–319

Young IR, Zieger S, Babanin AV (2011) Global trends in wind speed and wave height. Science 332:451–455