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The longer the better: the effect of substrate on sessile biota in Arctic kelp forests

Concise title: Sessile biota in Arctic kelp forest

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Abstract

Kelps are ecosystem engineers and thus enhance biodiversity and subsidize food-webs in nearshore areas. Numerous studies describing diversity and abundance of biota associated with kelp have focused on sub-tropical and temperate waters while kelp forests at high latitudes, where kelp is predicted to expand in distribution, remain mostly unexplored. Kelp forests contribute significantly to regional biodiversity, and associated fauna and the kelp themselves play ecologically important roles as habitat and feeding areas. Here, we report patterns in diversity, abundance and seasonal dynamics of fouling organisms associated with different regions of *Saccharina latissima* and nearby substrates (including stones of the barren ground). The study was conducted in Kongsfjorden, a high Arctic fjord on the west coast of Spitsbergen; and samples were taken five times between September 2013 and January 2015. Trends in species richness of epifauna were similar for stones and holdfasts: higher in winter (due the presence of rare species), and lower in spring and autumn. Species richness and abundance demonstrated a clear tendency to increase in accordance with substrate stability. Stones housed the most diverse biota compared to living substrates. Holdfasts demonstrated similar patterns in species composition and abundance as stones due their close spatial arrangement and presence of demersal larvae in the most of fouling organisms. Similarly, assemblages on blades in prostrate kelp forests are influenced by the species inhabiting stones of the barren ground. Both biotic and abiotic factors, including habitat stability and proximity to source populations, contribute to these spatial and temporal patterns in faunal abundance and diversity. .

Introduction

Kelp forests are widely distributed and highly productive marine coastal communities supporting diverse associated biota (Steneck et al. 2002). Being ecosystem engineers (Jones, et al. 1994), kelps serve as a food source, provide habitats for associated fauna and flora, and alter the hydrodynamic regime, sedimentation rates, and the ambient light climate below them. There is an extensive literature describing the influence of different environmental parameters on the flora and fauna associated with kelp forests, such as latitudinal gradients (e.g., Sheppard et al. 1977), seasonality (e.g., Christie et al. 2003), depth (Smith 1996; Smith et al. 1996), wave exposure (e.g., Schultze et al. 1990; Lippert et al. 2001; Spurkland and Iken 2011), and water flow (e.g., Duggins et al. 1990). These numerous studies have focused on kelp forests in subtropical and temperate waters, and only few have investigated kelp beds in the Arctic (Rozycki and Gruszczynski 1986; Lippert et al. 2001; Carlsen et al. 2007; Wlodarska-Kowalczuck et al. 2009). Most of published studies concern motile epifauna, while sessile organisms in such assemblage are often neglected (see Wlodarska-Kowalczuck et al. 2009 for a discussion of this).

Kelp beds are complex three-dimensional structures including both living and non-living substrates of varying longevity: ephemeral (blades), short-lived (holdfasts, stipes, understory macroalgae and large sessile organisms such as some bryozoans and cirripedians), and stable (stones). It was shown for different species of Laminariales that the number of epifouling species is often lower on blades and stipes than on holdfasts (Norton 1971; Withers et al. 1975; Schultze et al. 1990; Christie et.al. 2003, 2009; Blight and Thompson 2008; Wlodarska-Kowalczuk et al. 2009), nevertheless kelp beds were never addressed as entire structure – though every part of which has a specific fouling assemblage but they affect each other.

Sugar kelps (*Saccharina latissima*) form prostrate kelp forests that cover the bottom with their blades (Steneck et al. 2002). The meristemic growth site is located above the stipe, thus the older part of the blade is shifted towards its distal end (Hornsey and Hide 1976; Seed and Harris 1980). *S. latissima* and some other species of Laminariales are known to live up to five years in the Arctic (Lüning 1990; Carlsen et al. 2007), and their holdfasts and stipes are perennial regions. Blades of *Saccharina* and *Laminaria* spp., on the other hand, are usually thought to be ephemeral substrate with the longevity of about a year, their growth starts in winter and reaches its peak during late spring and midsummer. The oldest portion of the blade is lost through abrasion and necrosis which is especially intense during autumn and winter (e.g., Lüning 1979, 1993; Seed and Harris 1980; Schaffelke and Lüning, 1994; Makarov and Shoshina 1996; Wiencke and Amsler 2012). Some authors, however, have reported that individuals of *S. latissima* and *Laminaria digitata* found in summer along the Greenland and Svalbard coasts had perennial blades (2-3 years), with prominent annual differentiation (Lund 1959; Borum et al. 2002; Carlsen et al. 2007). Based on these data, therefore, we expect kelp blades to be quite suitable substrate to study recruitment patterns, including seasonality of the fouling assemblage.

Seasonal changes in species richness and diversity of the assemblage associated with kelp have been demonstrated in many studies performed in temperate waters, but mostly for motile fauna.. To our knowledge, however, there is only a single mention about winter state of kelp forests in the high Arctic (Berge et al. 2015). and data on seasonal changes in sessile epifauna at high latitudes are lacking since winter sampling under Arctic condition is logistically difficult. The recent evidence for reproduction in Arctic fauna throughout the year (e.g. Kuklinski et al. 2013), and activity across the food web in the middle of the Arctic winter (Berge et al. 2015), suggest seasonal studies can be revealing as to life-cycles of kelp-associated fauna, and food resources for nearshore food-webs.

Based on the relative lack of data on epifauna on kelp blades, and their potentially important roles in nearshore ecosystem functioning, we assessed patterns of diversity, abundance and seasonal dynamics of fouling organisms associated with different regions of *S. latissima* and accompanying substrates (including stones of the barren ground) according to their longevity. Results will fill important knowledge gaps regarding winter kelp community structure in high Arctic, its seasonal changes and sessile fouling fauna in general. Moreover, such data create a basis for fruitful comparison for studies concerning settlement patterns of benthic invertebrates on artificial substrates. These data are needed to establish a baseline against which to evaluate inter-annual variability and climate change as kelp beds are predicted to expand in a warmer, ice-free Arctic (Krause-Jensen et al. 2012).

Material and methods

Study area and sampling

The material was collected in Kongsfjorden (78^0 56'N 11^0 56'E, near Ny-Ålesund), a glacial fjord on the west coast of Spitsbergen. Kongsfjorden opens to the West Spitsbergen Shelf and is dominated by the influence of Atlantic waters (warm and saline), Arctic waters (cold and fresh), and glacial melt with pronounced seasonality (Cottier et al., 2005; Svendsen et al., 2002; Willis et al., 2006). During the last ten years, most of Kongsfjorden was free of fast-ice during winter (our observations, see also http://polarview.met.no).

Samples were taken by SCUBA diving in different seasons – first September 2013, then January, May and September of 2014, and finally January 2015. Sampling dates were chosen for several reasons: (*i*) we expected to experience a range of blade maturity, from little new growth in January to maximum in May (see Wiencke et al. 2007 and references therein); and (*ii*) these seasons represent a range of food supply and meroplankton abundance and composition (Willis et al., 2006; Piwosz, 2009; Walkusz et al., 2009; Kuklinski et al., 2013; Stübner et al. 2016).

At each season, we took from 7 to 10 sets of samples from 2 m depth. Each set included a stone (hereafter SL-stone) with one or several individuals of *S. latissima* and understory macroalgae, and a sediment sample (hereafter, Gr-samples) taken by a cogged grab (sampling area 0.025 m^2) near SL-stone. All stones found within sediment (grab) samples are referred hereafter as Gr-stones. In January and May, 2014 and in January, 2015 we also took six sets of samples at five meter depth. Stones with sessile organisms were selected from Gr-samples and weighed separately, the rest of Gr-samples were used for grain size analysis which was performed using the standard dry-sieve shaking method (Eleftheriou 2013).

When several individuals of *S. latissima* were attached to a single stone and it was impossible to separate their holdfasts we regarded the latter as a complex but single structure.

125   The thallus of *S. latissima* possesses several microhabitats corresponding to its region (blade, stipe, holdfast).
126 In several SL- and GR-samples understory macrolagae were present. Data from each substrate type were analysed
127 separately since their characters differ and are likely very important for fouling organisms. Substrate types were
128 divided into three categories according to their longevity: (*i*) ephemeral (about a year – blades of *S. latissima*); (*ii*)
129 short-living (about 3-4 years – holdfasts and stipes of *S. latissima*, understory macroalgae and large bryozoan
130 colonies); (*iii*) stable (stones). Only individuals of *S. latissima* that were older than 3 years were taken in the
131 analysis; age was determined according to Kain (1963).

132   Almost all blades of *S. latissima* in January and all blades in May possessed a very prominent constriction
133 which was lacking in September (Online Resource 1). This constriction divided a blade in two portions, proximal
134 and distal, which differed in thickness, colour and abrasion and hence were referred, respectively, as "0+" and "1+"
135 year-zones. Although both stipes and holdfasts continue to grow (though not so fast) during the whole life-span of a
136 kelp individual, it is impossible to divide these parts of *S. latissima* thallus into year-zones.

137   For each substrate type (blade, stipe and holdfast of *S. latissima*, thalli of other macroalgae and stones)
138 surface area was calculated. Blades (different year-zones separately), stipes, and holdfasts (preliminary split at
139 bifurcations into pieces) were photographed with a size scale, and the diameter of stipes and holdfast pieces was
140 measured. Area of blades and length of stipes and holdfast pieces were assessed using ImageJ 1.48v package. Thalli
141 area of other macroalgae was estimated using the same procedure. Surface area of stones and barnacle shells was
142 calculated using an inelastic net marked in a grid of cm^2.

143   All sessile macrobenthic organisms were identified to the lowest possible taxonomic level, counted and
144 weighed (wet-weight) with accuracy of 1 mg (except bryozoans). We measured a square of bryozoan colonies (in
145 mm^2) and calculated their weight using species-specific coefficient (Denisenko, 1983). For solitary organisms
146 density was estimated as the number of individuals per m^2, for colonial organisms as the number of colonies per m^2.
147 Since densities during our survey were rather low there were no difficulties with counting number of hydrozoan or
148 bryozoan colonies.

149   Whenever possible, we registered the presence of juvenile and adult stages: for bryozoans, ancestrula or small
150 colonies including ancestrula plus up to four zooids were assigned as juveniles; for spirorbid polychaetes, recruits
151 with tubes not yet coiled were ascribed as juveniles.

152
153 **Data analysis**
154   To estimate seasonal changes in the percentage of "0+" year-zone we used General Linear Model analysis
155 (GLM; continuous predictor – total area of blade, categorical factors – season, depth) and a post-hoc test (Fisher
156 LSD). We only included data from Januaries and May because in Septembers blades were composed of "0+" year-
157 zone.

158   Species richness (hereafter, SR) was assessed with both three-way main effects analysis of variance
159 (ANOVA; factors: substrate type, season, depth) based on all samples, and Spearmen correlation. For animals, we
160 calculated the Shannon diversity index (H'; log base e) and D-index (effective number of species; see Jost 2006)
161 based on density.

162   To compare assemblages on different substrates, we estimated density and biomass using the surface areas of
163 corresponding substrates. To calculate total density and total biomass we used the sum of substrate surface area of
164 all substrate types in the sample. The frequency of occurrence (*F*) was calculated for each taxon as a percentage of
165 samples where the taxon was found relative to the total number of samples. Rare species were defined as those
166 occurring in only one (unique) sample. We identified dominant and subdominant species based on their frequency of
167 occurrence (F≥75%) and density/or biomass (N≥15% or B≥15%) in at least one of the seasons.

168   Since macroalgal communities are usually quantified by biomass only, we used this parameter when we
169 referred to the fouling assemblage as a whole. When assessing animals' distributions we used both their density and
170 biomass values. Density of animals was chosen as a main abundance index when we traced seasonal changes.

171   ANOSIM (based on Bray-Curtis dissimilarity matrix) was used to test differences in fouling assemblages on
172 different substrates and in different seasons. ANOSIM tests were based on (*i*) biomass of all sessile organisms as
173 well as (*ii*) density and (*iii*) biomass of animals only, and were made for two and five meter depth separately.
174 Understory macroalgae from sediment samples from both depths as well as Gr-stones from five meter depth were
175 excluded from this analysis due their low frequency of occurrence. SIMPER (based on Bray-Curtis dissimilarity
176 matrix) analysis was also used to assess taxon contribution to sample heterogeneity at two meter depth.

177   We applied a three-way main effects ANOVA analysis (factors 'substrate type', 'season', 'depth') for
178 assessing (*i*) biomass distribution of animals and macroalgae; (*ii*) biomass of dominant and subdominant species.
179 Understory macroalgae from sediment samples were excluded from these analyses due their low frequency of
180 occurrence. Distribution of juvenile densities were tested with use of two-way ANOVA (factors substrate type and
181 season) based on the data from 2 m depth since we have a full seasonal set of samples. ANOVA tests were based on
182 fourth-root transformed data and were followed with post-hoc tests (Fisher LSD).

183   PCA analysis was based on fourth-root transformed data of average density of animals on each substrate type
184 per season. PCA analysis was chosen because it allows to estimate the portion of variation for each factor and to
185 trace loadings for each species.

186   GLM analysis, ANOVA and post-hoc tests, and Spearmen correlations were calculated with use of
187 STATISTICA 7.0 software package; ANOSIM, SIMPER and PCA analyses were made using PAST 3.12 software
188 package.
189
190   **Results**

Substrate characters

191
192   The main sediment fraction was categorized as pebbles and cobbles at two meters depth, and silted fine sand
193 at five meters depth. At five meters depth we found several individuals of *Saccharina latissima* with holdfasts
194 attached to very fine pebbles and almost entirely embedded within soft sediments. Such holdfasts were rather
195 thinner and longer than those attached to cobbles and boulders (Online Resource 2).
196   Frequency of occurrence of understory macroalgae (see the list in the legend in Online Resource 3) was
197 variable and quite low, and usually did not exceed 15-20% for each season, except for *Chaetopteris plumosa* – 30%
198 and 50% (January 2014 and 2015, respectively) and *Polyides rotundus* – 60% and 40% (September 2014 and
199 January 2015, respectively). Average surface area of each algal substrate type varied both within and among
200 seasons, but this value was several times larger for blades of *S. latissima* than for other substrates; average surface
201 area of stones sampled was comparable to that of holdfasts and stipes (Table 1).
202   Usually in January and always in May, blades of *S. latissima* included both "0+" and "1+" year-zones while
203 in September all blades lacked constriction and comprised only "0+" year-zone (Online Resource 1). In both
204 January samplings there were several individuals of *S. latissima* without "0+" year-zone of blade and occurrence of
205 such individuals was higher at five meters depth (5% and 30% in January 2014 at two and five meter depth,
206 respectively, and 30% at 5 m depth in January 2015). The percentage of "0+" year-zone varied according to the
207 season (GLM, $F_{2,156} = 112.7$, p<0.0001) but was independent from total blade surface area ($F_{1,156} = 0.21$, p=0.65)
208 and thus the growth pattern of *S. latissima* was considered to be isometric (Fig. 1). Depth did not affect the
209 percentage of "0+" year-zone ($F_{1,156} = 3.42$, p=0.07) but analysis revealed a significant interaction (season*depth;
210 $F_{2,156} = 5.53$, p=0.005). In Januarys at 5 m depth, the percentage of "0+" year-zone was lower than at 2 m (post-hoc
211 test; p<0.001) but this index was similar at both depths in May (post-hoc test, p=0.18). Post-hoc tests also
212 demonstrated that the percentage of "0+" year-zone was similar in January 2014 and 2015 (p=0.81 and p=0.48 for
213 two and five meter depth respectively).
214   Rarely, some substrates (more often, "0+" year-zone and stipe of *S. latissima*) were not colonized by sessile
215 organisms (i.e., they were empty) and their portion varied during the survey. All understory macroalgae were empty
216 in May, 2014.
217
218

Species richness and species composition

219
220   In total, 111 taxa of sessile biota were recorded including 80 taxa (57 to species level) of animals and 31 taxa
221 (23 to species level) of macroalgae; Online Resource 3 gives the full list of taxa. Such a huge gap between the
222 number of identified species and the number of registered taxa was due to numerous juveniles in the samples,
223 especially bryozoans, which often possess identification characters only at adult stage.
224   Species richness (hereafter, SR) on every substrate type was highly variable and ranged from 0 to 39 species
225 per sample. Among animals, Bryozoa was the most species-rich group (56 taxa and 43 species) and among epiflora,
226 brown algae (Orchophyta: Phaeophyceae – 16 taxa and 11 species) and red algae (Rhodophyta: Floridiophyceae –
227 11 taxa and 10 species) demonstrated the highest diversity. Mean and total values of SR of macrobenthos were the
228 lowest on blades and stipes and the highest on SL-stones (Fig. 2, Table 1, see also Online Resources 4 and 5). SR
229 pattern was similar both for animals and macroalgae and at the both depths (Spearmen correlation, p<0.05 for all
230 paired combinations).
231   A three-way main effects ANOVA demonstrated that SR of animals was significantly influenced by all three
232 factors: 'substrate type' ($F_{6,41}$=15.01, p<0.0001), 'depth' ($F_{1,41}$=10.96, p=0.002), and 'season' ($F_{4,41}$=2.9, p=0.038).
233 Substrate type had the highest effect size (63.2%) while effect sizes of season and depth were rather low (8.2% and
234 7.7%, respectively). SR of epiflora demonstrated similar patterns, but only substrate type had a significant effect
235 (three-way main effect ANOVA, $F_{6,41}$=17.32, p<0.0001; effect size = 68.5%). Post-hoc tests (Fisher LSD, p<0.05)
236 confirmed that SR of sessile macrozoobenthos on SL-stones and SR of macroalgae both on SL- and Gr-stones
237 differed significantly from other substrates.
238   Seasonal changes in total SR of animals at two meters depth were similar on SL-stones and holdfasts
239 (Spearman correlation, 0.98, p=0.0004) with the highest values of total SR detected in winter samples both in 2014
240 and 2015 (Fig. 3; Table 1). Contrary to this, we failed to trace any trend in seasonal fluctuations in SR of animals on
241 blades and stipes (Fig. 3) and total SR were considerably lower on these substrates (Table 1). Total SR of
242 macroalgae was the lowest in September, 2013 and January, 2014 but increased to the highest values in the same
243 seasons a year later (Fig. 3). SR of macroalgae varied on different substrate types with the lowest values registered
244 for stipes (a single species *Styctiosyphon tortilis* was found only once – in May, 2014).
245   Species composition was highly variable on each substrate type. Almost half (46%) of registered taxa
246 demonstrated substrate preferences (Online Resource 3). Two species (*Buskia nitens* and *Cerceis spirillum*) were
247 found only on understory macroalgae while about 66% of taxa never resided on them (the majority of such species
248 were recorded on stones). Nine species were found only on *Saccharina latissima* (seven only on holdfasts, two both

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249 on holdfasts and stipes) while 36 taxa were resided solely on stones, of which two species inhabited only Gr-stones,
250 21 taxa occurred only on SL-stones, and 13 taxa were found both on SL- and Gr-stones. There were no taxa specific
251 for blades or/and stipes. We registered 13 taxa residing on all regions of the *S. latissima* thalli and both SL- and Gr-
252 stones; the rest of the 56 taxa inhabited several substrate types in different combinations.
253   For animals, both Shannon diversity index (H') and D-index (effective number of species) had the highest
254 values for stones and the lowest for blades and stipes (Table 1), and demonstrated seasonal fluctuations both at two
255 and five meters depth. A three-way main effects ANOVA revealed that D-index was significantly influenced by
256 substrate type ($F_{6,44}$=16.94, p<0.0001; effect size=72.3%) but was independent of season ($F_{6,44}$=0.56, p=0.69) and
257 depth ($F_{6,44}$=0.63, p=0.43). Values of D-index for blades and stipes significantly differed from other substrates (post-
258 hoc test; Fisher LSD, p<0.05).
259   Within a sample, we found up to six species of understory macroalgae with different thallus morphologies
260 and surface area. SR tended to be higher when more understory algae were recorded, but the frequency of
261 occurrence of understory algae was too low to address this trend statistically.
262
263 **Occurrence and abundance of fouling organisms**
264   Total biomass of sessile organisms on blades and stipes was considerably lower than that on stones and
265 holdfasts (Fig. 4). During our survey we also found noticeable seasonal fluctuations in total biomass, which was
266 rather high in January, 2014 and September, 2014 and lower in other seasons. It is not surprising that biomass of
267 macroalgae on both blades and stipes was close to zero and was rather low on holdfasts (except for September, 2013
268 and January, 2014) compared to stones. Biomass on all parts of *Saccharina latissima* was dominated by animals. A
269 similar pattern was revealed for SL-stones in September, 2013 and January, 2014 while in the rest of the seasons the
270 biomass ratio of animals and algae was opposite. Gr-stones were dominated by macroalgae in May, 2014 and
271 January, 2015 but in September, 2014 biomass ratio of macrolgae and animals was almost equal. Total biomass of
272 sessile zoobenthos was the lowest in May, 2014 and the highest in January, 2014.
273   ANOSIM tests based on biomass of all sessile organisms, as well as on density and biomass of animals,
274 indicated that assemblages were significantly different on all substrate types at both depths (statistic R values varied
275 from 0.5 up to 0.61). Within each substrate type at 2 m depth, seasonal fluctuations were not so prominent (statistic
276 R values varied from 0.19 up to 0.3), while at 5 m depth the degree of dissimilarity among seasons was higher
277 (statistic R values varied from 0.42 up to 0.62).
278   We found the highest dissimilarities in biomass distribution among substrates at 2 m (Table 2), while
279 seasonal differences were somewhat lower (except for holdfasts). Sample heterogeneity was also high and
280 comparable with seasonal dissimilarities (Table 2).
281   A three-way main effects ANOVA demonstrated that biomass both of animals and macroalgae was
282 influenced by substrate type ($F_{5,294}$=24.7, p<0.0001; effect size = 27.2% for animals and $F_{5,294}$=35.07, p<0.0001;
283 effect size = 35.7% for algae) and season ($F_{5,294}$=6.9, p<0.0001; effect size = 6.1% for animals and $F_{5,294}$=3.19,
284 p<0.014; effect size = 2.6% for algae). Biomass distribution was independent of depth.
285   Both density and biomass of sessile zoobenthos demonstrated high correlations with substrate type. Thus, the
286 first component (21.4%) in the PCA analysis (based on average density of animals on each substrate type per
287 season) corresponded to substrate type since blades and stipes had the lowest scores (from -3.79 up to -2.69) and
288 SL-stones had the highest one (from 1.6 up to 8.9) while the rest of substrate types occupied intermediate positions
289 (Fig. 5). This correspondence was also confirmed by the lowest loadings for the species that were often registered at
290 the blades and stipes (-0.35 and -0.14 for *Celeporella hyalina* and *Circeis armoricana*, respectively), as well as by
291 the highest loadings for species found mostly on stones (0.89 for *Tegella arctica*; see also the right frame on Fig. 5).
292 Thus along the first component (from left to right) there was an "age-gradient" of substrates: from ephemeral
293 (blades) through short-living (stipes and holdfasts), towards stable (Gr- and SL-stones). The second principle
294 component (13.8%) corresponded to the differences between living and non-living substrates located directly on the
295 bottom: holdfasts and understory macroalgae had the highest scores (always positive) while scores of Gr-stones
296 (always) and SL-stones (usually) were negative. The lowest loadings were found for species more frequently
297 inhabiting stones, while the highest loadings were registered for species usually occupying understory macroalgae
298 and holdfasts (see the list in the left box on Fig. 5). Together, the first and second components explained about one
299 third of dispersion, the rest of the components corresponded to the seasonal variation of density of fouling animals
300 on stones.
301   We found high temporal heterogeneity in the structure of fouling community. Among macroalgae, dominant
302 species differed within each season on different substrates and changed on each substrate during the survey (Fig. 6,
303 Table 1, see also Online Resource 4) so we failed to trace any consistent pattern. Among animals, blades and stipes
304 were dominated in biomass by a single species (*Circeis armoricana* and *Celeporella hyalina*, respectively) during
305 the survey. Contrary to this, dominant species on other substrates varied in different seasons (Fig. 6, Table 1, and
306 Online Resources 4 and 5). And since a dominant species in one of the seasons was usually registered as a
307 subdominant in others, we refer to this collection of taxa as 'leading species'. All dominant and leading species were
308 found on at least three substrate types, among which stones and holdfasts were always represented (except for
309 *Alcyonidium gelatinosum* that was not registered on holdfasts). In addition to this group, we distinguished several
310 species (*Porella smitti, Tricellaria ternate, Crisia eburnea, Alcyonidium mamillatum, Porella minuta, Buschiella*

311 *quadriangularis*) with high frequencies of occurrence (F ≥ 70%), but with rather low density and biomass. Several
312 species were rather rare on a given substrate type (Online Resource 3).
313   A three way main-effects ANOVA demonstrated that substrate type and season significantly influenced
314 abundance indices of dominant and leading species (Table 3), but effect size of substrate type was higher. Only three
315 species were significantly influenced by depth and, moreover, effect size of this factor was extremely low (about 2%
316 of explained variation).
317
318 **Distribution of juveniles**
319   We found juvenile stages of bryozoans, barnacles and spirorbid polychaetes; and among them, eight taxa
320 were identified to species level and seven to genus level (Online Resource 3).
321   Juveniles usually demonstrated the same substrate preferences as adults, but in several cases they were also
322 registered on substrates where adults were absent (e.g., juveniles of *Dendrobeania* sp. were found on stipes,
323 *Tubulipora* sp. on stones, and *Balanus balanus* on blades). Juveniles of some taxa were recorded in specific
324 season(s), e.g., only in September (*Alcyonidium* sp.), both in September and in January (*Circeis armoricana*,
325 *Tubulipora* sp., *B. balanus*, and *Porella minuta*), both in January and May (*Tricellaria* sp.). Contrary to this,
326 juvenile stages of some taxa (e.g., *Callopora craticula*, *Cribrilina annulata*, *Celeporella hyalina*, *Crisiella producta*,
327 *Bushiella* sp., *Dendrobeania* sp.) were present in all seasons during the survey, and on at least one type of perennial
328 substrates. A two-way ANOVA (factors 'substrate type' and 'season'; $df_1 = 3$, $df_2 = 2$) demonstrated that the
329 distribution of juveniles of some taxa (*Bushiella* sp., *Dendrobeania* sp., *C. hyalina*, *C. armoricana*, *C. annulata*,
330 *C. producta*) was significantly influenced by both factors (p<0.001 in all cases except for *C. hyalina*, season,
331 p=0.024). Two taxa (*Alcyonidium* sp. and *Tricellaria* sp.) were significantly affected only by season (p<0.005 in
332 both cases), and some taxa (*Paradexiospira* sp., *B. balanus*, *C. craticula*, *Patinella* sp.) were only influenced by
333 substrate type (p<0.005 in all cases). Distribution of juveniles of several species (*C. hyalina*, *C. armoricana*,
334 *C. annulata*, *C. producta* and *Bushiella* sp.) were also influenced by interactions of factors (substrate*season), and
335 highest densities of juveniles were recorded for different substrates in various seasons.
336   On blades, we recorded juveniles of six taxa (*C. armoricana*, *C. hyalina*, *C. producta*, *Patinella* sp.,
337 *C. annulata*, *Tubulipora* sp.) but not in May, when they were registered on perennial substrates. During the survey,
338 their densities were about half that of adults (Fig. 7). In Januarys, juveniles of all species were found within the '1+'
339 year-zone of blades.
340
341
342 <center>**Discussion**</center>
343 **Methodological issues**
344   Traditionally, abundance of sessile biota is estimated using percent cover as a main index. The principal
345 advantage of this method consists in possibility to describe both community structure and abundance without time-
346 consuming procedure of calculating density and biomass, particularly since colonial animals present challenges
347 here. Doubtless, spatial competition on stable substrates may be very high and sometimes it can be difficult to count
348 the number of colonies of hydrozoans or bryozoans. However, percent cover data are only comparable when
349 substrates are more or less equal in size, which is not always the case. Therefore, different methods for assessing
350 species number and/or abundance of epibionts were used in previous studies, such as number of epifaunal organisms
351 per plant (Norton 1971), area of substrate surface (e.g., Rozycki and Gruszczynski 1986), weigh of basibiont (e.g.,
352 Kain 1971; Lippert et al. 2001), volume of basibiont (e.g., Edwards et al. 1980; Smith et al, 1996; Christie et al.
353 2003, 2009; Blight and Thompson 2008) or length of stipe (e.g., Christie et al. 2003). Such a diversity of methods
354 hinders the comparability of different studies of species abundance. Most of these methods are applicable to the
355 study of abundance of mobile epifauna, but one of the most important factors for studying the distribution of sessile
356 organisms is the area of substrate surface,. This method is also of particular importance when comparing diversity
357 and abundance across different substrates.
358
359 **Phenology of blade extension**
360   We documented growth of *Saccharina latissima* in Kongsfjorden in early January (though not all individuals
361 had started to grow by mid-January).The blade at this time includes a small '0+' year-zone and a large '1+' year-
362 zone. Growth slows down in autumn and the distal part of the blade is destroyed due to physical forces, so by the
363 end of September the blade is composed only of '0+' year-zone.
364   Our results are in agreement with previously reported data from European coast (e.g., Lüning 1993;
365 Schaffelke and Lüning 1994; Makarov and Shoshina 1996). Carlsen et al. (2007), however, reported 3-year-old
366 blades both of *S. latissima* and *Laminaria digitata* from the same locality (Kongsfjorden, west Spitsbergen), and
367 blades of 2-3 years were also reported from Greenland coast (Lund 1959; Borum et al. 2002). Such a difference is
368 quite surprising and difficult to explain. Perhaps such individuals were rather rare and were collected in sheltered
369 localities and/or deeper where blade abrasion is rather slow. In addition they probably were a specific target in these
370 studies while we sampled randomly and did not find such old blades. However, since in all these cases material was
371 collected in high Arctic glacial fjords with mid-summer decreases in light and nutrient loads due to glacial runoff,
372 one can speculate that such abrupt changes in abiotic drivers might cause non-cyclic slowing down or even stoppage
373 of blade growth, resulting in constriction formation. Although such a phenomenon was never reported for

374 Laminariales species, interaction of environmental factors (such as irradiance, temperature, nutrients, etc.) can affect
375 algal growth in ways that are not fully understood (reviewed in Wiencke et al. 2007, 2009; Gomez et al. 2009;
376 Wiencke and Amsler 2012).
377
378 **Assessment of species richness**
379   Epifauna associated with all Laminariales species often demonstrate large similarities across studies,
380 especially regarding SR and species composition (Schultze et al. 1990; Lippert et al. 2001; Carlsen et al. 2007;
381 Wlodarska-Kowalczuk et al. 2009). Based on this, we expected to find similar levels of species diversity in our
382 survey and earlier studies, especially those conducted in the same region and locality (Kongsfjorden, west coast of
383 Spitsbergen). Data from two previous studies (Lippert et al. 2001, Carlsen et al. 2007) allow a detailed comparison
384 with our results for sessile epifauna. Strikingly, the number of zoobenthic taxa recorded on *S. latissima* in our survey
385 was at least two times higher than in either of the other studies. Nevertheless, the higher level taxonomic
386 compositions found the present study and reported by Lippert et al. (2001) are consistent, and the most abundant
387 taxonomic groups are similar, e.g. we registered 80% of the bryozoan species listed by Lippert and coauthors. On
388 the other hand, species composition reported by Carlsen et al. (2007) differs significantly: sponges, barnacles and
389 hydrozoans were not mentioned in their study, only about 50% of bryozoan species coincided, and spirorbid
390 polychaetes were represented by other species. Data reported by Rozycki and Gruszczynski (1986) for four species
391 of overstory kelp collected on the west coast of Spitsbergen revealed a similar pattern: SR in our survey is three
392 times as high while taxonomic composition is comparable. Such differences in both cases are most likely due the
393 combination of two factors: small numbers of samples in these studies (8, 20 and 56, respectively) and spatial
394 heterogeneity. Even at small scales (one to few meters) it is typical for the distribution of biota and assemblage
395 composition to vary considerably (e.g., Arroyo et al. 2004; Anderson et al. 2005; Kuklinski et al. 2006; Yakovis et
396 al. 2008; Miguel et al. 2010).
397   In our survey we found 111 taxa in 68 samples including 110 individuals of *S. latissima* which is quite far
398 from assessing true species richness. Even in an extensive study of motile and sessile epifauna associated with
399 macroalgae, and based on rather numerous samples (in total, 403 samples including 356 individuals of three species
400 of overstory kelp), the observed number of motile and sessile taxa was 208, a value much lower than Chao2
401 estimated value (Wlodarska-Kowalczuk et al. 2009). This research was also performed in Svalbard waters
402 (Hornsund), and demonstrated diverse sessile fauna among which Bryozoa and Hydrozoa were the most species rich
403 groups, with 70 and 37 species, respectively (compared to 56 and 8 species in the present study). Unfortunately,
404 Wlodarska-Kowalczuk and coauthors did not provide any details of epifauna distribution on a given species of
405 macroalgae (or at least mention them to be located either on overstory or understory kelp) and this prevents us from
406 further comparison. Besides differences in number of samples, such a huge gap in the species richness probably
407 resulted from different sampling depth and larger number of sites sampled.
408   Habitat complexity and structural heterogeneity are well known to beget diversity and increase richness and
409 abundance in different habitats (e.g., Dean and Connell, 1987; McCoy and Bell 1991; Gee and Warwick 1994;
410 Knowles and Bell 1998; Kelaher and Castilla 2005; Matias et al. 2010; Kovalenko et al. 2012; St.Pierre and
411 Kovalenko 2014; Loke and Todd 2016). Abundance, biomass, and diversity of motile epifauna are directly related to
412 algal species composition (e.g. Attrill et al. 1996; Parker et al. 2001; Christie et al. 2003; Norderhaug et al. 2007).
413 As shown by Leclerc et al. (2015), the abundance of mobile fauna in kelp epiphytes may interfere with habitat
414 complexity on the understory and kelp size-density structure (density of adults hosting abundant epiphytes).
415 Armitage and Sjøtun (2016) demonstrated that shared macroalgal epiphytes lead to higher similarity between the
416 zoobenthic communities associated with *Codium fragile* and *Fucus serratus*. Unfortunately, such data lack for
417 sessile epifauna, anyway, one can speculate that (*i*) substrate surface area available for recruits increases with the
418 habitat complexity; (*ii*) understory macroalgae alter hydrodynamic regime within the bottom water layer making it
419 more turbulent which is supposed to facilitate in the food uptake by suspension feeders (e.g., Shimeta and Jumars
420 1991; Vogel 1994).
421   Thus, the higher values of SR and somewhat different species lists reported by Wlodarska-Kowalczuk and
422 coauthors (2009) may be due to higher habitat complexity and structural heterogeneity owing to the presence of
423 more numerous understory macroalgae with diverse thallus structure in their samples. Understory macroalgae in our
424 survey were dominated by filamentous and branching forms (see species list in Online Resource 3), and their
425 morphology and limited surface area impede settlement by sessile biota. Although the occurrence of understory
426 macroalgae in our samples was rather low, we noted that SR tended to be higher when more understory algae were
427 recorded. This observation, and the quite different species lists of understory algae in the present study and that
428 reported by Wlodarska-Kowalczuk et al. (2009), we suggest that SR and diversity of sessile biota associated with
429 overstory kelp is also highly influenced by species composition and abundance of understory macroalgae.
430
431 **Effect of substrate type**
432   It has been shown that the number of fouling species on different species of Laminariales is often lower on
433 blades and stipes than on holdfasts (Norton 1971; Withers et al. 1975; Schultze et al. 1990; Christie et.al. 2003,
434 2009; Blight and Thompson 2008; Wlodarska-Kowalczuk et al. 2009); and our data confirm this observation (see
435 Fig. 2). In the present study, SR, density and biomass of epibionts on blades and stipes were two orders of
436 magnitude lower than on other substrate types (see Fig. 2, 3, 4). According to our results, substrate type, reflecting

437 longevity, surface characteristics, and likelihood of disturbance, among other factors, more strongly influenced
438 distribution of fouling biota than seasonality or depth. This hierarchy of factors was found for SR, diversity, and
439 abundance indices of the whole assemblage, as well as for dominant and leading species (see Table 3, Fig. 6).
440   Numerous studies have demonstrated the effect of substrate type on SR, diversity, species composition of
441 epifauna (e.g., Seed and O'Konnor 1981; Lippert et al. 2001; Kuklinski and Barnes 2005; Villegas et al. 2008). Our
442 data are in agreement with them. In the present study, SL-stones housed the most diverse biota compared to living
443 substrates (97 and 61 taxa, respectively, out of 111 – see Online Resource 3), which is probably due to higher
444 substrate stability and, perhaps, surface quality, in particular, rugosity. Numerous fouling settlers prefer small
445 cavities, and rough and convex surfaces (e.g., Seed and O'Connor 1981; Ward and Thorpe 1989; Kuklinski and
446 Barnes 2005). Gr-stones demonstrated a lower ratio of substrate-confined species and lower values of total SR
447 compared with SL-stones, making GR-stones more similar to ephemeral substrates. Although species composition,
448 density, and biomass of fouling biota on Gr-stones were similar to those on SL-stones, their values were highly
449 variable during the survey so that Gr-stone samples formed an elongated cluster along first component axis in PCA
450 analysis (see Fig. 5) which corresponded with an "age-gradient" of substrate type. Such features are very likely to be
451 explained by somewhat smaller size of some Gr-stones (see Table 1) and their lower weight resulting in more
452 frequent overturning caused by strong wave action, and, in addition, smaller surface area available for recruits. We
453 have indirect confirmation of disturbance (overturning) frequencies of small Gr-stones during our survey as the
454 presence of dead bryozoan colonies with destroyed frontal walls of zooids which were more numerous in samples
455 collected in September, 2014 and January, 2015, sampling periods that were preceded by strong storms. These
456 results confirm the data of numerous previous studies reported that the stone size is of prime importance for
457 colonization patterns (e.g., Osman 1977; Sousa 1979; Wilson 1987; Kuklinski et al. 2006; Grzelak and Kuklinski
458 2010). As suggested before, assemblages on small stones are likely in a state of constant transformation and are
459 composed of opportunistic species with very short life cycles (Kuklinski et al. 2006; Kuklinski 2009).
460   Bryozoans in Svalbard waters show no indication of being substrate-specific (Kuklinski and Barnes 2005).
461 Contrary to this, some bryozoan species in this study were only found on a single substrate type (Online Resource
462 3). Realizing that we had a smaller number of samples, a limited depth range of sampling, and a single sampling
463 site, we do not suggest such species are substrate-specific, but instead designate them as 'substrate-confined'. The
464 proportion of such substrate-confined species was higher for stones compared to *Saccharina latissima* and, they
465 resided on perennial regions of kelp thallus and not on blades. Absence of substrate-confined species on blades
466 probably resulted from the ephemeral and unstable nature of the substrate, which prevents the majority of sessile
467 animals from finishing their life-cycles.
468   Although the percentage of empty substrate was rather low during the survey (see Table 1), we never
469 registered examples of spatial competition (overgrowth), even on stones. This suggests that epifaunal communities
470 on all substrates were in early stages of colonization.
471   Among animals, we can distinguish two groups of dominant and leading species: the first was specific for
472 blades+stipes and the second for stones, while the list of leading species on holdfasts was a mixture of both groups
473 (see Table 1, Online Resources 4 and 5). Since the same trend was also found for species composition, we suggest
474 that assemblage of epibionts on holdfasts is highly influenced by that on stones.
475   Some dominant species are consistent with those previously mentioned for Svalbard waters. Thus,
476 *Celeporella hyalina* was reported to dominate macroalgae (Lippert et al. 2001; Kuklinski and Barnes 2005) and in
477 the present study this species dominated on stipes of *S. latissima* and was a subdominant on blades and holdfasts,
478 and on understory kelp. The bryozoan assemblages on shallow subtidal stones in Arctic waters were dominated by
479 *Harmeria scutulata* (e.g., Barnes and Kuklinski 2003; Kuklinski and Barnes 2005; Kuklinski et al. 2006; Kuklinski
480 2009). During our survey, *H. scutulata* was dominant or subdominant species on SL-stones, and only once took a
481 subdominant position on Gr-stones. The other leading species on stones (*Cribrilina annulata*, *Tegella arctica*,
482 *Electra arctica*) have also been shown to be abundant in some studies, but contrary to our data, their density was
483 reported to be at least an order of magnitude lower compared to that of *H. scutulata* (e.g., Barnes and Kuklinski
484 2003; Kuklinski and Barnes 2005; Kuklinski et al. 2006; Kuklinski 2009).
485   In the present study, SR and abundance demonstrated a clear tendency to increase in accordance with
486 substrate longevity, from ephemeral (blades) through short-lived (holdfasts and understory macroalgae) towards
487 stable (stones) substrate. Short-lived substrates are quite specific: they are perennial and grow during their life-span,
488 increasing their surface area which provides empty space for recruits. On the other hand, different parts of the
489 *S. latissima* thallus vary in rigidity; morphology (shape); and, as a consequence, local water flow velocity and
490 regime; and also exometabolite composition (some of them may attract recruits and some may prevent them from
491 settlement). All these points may affect the attractiveness of different parts of kelp thallus and result in higher
492 diversity and abundance of biota associated with the holdfast.
493
494 **Seasonal dynamics and recruitment**
495   During the survey, we found the highest values of SR of sessile zoobenthos in both Januaries but we
496 registered very low values of epifloral SR in January, 2014 and the highest in January, 2015. Unfortunately there are
497 scarce data on seasonal changes of sessile biota associated with kelp and mainly they concern temperate waters.
498 Contrary to our findings, Withers et al. (1975) mentioned richer epifauna in summer comparing to winter, and
499 Christie et al. (2003) specified that SR was not affected by seasonal changes but abundance of epifauna was

500 significantly related to season. Carlsen et al. (2007) reported that total SR of epifauna on blades of *Saccharina*
501 *latissima* and *Laminaria digitata* was significantly higher in May than in late August (considering only sessile
502 species from their list, 15 and 6 taxa, respectively). We sampled in May and late September and found an opposite
503 pattern (Fig. 3). There are several possible explanations for these dissimilarities: (*i*) interannual variability; (*ii*)
504 spatial heterogeneity; (*iii*) the difference of one month between autumn sampling dates (we sampled a month later)
505 resulting in colonization of blades by newly settled recruits which probably had not yet appeared in August.
506   SR of epifauna in the present study demonstrated seasonal trends that were similar for SL- and Gr-stones and
507 holdfasts: it was higher in both Januarys and lower in May and both Septembers with comparable values of the same
508 seasons in subsequent years (see Fig. 3). Collation of species lists for these substrates reveals that the highest values
509 of SR in Januarys were due the presence of rare species (Online Resource 3), which most likely results from their
510 settlement between September and January. The decrease of SR in May and September may be caused by the effect
511 of abiotic factors (e.g., abrupt drop of salinity and increase of sedimentation rate in summer are quite typical in
512 glacial bays, and runoff from the Red River in autumn flows directly over the kelp bed we studied), juvenile
513 mortality and/or predation impact.
514   Seasonal fluctuations in total biomass of fouling assemblages were connected with different relative
515 importance of macroalgae and zoobenthic organisms' abundance in different seasons. The fouling community in
516 May and September, 2014 was dominated in biomass by understory macroalgae due their intensive growth during
517 spring and summer. Low values of macroalgal biomass recorded in September, 2013 are probably explained by
518 interannual variability and spatial heterogeneity of a small scale. The same factors seem to be more probable to
519 affect also the biomass ratio of macroalgae and animals in corresponding seasons (Septembers and Januarys). Low
520 frequency of occurrence of all species of understory macroalgae in the samples and short period of our observations
521 prevent us from any further speculation.
522   Seasonal variability in the abundance of juvenile forms on holdfasts and stones registered in the present study
523 (see Fig. 6) likely reflects spatial patterns in adult populations, seasonal recruitment, and/or differential juvenile
524 mortality. Unfortunately, data on life cycles or life history of many benthic species from the Arctic are limited, but
525 life-history strategies of dominant taxa in this study varied considerably. Settlement peaks of some taxa in mid-
526 winter, and lack of distinct seasonality in other taxa, highlight the little-recognized complexity of larval strategies
527 for Arctic benthos, where larval appearance is often presumed to be associated with the spring phytoplankton bloom.
528   We found distinct seasonality in occurrence of some juvenile stages that likely reflects seasonality in the
529 reproduction of such species. Similarly, those species with juveniles found in both in September and January likely
530 have either a long recruitment period with very slow growth, or stoppage of growth when food supply is low. The
531 presence of juveniles of some taxa in all seasons at least on one type of perennial substrates indicates year-round
532 reproduction in such species, which was also confirmed by presence of larvae in the ovicells of some bryozoans
533 (e.g., *Callopora craticula*, *Cribrilina annulata*, *Celeporella hyalina*) during every sampling period. These species
534 are known to be opportunists with fast growth. Absence of juveniles of these species on blades in May (see Fig. 7)
535 despite their presence on perennial substrates at the same time let us suggest a year-round reproduction of these
536 species and, at the same time it is very likely that their larvae avoid blades during spring presumably due a specific
537 exometabolites composition and biofilm on them. Many authors pointed the differences of epifaunal assemblages
538 associated with different species of macroalgae (e.g., Seed and O'Connor, 1981; Blight, Thompson, 2008; Parker et
539 al., 2001; Christie et al., 2009; Grzelak and Kuklinski, 2010). For example, even for kelp species with similar thallus
540 structure difference in SR of epibionts was reported; this was explained by higher production of antifouling
541 chemicals by *Laminaria ochroleuca* compared to *L. digitata* (Bligth, Thompson, 2008). Later, Hellio et al. (2000,
542 2002) found that exudates of *L. ochroleuca* had higher levels of antimicrobial activity comparing to *L. digitata*,
543 particularly against microalgae and marine fungi which together with bacteria are significant contributors to biofilm
544 formation and thus affect the subsequent attachment of other epibiont organisms.
545   Only a few of the animals recorded in our study (bryozoan *Electra arctica*, cirripedian *Balanus balanus*) have
546 planktotrophic larvae which spend quite long periods in the water column (pelagic larvae), while the rest of sessile
547 epifauna – spirorbid polychaetes, ascidians, sponges, hydrozoans and the rest of bryozoans – have lecithotrophic
548 larvae. Spirorbid larvae are regarded as pelagic in spite of their very short swimming period (e.g., from 15 minutes
549 up to few hours reported for *Spirorbis spirorbis* – Knight-Jones 1951, 1953; see also an extensive review in
550 Kupriyanova et al. 2001). However, it was shown that presence of a favourable substrate reduced the duration of
551 pelagic phase, for example, up to 91% of released larvae of *Spirorbis rupestris* metamorphosed even without
552 becoming pelagic (Gee 1963). Swimming period of both sponge and solitary ascidian larvae varies in different
553 species within 2-24 hours (e.g., Berrill 1930; Svane and Young 1989; Ereskovsky, 2010), and although they are
554 assumed to be pelagic, they have not been registered in meroplankton samples in Kongsfjorden (e.g., Piwosz, 2009;
555 Walkusz et al. 2009; Kuklinski et al. 2013; Grenvald et al. 2016; Stübner et al. 2016). In the few studies concerning
556 behaviour of hydrozoan planulae, it was demonstrated that they have short swimming or crawling period (usually
557 10-12 hours but up to 2-3 days – Williams 1965; Sommer 1992; Orlov 1996, 1997; Migotto 1998) and only very
558 rarely can they be transported by ambient currents (see Migotto 1998). Bryozoan lecithotrophic larvae also have a
559 short swimming period which they spend within the bottom water layer (for different bryozoan species, from several
560 hours up to 3-4 days – Shunatova, unpublished data; see also Ryland 1974, 1976; Reed 1991). Pearse (1969) and
561 Mileikovsky (1971) termed such larval type as demersal and both of them suggested that it may be more common
562 for benthic invertebrates than previously thought (see also Gerrodette 1981).

Based on these data, it is likely that the distance traveled by demersal larvae does not exceed a few meters (and usually is less than one), so that they are more or less restricted to the area where maternal colony (or individual) is located. This perspective can help to explain (*i*) the higher similarity of SR, species composition, and abundance of sessile epifauna associated with SL-stones and holdfasts, and (*ii*) the lower SR and abundance on blades and stipes. This is consistent with observations of Christie et al. (2003) who found that epifauna on the stipe of *Laminaria hyperborea* was richer in regions closer to the holdfast. Meyer et al. (2017), also noted very high spatial heterogeneity of settlement on panels deployed for different periods in a 12-month period in several Svalbard fjords, which they interpreted to reflect short larval periods and, thus, close relationships between settlers and nearby adult residents. Thus, larval characteristics are likely of the primary importance for colonization patterns of fouling assemblages. The presence of demersal larvae in most registered species and close spatial arrangement of holdfasts and SL-stones, as well as blades and stones of the barren ground, result in similar patterns in species composition and abundance for each pair of substrates.

Conclusions

This study demonstrated that SR, diversity, and abundance were higher on holdfasts than on blades or stipes of kelp in a Svalbard fjord. Substrate type, reflecting longevity, surface characteristics, and likelihood of disturbance, among other factors, more strongly influenced distribution of fouling biota than seasonality or depth. This hierarchy of factors was found for SR, diversity, and abundance indices of the whole assemblage, as well as for dominant and leading species. Among numerous differences between discussed, substrate types their longevity had quite prominent effects on species composition. Additionally, presence of demersal larvae in most fouling species and close spatial arrangement of holdfasts and SL-stones as well as blades and stones of the barren ground result in similar patterns in species composition and abundance for each pair of mentioned substrates. Based on the data reported for motile epifauna and our qualitative observations, we suggest that SR and diversity of sessile biota associated with overstory kelp is also highly influenced by species composition and abundance of understory macroalgae. But this point deserves to be a subject of a separate study.

Conflict of interest

The authors declare that they have no conflict of interest.

Ethical approval

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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Figure captions

813
814   **Fig. 1** Portion of "0+" year-zone of the blades of *Saccharina latissima* (percentage of total surface area of blade)
815   *Error bars* show standard error.
816
817   **Fig. 2** Average and total species richness on different substrate types (all seasons together)
818   *Error bars* show standard error.
819
820   **Fig. 3** Seasonal dynamic of species richness in zoo- and phytobenthos at 2 m depth
821
822   **Fig. 4** Seasonal dynamic of total biomass of macrobenthic organisms at 2 m depth
823
824   **Fig. 5** Biplot of substrates distribution in Principal Component Analysis (based on four-root transformed data on
825   density of macrozoobenthos at 2 m depth)
826   Dotted lines correspond to loading vectors of species that significantly contributed to the first and second
827   components.
828
829   **Fig. 6** Seasonal dynamic of total biomass of dominant and leading species (left column – animals, right column –
830   algae) at 2 m depth
831
832   **Fig. 7** Distribution of adults and juveniles of leading species on blades of *Saccharina latissima*
833   "0+" and "1+" year-zones of the blades of *Saccharina latissima* are marked as "0+" and "1+", correspondingly.
834   *Error bars* show standard error.