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Macrofauna associated with macroalgae in the Kongsfjord (Spitsbergen)

Abstract Macrofauna associated with six abundant macroalgal species was investigated in Kongsfjord, Spitsbergen, in order to qualitatively and quantitatively describe macroalgal epifauna composition. A total of 104 invertebrate species were identified, with bryozoans and amphipods representing the most abundant taxa. Analysis of similarity of epifaunal composition showed differences between algal species, and four groups could be distinguished: a *Laminaria-Alaria* group, a *Ptilota-Phycodrys* group, *Desmarestia aculeata* and *Acrosiphonia* aff. *flagellata*. Abiotic factors such as temperature and salinity were found to play a minor role in structuring epifaunal communities, while wave action and ice abrasion at least partially determine the epifauna on plants growing in the upper sublittoral. Major factors influencing composition of associated epifauna are the overall growth form and the three-dimensional thallus structure of macroalgae. None of the epifaunal species showed high host specificity. Patterns of dominating animal taxa and distribution among algal groups in Kongsfjord are similar compared to other biogeographic regions, although epifauna associated with Arctic macroalgae seems to be less rich in species.

Introduction

The Arctic Ocean is essentially characterised by low, but relatively constant, water temperatures, long periods of ice cover, as well as strong seasonality in light regime and primary production and, hence, generally only low

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biological activity (Hempel 1985; Kendall and Aschan 1993). Arctic benthic communities are assumed to have a lower biodiversity compared to other marine systems, especially tropical regions, and also the Antarctic (Arntz et al. 1997; Starmans et al. 1999) although, locally, communities can be rich in biomass and diversity (Brandt 1997). This low biodiversity is thought to be mainly due to the evolutionary history of the Arctic Ocean and the often uniform habitats dominated by soft bottoms, which provide little structure and variety to benthic organisms. Most studies on the Arctic benthos are comparative investigations of soft-bottom communities (e.g. Piepenburg et al. 1996; Holte and Gulliksen 1998; Wlodarska-Kowalczuk et al. 1998). Among these, faunal assemblages at inner-fjord locations were found to be particularly poor because of high glacial sedimentation impact (Elverhøi et al. 1983; Piepenburg et al. 1996; Wlodarska-Kowalczuk et al. 1998). Shallow Arctic coastal regions, however, can be very diverse in structure. Beside soft bottoms, hard substrates occur in steeply declining slopes or wide flat areas. Rocky shores down to about 25 m can be populated by a rich community of macroalgae (Svendsen 1959; Weslawski et al. 1997). Macroalgae add a major structural component to shallow-water ecosystems, and they may also serve as specific habitats for invertebrates (Hayward 1980; Seed and O'Connor 1981). From other geographic regions, it is known that epifaunal communities on macroalgae show higher numbers of individuals compared to infaunal communities of soft bottoms (Hagerman 1966) or terrestrial soils (Colman 1939). Macroalgae may offer different resources to inhabiting fauna, e.g. substrate for sessile animals (Hayward 1980), shelter from predation (Duffy and Hay 1991; Schneider and Mann 1991a, b; Martin-Smith 1993; Gosselin and Chia 1995), protection against wave action, currents and desiccation (Wieser 1952; Seed and Harris 1980) or directly as a food source (e.g. Dayton 1985; Iken et al. 1997; Iken 1999).

Only a few studies so far have mentioned macroalgal epifauna at Arctic coasts (Thorson 1933; Ockelmann 1958; Gulliksen 1974; Rózycki and Gruszczynski 1986;

Weslawski et al. 1997), and even less is known on species richness and diversity of epifaunal communities inhabiting macroalgae (Curtis 1975). Therefore, the first aim of our study was to describe qualitatively and quantitatively the epifauna associated with abundant macroalgae in an Arctic fjord.

The attractiveness of the various macroalgal species for the inhabiting fauna differs considerably, and epifaunal species can also have different requirements on their host algae. For example, invertebrates may not discriminate, and settle on any available substrate or they may select specific substrates for settlement, e.g. individual algal species (Seed and Boaden 1977). The second aim of our study, therefore, was to investigate the epifauna associated with specific macroalgal species and to determine differences and similarities among these epifaunal communities. We also wanted to evaluate the abiotic and biotic factors that influence distribution, composition and preference of epifaunal organisms on specific algal species.

Materials and methods

Study site

The study was carried out in Kongsfjord at the northwestern part of Spitsbergen (79°N, 12°E) in summer 1997 (June – July) (Fig. 1). The fjord is 26 km long, has a width between 3 and 8 km, and its maximum depth reaches 400 m. The shores consist of a steep rocky bottom, as well as weakly declining slopes with, mostly, soft glacier sediments. The tidal range is about 2 m with weak currents (Ito and Kudoh 1997). Four glaciers and a number of glacier run-offs add terrestrial sediments (Elverhøi et al. 1983) and freshwater to the fjord, which may locally reduce salinity from an average 34 psu down to 20 psu. The annual mean water temperature is slightly above 0°C (Ito and Kudoh 1997); however, in summer we measured maximum temperatures of about 6°C at the surface and 3.6°C at 20 m depth (for details see Hanelt et al. 2001).

The sampling site (Hansneset) is located at the western side of the island, Blomstrand, in the central part of Kongsfjord (Fig. 1), and has steeply declining rocky shores. The impact of ice at Hansneset is relatively low for macroalgae because there is often no sea-ice formation in winter or the ice cover breaks up early in the year due to winds and currents, which in turn prevent ice from accumulating at this exposed location. Hansneset is densely populated by a relatively rich macroalgal community, with 27 different species reported (Vögele, unpublished data).

Sampling

Six abundant macroalgal species typical for the location, namely the brown algae *Laminaria digitata*, *Alaria esculenta*, *Desmarestia aculeata*, the green alga *Acrosiphonia* aff. *flagellata* and the red algae *Phycodrys rubens* and *Ptilota gunneri* (characteristics of species summarised in Table 1), were collected from their natural habitat by scuba diving. Individual algae were carefully enclosed in hand nets (mesh size 1 mm) together with the associated epifauna. Between two and four individual plants of each species were sampled for the investigation of the associated macrofauna. In the laboratory, mobile fauna was separated from individual algae, counted and fixed in 5% formaldehyde-seawater solution for later identification. Sessile epifauna was counted directly on the algae, and colonial species were regarded as individuals. Most sessile species were identified immediately unless they had to be preserved for later taxonomic identification. For determination of fresh weight (FW), algae were blotted to remove extracellular water and weighed. The number of species and individuals of epifauna were then calculated per 100 g algal FW.

Statistical treatment

Data on epifaunal composition, i.e. individuals and species of epifauna per 100 g FW algae, were transformed by double square root prior to analysis of similarity, which was assisted by the computer program PRIMER 4.0 (Clarke and Warwick 1994). The Bray-Curtis Index (Bray and Curtis 1957) was used for a pairwise comparison of all samples to analyse the similarity of epifaunal composition associated with individual macroalgae. The results of the similarity analysis were plotted by multidimensional scaling. Due to the difficult taxonomy of Nemertini, Nematoda and species of the bryozoan genus *Lichenopora*, these taxa were treated as groups in the similarity analysis.

Results

A total of 104 species of epifauna belonging to 11 higher taxonomic groups were identified on the 6 investigated

Fig. 1 General view of Spitsbergen, showing Kongsfjord and the study site Hansneset (indicated by *star*)
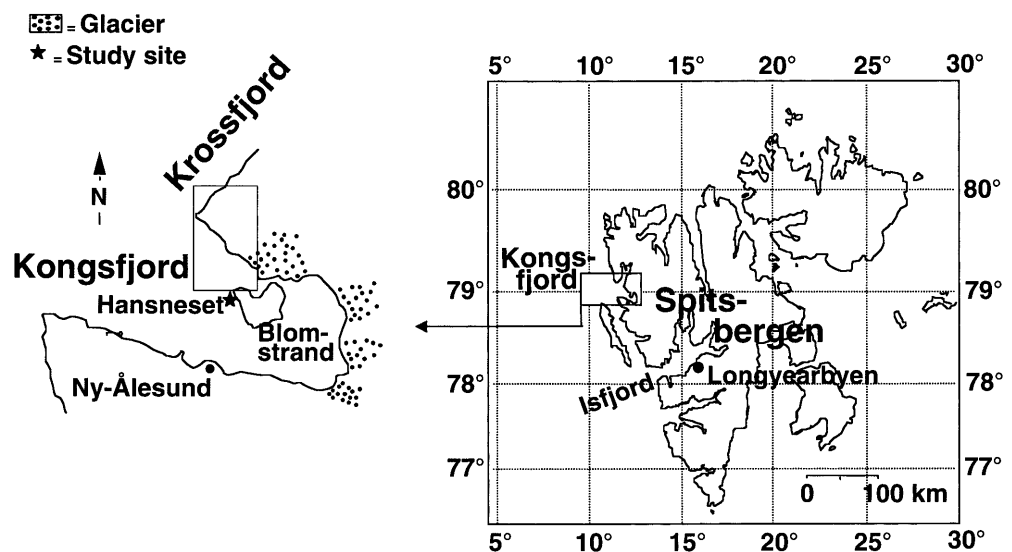
Table 1 Investigated macroalgal species, life form type, thallus morphology (cf. Fig. 2), thallus size, zonation and depth of sampling

Species	Geographic distribution	Life form type	Thallus morphology	Maximum thallus length (m)	Depth of distribution (m)	Depth of sampling (m)
Chlorophyta						
Acrosiphonia aff. *flagellata* Kjellman	Boreal-arctic	Pseudoperennial	Branched uniserate filaments	0.1	0–5	4
Phaeophyta						
Laminaria digitata (Hudson) Lamouroux	Boreal-arctic	Perennial	Leathery large surface area	2	2–12	4–7
Alaria esculenta (L.) Greville	Boreal-arctic	Perennial	Membranous with solid midribs, large surface area	3	2–13	11–12
Desmarestia aculeata (L.) Lamouroux	Boreal-arctic	Perennial	Terete, highly branched	1.3	12–18	14–17
Rhodophyta						
Phycodrys rubens (L.) Batters	Boreal-arctic	Pseudoperennial	Foliose with midrib and side veins	0.2	10–22	15–19
Ptilota gunneri (L.) Agardh	Boreal-arctic	Perennial	Finely branched, compressed	0.3	6–22	10–12

macroalgal species. Table 2 lists all species and their occurrence on the specific algae. Not all animals could be identified to species level, and hence the actual number of species given here is underestimated. Of the 11 taxonomic groups, the Bryozoa and Crustacea dominated quantitatively with 34 and 25 species, respectively. Most of the Crustacea were Amphipoda (16 spp.) and Decapoda (6 spp.). Other taxa with numerous species were Mollusca (16 spp. divided into 8 Gastropoda, 6 Bivalvia, 2 Polyplacophora) and Polychaeta (13 spp.). Beside macrofaunal organisms, Nemathelminthes (Nematoda), classically regarded as meiofauna, were found in some algal samples and were included in the analysis.

Faunal species composition on different algal taxa

Figure 2 gives an overview of the number and density of epifaunal species for the investigated algal species, as well as the dominant animal species with its relative abundance. The highest number of epifaunal species (51 spp.) was found on *Alaria esculenta*; however, their density was relatively low (204 ind. 100 g^{-1} FW) on this alga. In contrast, *Ptilota gunneri* harboured a similarly high number of animal species (48 spp.), but exhibited the highest total number of individuals of all studied algal species (16,277 ind. 100 g^{-1} FW). On *Acrosiphonia* aff. *flagellata*, the number of associated species was lowest (10 spp.), while lowest number of individuals was observed on *L. digitata* (32 ind. 100 g^{-1} FW). The epifauna of *D. aculeata* and *Acrosiphonia* aff. *flagellata* was dominated by the amphipod *Ischyrocerus anguipes* whereas dominant species on all other algal species were

Algal species	Number of epifauna species	Individuals 100g^{-1} FW	Dominant species and maximum dominance
A. aff. *flagellata*	10	746	*Ischyrocerus anguipes* 92,1 %
L. digitata	32	32	*Celleporella hyalina* 37,4 %
A. esculenta	51	204	*Celleporella hyalina* 53,8 %
D. aculeata	36	790	*Ischyrocerus anguipes* 32,1 %
Ph. rubens	23	7583	*Spirorbis* cff. *spiryllum* 44,8 %
Pt. gunneri	48	16277	*Hippothoa divaricata* 33,3 %

Fig. 2 Algal species, number and density of epifaunal species, dominant species and their degree of dominance

Table 2 Taxonomic groups and epifaunal species associated with the different macroalgal species (*Acr Acrosiphonia* aff. *flagellata, Lam Laminaria digitata, Ala Alaria esculenta, Des Desmarestia aculeata, Pti Ptilota gunneri, Phy Phycodrys rubens, X* present, *O* not present)

Epifauna				Algal species					
				Acr	Lam	Ala	Des	Pti	Phy
Porifera			*Haliclona* sp.	O	O	O	O	X	X
			Sycon sp.	O	O	O	O	X	O
			aff *Tethya.*	O	O	X	O	O	O
			Porifera sp.	O	O	X	O	O	O
Cnidaria		Hydrozoa	*Campanularia integra* Mac Gillivray, 1842	O	X	X	O	X	X
			Campanularia volubilis (Linnaeus, 1758)	O	O	O	O	X	O
			Campanularia syringa (Linnaeus, 1767)	O	X	X	O	X	O
			Halecium curvicaule	O	X	O	O	O	O
			Lafoea fruticosa Sars, 1851	O	O	O	O	X	O
			Sertularella rugosa (Linnaeus, 1758)	O	X	O	O	O	O
			Hydrozoa sp.	O	X	O	O	X	O
Tentaculata		Bryozoa Cyclostomata	*Crisiella diversa*	O	X	O	O	X	O
			Cyclostomata sp.	O	O	O	O	X	O
			Lichenopora spp. (mixed group: *Lichenopora verrucaria* (Fabricius, 1780), *Lichenopora crassiuscula, Lichenopora* sp. Defrance, 1823, *Lichenopora* juv.)	O	X	X	X	X	X
			Onousoecia diastoporides (Norman, 1869)	O	O	O	O	O	X
			Tubulipora flabellaris (Fabricius, 1780)	O	O	O	O	X	X
		Ctenostomata Cheilostomata	*Alcyonidium mytily* Dalyell, 1848	O	O	X	O	O	O
			Callopora aurita (Hincks, 1877)	O	O	X	O	O	O
			Callopora craticula (Alder, 1856)	O	O	X	O	O	X
			Callopora smitti Kluge, 1946	O	X	X	O	O	O
			Callopora sp. Gray, 1848	O	O	O	O	X	O
			Cauloramphus intermedius	O	O	X	O	X	O
			Celleporella hyalina (Linnaeus, 1776)	O	X	X	X	X	X
			Cribrilina annulata (Fabricius, 1780)	O	X	X	O	O	O
			Cribrillina spitzbergensis Norman, 1903	O	X	O	O	O	O
			Cylindroporella tubulosa (Norman, 1868)	O	O	X	X	O	X
			Dendrobeania fruticosa (Packard, 1863)	O	O	X	X	O	O
			Dendrobeania murroyana (Johnston, 1847)	O	X	O	O	X	O
			Doryporella spatulifera (Smitt, 1868)	O	O	O	X	O	O
			Eucratea loricata (Linnaeus, 1758)	X	X	X	X	X	O
			Harmeria scutulata (Busk, 1855)	O	X	O	O	X	O
			Hippothoa divaricata var. *arctica* Kluge, 1906	O	O	O	O	X	X
			Rhamphostomella bilaminata (Hincks, 1877)	O	O	X	O	O	O
			Schizomavella auriculata var. *lineata* (Hassall, 1842)	O	O	O	X	X	O
			Scrupocellaria arctica (Busk, 1855)	O	O	X	O	O	O
			Scrupocellaria scabra (Van Beneden, 1848)	O	O	O	O	X	O
			Scrupocellaria sp. Van Beneden, 1845	O	O	O	X	O	O
			Tegella arctica (D'Orbigni, 1850–1852)	O	O	X	O	O	O
			Tegella armifera (Hincks, 1880)	O	O	X	O	O	O
			Tegella nigrans (Hincks, 1882)	O	O	X	O	O	O
			Tricellaria ternata (Ellis & Solander, 1786)	O	X	X	X	X	X
			Bryozoa spp.	O	O	X	O	X	O
Nemertini		Nemertini spp.		O	X	X	O	O	O
Nemathelminthes	Nematoda	Nematoda spp.							
Mollusca	Polyplacophora		*Tonicella marmorea* (Fabricius, 1780)	O	O	O	O	O	X
			Tonicella rubra (Linnaeus, 1767)	O	X	X	O	O	O
	Gastropoda		*Lepeta caeca* (Muller, 1776)	O	O	O	X	O	O
			Margarites groenlandicus (Gmelin, 1791)	O	X	X	X	X	O
			Margarites helicinus (Fabricius, 1780)	X	X	X	X	X	X
			Onoba mighelsi (Stimpson, 1851)	O	O	O	X	X	O
			Punctulum sp.	O	O	O	X	O	O
			Puncturella noachina (Linnaeus, 1771)	O	O	X	O	O	O
			Volutopsis aff. *norvegicus* (Gmelin, 1791)	X	O	O	O	O	O
			Gastropoda spp.	O	O	X	O	O	O
	Bivalvia		*Chlamys* sp. juv.	O	O	O	O	O	X
			Musculus corrugatus (Stimpson, 1851)	O	O	O	X	O	O
			Musculus laevigatus (Gray, 1824)	O	X	X	O	O	O
			Musculus sp. juv.	X	O	X	O	X	O
			Saxicava arctica (Linnaeus, 1767)	O	X	X	X	X	X
			Bivalvia sp.	O	X	O	O	X	O

Table 2 (Contd.)

Epifauna				Algal species					
				Acr	Lam	Ala	Des	Pti	Phy
Annelida	Polychaeta Errantia								
		Phyllodocida	Autolytinae sp. juv.	O	O	X	O	X	O
			Harmothoe imbricata Linnaeus, 1767	O	X	X	X	X	X
			Nereis zonata Malmgren, 1867	O	O	X	O	O	O
			Nereis pelagica Linnaeus, 1758	O	O	X	O	O	O
			Nereis sp. juv.	X	O	O	O	O	O
			Nereis sp.						
		Sedentaria							
		Orbiniida	*Naineris quadricuspida* (Fabricius, 1780)	O	O	X	O	O	O
		Capitellida	*Nicomache trispinata* Arwidsson,1906	O	O	X	O	O	O
		Terebellida	Ampharetidae sp. juv.	O	O	O	X	X	O
		Sabellida	*Chitinopoma serrula* (Stimpson, 1854)	O	O	O	O	X	O
			Chone infundibuliformis juv. Kroyer, 1856	O	X	X	O	O	O
			Spirorbis aff. *spiryllum* Linnaeus, 1758	O	X	X	X	X	X
		Polychaeta spp.		O	O	O	O	X	X
Arthropoda	Chelicerata	Pantopoda	Pantopoda sp.	O	X	O	O	X	O
	Crustacea	Cirripedia	*Balanus crenatus* (Bruguiere, 1789)	O	O	X	O	O	O
		Malacostraca Peracarida							
		Mysidacea	*Mysis oculata* (Fabricius, 1780)	O	O	O	X	O	O
		Amphipoda							
		Gammaridae	*Apherusa jurinei* (Milne-Edwards, 1830)	O	O	O	X	O	O
			Apherusa sp.	O	O	X	X	X	O
			Gamarellus homari (Fabricius, 1779)	O	O	X	X	O	O
			Gitanopsis inermis (Sars, 1882)	O	O	O	X	O	O
			Halirages fulvocinctus (Sars, 1858)	O	O	O	X	O	O
			Ischyrocerus anguipes (Kroyer, 1838)	X	X	X	X	X	X
			Parapleustes aff. *assimilis* Sars, 1882	O	O	O	O	X	O
			Parapleustes bicuspis (Kroyer, 1836)	O	O	X	X	O	X
			Pleusymtes glaber (Boeck, 1861)	O	O	O	X	X	X
			Pleustidae sp. juv.	O	O	X	O	O	X
			Pleustidae sp.	O	X	O	X	O	O
			Weyprechtia pinguis (Kroyer, 1838)	X	O	O	X	X	O
			Amphipoda sp. juv.	O	O	X	X	O	O
			Amphipoda sp.	X	O	X	O	O	X
		Caprellidae	*Caprella septentrionalis* Kroyer, 1838	O	O	X	X	X	O
			Caprella sp. juv.	X	O	O	X	X	O
		Isopoda	*Munna spitzbergensis*	O	X	O	O	X	O
		Eucarida Decapoda							
		Natantia	*Eualus gaimardii* (Milne Edwards, 1837)	O	O	X	O	O	O
			Hippolytidae sp. juv.	O	O	O	O	X	O
			Sabinea septemcarinata (Sabine, 1821)	O	O	O	X	O	O
			Spirontocaris turgida (Kroyer, 1842)	O	O	X	X	X	O
			Shrimp sp.	O	O	O	X	O	O
		Reptantia							
		Brachyura	*Hyas araneus* (Linnaeus, 1766)	O	O	O	O	X	O
Echinodermata		Ophiuroidea	*Ophiopholis aculeata* (Linnaeus, 1767)	O	O	X	O	O	O
Chordata		Ascidiacea	*Synoicum turgens* (Phipps, 1774)	O	X	O	O	X	O
			Ascidiacea sp.	O	X	O	O	X	O

sessile Bryozoa and Polychaeta. In general, the most common taxa found were Bryozoa, Crustacea, Mollusca, Polychaeta and Hydrozoa. The relative share of these taxa on total taxa number, however, varied greatly among the macroalgal species investigated.

Analysis of similarity

The results of the analysis of similarity are plotted by multidimensional scaling (Fig. 3). Epifaunal composition showed highest similarity within replicate samples of individual algal species (shaded circles in Fig. 3) even when they were sampled in different depths. Furthermore, the brown algae *L. digitata* and *Alaria esculenta*, and the red algae *Ptilota gunneri* and *Phycodrys rubens*, respectively, had similar epifaunal communities. Epifauna on *D. aculeata* is located, in similarity, between the *Laminaria-Alaria* group and the *Ptilota-Phycodrys* group. The epifauna associated with the green alga *Acrosiphonia* aff. *flagellata* showed low similarity to the epifauna of all other algal species investigated. Consequently, four different groups of algal epifauna were distinguished by the analysis of similarity: the *Laminaria-Alaria* group, the *Ptilota-Phycodrys* group, *D. aculeata* and *Acrosiphonia* aff. *flagellata*.

Mobile and sessile epifauna

The macroalgal species *Alaria esculenta*, *L. digitata*, *Phycodrys rubens* and *Ptilota gunneri* were inhabited by more sessile species and individuals than mobile epifauna organisms (Fig. 4a, b). Although the similarity analysis did not show high similarity of invertebrates associated with *Acrosiphonia* aff. *flagellata* and *D. aculeata*, the epifauna of these two species had two things in common: the dominance of the amphipod *Ischyrocerus anguipes*, and a great abundance of mobile animals.
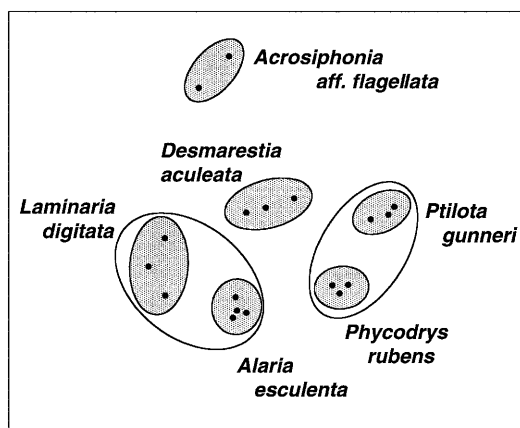

Fig. 3 Multidimensional scaling of epifauna composition on the various algal species studied (● = one sample)
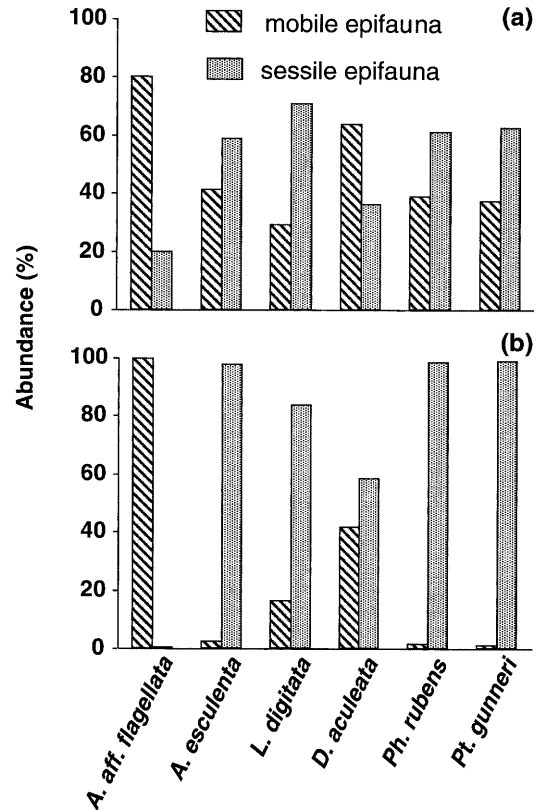

Fig. 4 Abundance of mobile and sessile epifauna on the various algal species studied: **a** species; **b** individuals

Discussion

Methods

For quantitative comparison of epifaunal density associated with different algal species, we used fresh weight as reference parameter. Considering sessile organisms, however, available surface and not weight of an alga is probably of primary importance for settlement. For example, 100 g FW of the thin leaf-like blades of *Phycodrys rubens* provides more colonisable surface than 100 g FW of the leathery blade of *L. digitata*. Total surface of complete plants, however, is extremely difficult to determine, especially under limited field conditions, as in the present study. Therefore, weight as reference unit is more practicable, even though problems in comparative quantification have to be considered. Colman (1939) and Sloane et al. (1957) also used algal FW to measure the quantity of epifauna on different algal species and found only minor differences between the number of individuals per unit algal FW and the number of individuals per unit bottom surface or per unit algal surface, respectively. Additionally, we also performed an analysis of similarity, only considering qualitative species composition associated with algal species, and found results highly comparable to our quantitative analysis (H. Lippert, unpublished results). Therefore, we found algal FW to be

a useful reference parameter for comparison of epifaunal density among different algal species.

Factors influencing the distribution of epifauna on macroalgal species

Various abiotic and biotic factors can influence the attractiveness that an algal species has for invertebrates, and these factors may be very different for sessile and mobile fauna. Abiotic factors of special importance could be water motion due to currents or wave action (Sloane et al. 1957; Schultze et al. 1990), salinity, depth (Wieser 1952) or sediment load (Boaden et al. 1975; O'Connor et al. 1979; Edwards 1980). Important biotic factors are structural characteristics of algal species such as size, surface characteristics (e.g. roughness) or thallus structure (leaf-like vs branched). Also, the lifetime of a plant (Hayward 1980), growth rates (Seed and O'Connor 1981), as well as interactions between animals and algae (e.g. grazing, antifouling) and between animals (e.g. competition, predation, parasitism), can significantly influence the association of invertebrates with macroalgae (Hay and Steinberg 1992).

Influence of abiotic factors

The epifaunal communities inhabiting the six algal species investigated in Kongsfjord showed marked differences in composition, abundance and dominance of species and individuals. At first sight, a correlation between abiotic factors related to the depth in which algal species grow and their associated epifauna could be expected. Wieser (1952) found an increase in species number and density of individuals of algal-associated epifauna with increasing water depth from the eulittoral to the upper sublittoral in southern England, and hypothesised this as being due to the increasing stability of abiotic factors in deeper waters. Even though we found trends of low species numbers in shallow waters (*Acrosiphonia* aff. *flagellata*) and high individual numbers in deeper waters (*Phycodrys rubens* and *Ptilota gunneri*), our data do not support the observations of Wieser (1952). In summer 1997, temperature and salinity varied significantly between 0 and 12 m depth, while below 12 m conditions were stable (Hanelt et al., in press). There was no continuous gradient and therefore there does not seem to be a strong correlation between number of species, as well as number of individuals, and exposure to variable physical conditions.

Beside density of individuals and species number, composition of species shows that factors other than those related to water depth must have an important influence on the epifauna inhabiting different algal species. Epifaunas of *Alaria esculenta* and *L. digitata* sampled at different depths exhibited a higher similarity than epifaunas of *Alaria esculenta* and *Ptilota gunneri*

collected at the same depth (see Fig. 3). Although this shows that salinity and temperature fluctuations are unlikely to strongly determine epifaunal species composition, the impact of wave action and ice abrasion is especially high in very shallow waters and might be one reason for the low species number of epifauna on *L. digitata* and *Acrosiphonia* aff. *flagellata*. The dominance of mobile fauna on *Acrosiphonia* aff. *flagellata* especially might be due to these strong physical factors. Mobile animals are able to escape unfavourable conditions such as wave action and ice abrasion. However, below 4 m depth, wave action and abrasion by ice are unlikely to be major factors influencing epifaunal species composition, and individual numbers at the study site and also other abiotic factors such as temperature and salinity obviously play a minor role in structuring epifauna communities on different species of macroalgae.

Influence of thallus morphology

General models categorising thallus forms of macroalgae have been developed to explain and predict physiological characteristics and ecological interactions of macroalgae (Littler and Littler 1980; Steneck and Watling 1982). These functional-form models base on algal morphology and anatomy, and should allow, among others, prediction of plant-animal interactions. Considering their general thallus structure, the six macroalgal species investigated in this study could be distinguished into two major groups: leaf-like species comprising *L. digitata*, *Alaria esculenta* and *Phycodrys rubens*, and branched species comprising *Acrosiphonia* aff. *flagellata*, *D. aculeata* and *Ptilota gunneri*. A more detailed distinction of morphological characteristics, however, as suggested by Littler and Littler (1980) and Steneck and Watling (1982), would yield four groups: filamentous species (*Acrosiphonia* aff. *flagellata*), foliose to membranous species (*Phycodrys rubens*, *Alaria esculenta*), branched corticated species (*D. aculeata*, *Ptilota gunneri*) and leathery species (*L. digitata*). According to the functional-form model, groups of algal species should be similar in their associated epifauna. Our similarity analysis, however, shows distinct differences from these groupings based on functional-form models. The epifauna on the foliose-membranous species *Alaria esculenta* is more similar to that on the leathery species *L. digitata* than to other foliose-membranous species. The epifaunal composition on *Ptilota gunneri* also shows a higher similarity to the epifauna associated with *Phycodrys rubens* and not to species predicted by the functional-form model. Epifauna associated with *D. aculeata* is separated from other investigated algal species, which was not predicted by the model. Hence, the classification of macroalgae by growth form and morphology as suggested by Littler and Littler (1980) and Steneck and Watling (1982) in order to predict similarity of associated epifauna does not seem to be an appropriate

approach. A recent review on the applicability of these functional-form models to ecological questions drew the similar conclusions that model predictions often obscure individual interactions of species (Padilla and Allen 2000), e.g. in plant-animal interactions such as grazing by herbivores (Iken 1999). We suggest that this may also be the case with algal-associated epifauna. The overall growth form and three-dimensional thallus structure may well have an influence on the ability of macroalgae to provide a suitable habitat or substrate for invertebrates; however, animal species' specific requirements will have to be considered. The epifauna associated with the two brown algae, *L. digitata* and *Alaria esculenta*, was grouped in our analysis of similarity. Both algal species show similarities in thallus morphology (leafy phylloids) and size (1–2 m in height). Most striking in similarity of associated epifauna are the dominance of the bryozoan *Celleporella hyalina* and the high percentage of other sessile suspension feeders on both algal species. We suggest that the large colonisable surface area of these algal species is a major factor facilitating settlement and growth of sessile organisms. Total numbers of species and individuals, however, are lower on *L. digitata* compared to *Alaria esculenta*, suggesting that *L. digitata* may generally be a less preferred substrate for epifauna. However, the surface of *L. digitata* is much smoother than the surface of *Alaria esculenta*, and a preference of many sessile epifaunal species for crinkled or rough surfaces has been reported in different studies (Colman 1939; Fletcher and Day 1983; Crisp 1984). Moreover, chemical characteristics of algal surfaces, such as slimes or exuded deterrent metabolites, may determine their suitability as substrates for epifauna (e.g. Bakus et al. 1986; Steinberg 1992). A high similarity of epifauna associated with the two red algae *Phycodrys rubens* and *Ptilota gunneri* surprises since the general thallus form of these algal species is very different. Epifauna of both red algal species is dominated by sessile filter feeders, *Phycodrys rubens* by the polychaete *Spirorbis* aff. *spiryllum*, and *Ptilota gunneri* by the bryozoan *Hippothoa divaricata* (which occurred exclusively on the red algae). Since the branched phylloids of *Ptilota gunneri* do not seem to provide a homogenous, flat surface favourable for settlement and growth of colonial epifauna species, the dominance and high percentage of sessile epifauna on this red alga is surprising. Obviously, the very dense and mono-planar branching of *Ptilota gunneri* creates a sufficiently homogenous surface, suitable for colonisation. A major difference in epifauna composition of both red algal species is the twofold-higher number of species and individuals on *Ptilota gunneri*. This may be due to differences in life history of the two species. While *Ptilota gunneri* is perennial and survives winter as an intact plant, the foliose parts of the blades of the pseudo-perennial *Phycodrys rubens* degenerate in winter, leaving only midribs and rhizoids as remaining structures. Growth of new blades begins in spring. Consequently, parts of the sessile animals are lost together with the phylloids, and epifauna

has to re-colonise the new fronds of *Phycodrys rubens* every year. However, information on the time period necessary for colonisation of new substrates in Arctic waters is lacking.

The higher abundance of epifauna on the two red algal species compared to *L. digitata* and *Alaria esculenta* might be related to the higher degree of branching and smaller leaf area in the red algae. This may provide a higher degree of shelter from wave action and predation for the inhabiting fauna (Wieser 1952; Schneider and Mann 1991a, b). The large flattened thalli of leaf-like seaweeds such as *L. digitata* and *Alaria esculenta* offer almost no protection to their inhabitants (Wieser 1952).

D. aculeata and *Acrosiphonia* aff. *flagellata* have similar growth forms with erect branched thalli and a bushy appearance. Analysis of similarity of associated epifauna, however, showed these species to be very different. Although on both algal species percentage of mobile fauna is high and the amphipod *Ischyrocerus anguipes* dominates epifaunal composition, epifauna on *D. aculeata* is more diverse. It comprises both mobile and sessile species (e.g. *Caprella septentrionalis* (Amphipoda) and *S.* aff. *spiryllum* (Polychaeta)/*Celleporella hyalina* (Bryozoa), respectively) while *Acrosiphonia* aff. *flagellata* is almost exclusively inhabited by mobile fauna. This also results in distinct differences in dominant feeding types, with a mixture of feeding types occurring on *D. aculeata* (suspension feeders, detritivores, predators) while invertebrates on *Acrosiphonia* aff. *flagellata* are almost exclusively detritivores (H. Lippert, unpublished results). The branches of *D. aculeata* are mechanically more stable, which may favour settlement of sessile organisms while the uniseriate branched filaments of *Acrosiphonia* aff. *flagellata* give little support for attachment of sessile organisms. Moreover, *Acrosiphonia* aff. *flagellata* is a shallow-water species and is more exposed to wave action, which may hamper colonisation by sessile invertebrates (see above). Additionally, most of the thallus of *Acrosiphonia* aff. *flagellata* degenerates in winter, thereby significantly reducing the chances of survival for sessile species.

We suggest that thallus morphology of macroalgae is, in fact, a major factor influencing composition of associated epifauna. However, general functional-form model predictions as suggested by Littler and Littler (1980) and Steneck and Watling (1982) cannot fully explain epifauna distribution. Considerations of species-specific interactions and the ecology of invertebrate species are necessary to understand the interaction between algal thallus form and associated epifauna. Chemically mediated interactions between marine animals and plants, such as nutritional associations (de Burgh and Fankboner 1978), antifouling (Davis et al. 1989; Pawlik 1992) or antifeeding (Hay 1992; Paul 1992; Steinberg 1992), which have not been part of the present study, would also have to be considered as important factors controlling algal-epifauna relationships.

Epifaunal settlement preference

According to Seed and Boaden (1977) and Martin-Smith (1993), there are two extremes in the choice of a substrate: one is to settle randomly on any available substrate; the other is to settle exclusively on one specific substrate, such as on a particular algal species. In our study, none of the epifaunal species showed very high host specificity. Among sessile epifauna, the two bryozoans *H. divaricata* var. *arctica* and *Tubulipora flabellaris* were found exclusively on the red algae *Ptilota gunneri* and *Phycodrys rubens*. However, both bryozoans are reported to occur also on stones and mollusc shells in other geographic regions (Hayward and Ryland 1979, 1985). The bryozoan *Celleporella hyalina* was found on all investigated macroalgae except *Acrosiphonia* aff. *flagellata*. This invertebrate has a preference for areas sheltered from currents (Sloane et al. 1957). Among mobile invertebrates, the amphipod *Caprella septentrionalis* was very abundant, especially on the brown alga *D. aculeata*, which may offer especially good structures for attachment, as well as a high degree of camouflage. Branches of *D. aculeata* are similar in shape and colour to the body of the amphipod. Hagerman (1966) found *Caprella septentrionalis* on filamentous red algae that also resemble the animal in colour.

Comparison with other biogeographic regions

Composition of epifauna associated with macroalgae is determined by a variety of abiotic and biotic factors. These factors may be of different importance in different biogeographic regions. Only a few studies have investigated macroalgal-associated epifauna in the Arctic, and a comparison with other systems will be of interest although comparisons in some cases may be difficult due to different sampling methods.

In the Kongsfjord, the epifauna of the green alga *Acrosiphonia* aff. *flagellata* was characterised by a low number of species and a high percentage of mobile individuals, especially amphipods. Weslawski et al. (1997) described similar communities on sublittoral filamentous green algae such as *Acrosiphonia*, *Enteromorpha*, *Ulothrix* and *Urospora* from Bear Island, which were also dominated by amphipods. This is in agreement with the study of Seed and O'Connor (1981), who found green algae in Wales to be a suitable habitat for many mobile invertebrates, but only a few sessile species.

The most frequently investigated algal epifauna is that associated with Laminariales (Colman 1939; Sloane et al. 1957; Norton 1971; Edwards 1980; Fletcher and Day 1983; Rózycki and Gruszczynski 1986; Schultze et al. 1990). Rózycki and Gruszczynski (1986), as well as Gulliksen (1974), found bryozoans, polychaetes and amphipods to be the most species-rich taxa associated with members of the Laminariales around Spitsbergen and Jan Mayen. This taxon composition, as well as species numbers reported in those studies, are similar to our results. At Helgoland, epifauna of *L. digitata* and

L. saccharina was similarly dominated by polychaetes, amphipods and bryozoans (Schultze et al. 1990). However, species numbers were much higher there (125 species), as well as on *Saccorhiza polyschides* from Scotland (89 species; Norton 1971). This might indicate that algal-associated epifauna is less diverse in Arctic shallow waters than in comparable temperate habitats.

Investigations of the epifauna associated with *Desmarestia* spp. are rare. Richardson (1977) studied the epifauna of *D. anceps* at Signy Island and Iken (1996) of *D. anceps* and *D. menziesii* at King George Island, both Antarctica. However, these two studies did not consider sessile fauna. The most common mobile taxa found in these studies were molluscs and amphipods. Richardson (1977) described 84 associated macrofaunal species, which is high, compared to the number of species in Kongsfjord (23 mobile species on *D. aculeata*).

Seed and O'Connor (1981) reported red algae in Wales to be inhabited by small and specialised invertebrates and to be only densely colonised when brown algae were missing in the habitat. That would suggest that red algae are a less preferred substrate for epifauna. In Kongsfjord, however, highest epifaunal densities were found on red algae. Similar results are reported by Remane (1940, North Sea and Baltic Sea), Colman (1939, southern UK), and Iken (1996, Antarctic Peninsula), who described highest epifaunal abundance on red algae compared to other macroalgal groups.

Generally, epifauna associated with macroalgae in an Arctic fjord seem to be less rich in species compared to most other geographic regions. General patterns of dominating taxa and distribution among algal groups, however, seem to be similar in different systems.

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