HELGOLÄNDER MEERESUNTERSUCHUNGEN
Helgoländer Meeresunters. 44, 39–51 (1990)

The macrofauna and macroflora associated with *Laminaria digitata* and *L. hyperborea* at the island of Helgoland (German Bight, North Sea)

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ABSTRACT: This paper describes the macroflora and macrofauna associated with two bull kelp species, *Laminaria hyperborea* and *L. digitata*, at the island of Helgoland, North Sea. During a study period of seven months (March–September 1987), 29 macroflora species and 125 macrofauna species were found. The dominant taxonomic groups were Polychaeta (25 species), Bryozoa (17), Amphipoda (14), Hydrozoa (10) and Ascidiae (8). The species maximum was in July. In general, *L. hyperborea* was preferred as a substrate for settlement to *L. digitata*. Composition of the communities associated with kelp changed during the season according to exposure to wave action, and according to location on the kelp thallus. The rhizoid community of both kelps bore more species at exposed locations. Wave-exposed *L. digitata* lacked obvious faunal settlement on both phylloid and cauloid. Phylloid and cauloid of *L. hyperborea* were chosen as an attractive substrate at both sheltered and wave-exposed locations, showing an association of encrusting bryozoan and hydrozoan colonies.

INTRODUCTION

Laminariaceae frequently dominate rocky coasts in temperate waters. They are widely distributed around the island of Helgoland, and there provide a suitable habitat for a wide variety of flora and invertebrate fauna.

Studies of epifaunal communities associated with Laminariales have already been published (see Ebling et al., 1948; Sloane et al., 1957; Ghelardi, 1971; Wing & Clendenning, 1971; Moore, 1973; Norton, 1971; Seed & Harris, 1980).

Most of them compare marine hard-bottom communities and those on intertidal macroalgae, *Fucus serratus* (Hagerman, 1966; Boaden et al., 1975, 1976; Haage & Jansson, 1970; Stebbing, 1973; Seed & O'Connor, 1981a, b; Seed et al., 1981; Seed, 1985; Janke, 1986; Oswald & Seed, 1986).

This paper describes epifaunal communities associated with *Laminaria digitata* and *L. hyperborea*. We focussed on the following questions:

Which flora and fauna are associated with *L. hyperborea* and *L. digitata*?

Is there a different association on *L. hyperborea* and *L. digitata*?

Are there different communities associated with phylloid, cauloid, and rhizoid?

How does the composition of the epifaunal association change with exposure to wave action?

Is there any change in the composition of the communities during the season?

Are overgrowth and biological patterns important for the composition of the communities?

MATERIAL AND METHODS

Kelps were sampled from two locations (Fig. 1):

(a) Südhafen: sheltered from wave action, low turbidity;

(b) NE-Reede: exposed to wave action, high turbidity.

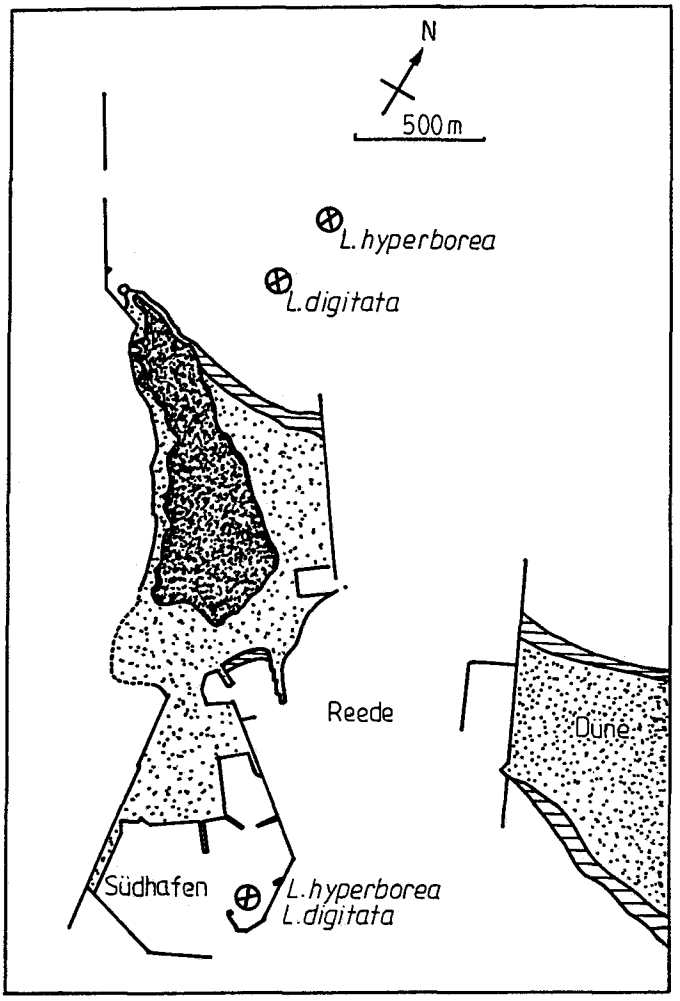

Fig. 1. Map of the island of Helgoland showing the sample sites (x) "Südhafen" (sheltered) and "NE-Reede" (exposed)

In March/April, July and September, 8 kelp plants of each species were taken from their natural habitat by *SCUBA* divers, carefully enclosed in large plastic sacks kept damp whilst being transported to the laboratory.

The flora and fauna found on phylloid and cauloid were identified immediately. Species from the rhizoid were fixed in 4 % formaldehyde/seawater and the mobile species were retained by sieving the fixed samples through a gauze of 500×10^{-6} m. Number of individuals and colonies on the thallus and the degree of cover of encrusting species were divided into three classes:

(a) individuals or colonies: 1–10
11–100
101–1000

(b) cover (%): 1–10
11–50
51–100

A similarity analysis of the macrofaunal associations in the rhizoids of both *Laminaria hyperborea* and *L. digitata* was made by using the Sørensen-index for a pairwise comparison of all samples. The results were clustered by using the furthest neighbour method.

RESULTS

In Table 1, all the macroflora and fauna species are listed that were found in association with *Laminaria digitata* or *L. hyperborea* between March and September 1987 at the two study sites.

Organisms marked with an "*" were found only in a preliminary study, in September 1986 and January 1987, but they were not considered for the results. Species marked with a "+" were not found on *L. digitata*.

29 macroflora and 125 macrofauna species were found in association with *L. digitata* or *L. hyperborea*. The maximum of species were found in July.

The Rhodophyceae (50 % of all flora species) dominated throughout the year. The most abundant taxa were: Polychaeta (20 % of all diverse fauna species), Bryozoa (14 %), Amphipoda (11 %), Hydrozoa (8 %), Ascidiae (6 %), Bivalvia (6 %), Nemertini (5 %), Prosobranchia (5 %), Porifera (4 %), Opisthobranchia (3 %) and Pantopoda (3 %). Other regularly occurring groups were: Anthozoa, Pantopoda, Cirripedia, Isopoda, Anomura, Brachyura, and Echinodermata.

Tables 2 and 3 show the distribution and abundance of dominant macroflora and macrofauna species on *L. digitata* and *L. hyperborea* 1987 at the two study sites.

The different abiotic factors from the "Südhafen" and "NE-Reede" influenced the composition of the communities. The number of species and their abundance were higher at sites of fast flowing, turbulent water (NE-Reede). In slow moving water (Südhafen), especially the calcified and sensitive members of the community (some bryozoans, ascidians, mobile forms) were most abundant.

The association on *L. digitata* and *L. hyperborea* at the same study site showed a very similar composition. At both study sites, especially on the "NE-Reede", the rhizoids were settled by more diverse communities than cauloids and phylloids.

At the exposed site, the fauna on the phylloid surface of *L. hyperborea* was dominated by *Membranipora membranacea, Obelia geniculata* and *Gibbula cineraria.*

Table 1. The macroflora and macrofauna associated with *Laminaria digitata* and *L. hyperborea* at two different sites at Helgoland (March – September 1987). Organisms marked with an "*" were found in a previous examination (September 1986 – January 1987). Species marked with a "+" were not found on *L. digitata*

Macroflora and macrofauna
Chlorophyceae
Acrosiphonia centralis (Lyngb.)
Acrosiphonia sonderi (Kütz.)
Cladophora sericea (Huds.)
Chaetomorpha melagonium (Web. et Mohr)
Rhizoclonium kochianum Kütz.+
Ulva sp. (juv.) Linné
Enteromorpha spp. Link+
Phaeophyceae
Ectocarpus fasciolatus Harv.
Laminariocolax tomentosoides (Farl.)
Litosiphon filiformis (Reinke)
Desmarestia aculeata Lamarck
Desmarestia viridis (O. F. Müll.)
Laminaria digitata (Huds.)
Laminaria hyperborea (Gunn.)
Rhodophyceae
Audouiniella membranacea (Magn.)
Trailliella intricata Batters
Cystoclonium purpureum (Huds.)+
Phyllophora sp. Greville
Chondrus crispus Stackh.+
Corallina officinalis Linné
Dermatolithon pustulatum (Lamarck)
Melobesia membranacea (Esper.)
Hildenbrandia rubra (Sommerf.)
Ceramium rubrum (Huds.)
Plumaria elegans (Bonnem.)
Delesseria sanguinea (Huds.)
Membranoptera alata (Huds.)
Polysiphonia urceolata (Lightf. et Dillw.)
Rhodomela sp. C. Agardh
Porifera
Leucosolenia botryoides (Montagu, 1812)+
Scypha ciliata (Fabricius, 1780)+
Scypha coronata (Ellis & Solander, 1786)+
Halichondria panicea (Pallas, 1766)
Halisarca dujardini Johnston, 1842+
Hydrozoa
Coryne pusilla Gärtner, 1774
Plumularia setacea (Linné, 1758)
Sertularella rugosa (Linné, 1758)+
Hydrallmania falcata (Linné, 1758)+
Dynamena pumila (Linné, 1758)
Sertularia cupressia Linné, 1758*
Laomedea flexuosa Hincks, 1868+
Obelia geniculata (Linné, 1758)
Obelia longissima (Pallas, 1766)
Obelia dichotoma (Linné, 1758)
Obelia gelatinosa (Pallas, 1766)
Scyphozoa
Aurelia aurita (Scyphopolyp) Linné, 1746+
Anthozoa
Actinia equina (Linné, 1758)+
Metridium senile (Linné, 1761)
Sargatia elegans (Dalyell, 1848)*
Sargatiogeton undatus (Müller, 1788)*
Bryozoa
Crisia eburnea (Linné, 1758)
Tubulipora sp. Lamarck, 1816
Alcyonidium gelatinosum (Linné, 1761)
Flustrellidra hispida (Fabricius, 1780)
Bowerbankia imbricata (Adams, 1800)
Bowerbankia gracilis (Linné, 1767)
Cribrilina punctata (Hassall, 1841)*
Cryptosula pallasiana (Moll, 1803)
Escharella variolosa (Johnston, 1838)
Celleporella hyalina (Linné, 1767)
Membranipora membranacea (Linné, 1767)
Conopeum reticulum (Linné, 1767)*
Electra pilosa (Linné, 1767)
Flustra foliacea (Linné, 1758)+
Callopora lineata (Linné, 1767)
Callopora aurita (Hincks, 1877)+
Membraniporella nitida (Johnston, 1883)+
Scrupocellaria scruposa (Linné, 1758)
Bugula stolonifera Ryland, 1960+
Sipunculida
Golfingia minuta (Keferstein, 1862)+
Nemertini
Procephalothrix filiformis (Johnston, 1828–29)+
Lineus ruber (Müller, 1774)
Lineus viridis (Müller, 1774)*
Amphiporus bioculatus McIntosh, 1873
Micrura fasciolata Ehrenberg, 1831+
Oerstedia dorsalis (Abildgaard, 1806)
Tetrastemma candidum (Müller, 1774)*
Tetrastemma vermiculus (Quatrefages, 1846)
Mollusca/Prosobranchia
Gibbula cineraria (Linné, 1758)
Rissoa parva (Da Costa, 1779)
Onoba aculeus (Gould, 1841)

Table 1 (Continued)

Macrofauna
Mollusca/Prosobranchia
Hydrobia ulvae (Pennant, 1777)
Hydrobia ventrosa (Montagu, 1803)•
Lacuna divaricata (Fabricius, 1780)
Lacuna pallidula (Da Costa, 1879)
Littorina mariae Sacchi & Rastelli, 1966•
Mollusca/Opisthobranchia
Retusa truncata (Bruguière, 1792)•
Onchidoris bilamellata (Linné, 1767)+
Onchidoris muricata (Müller, 1767)
Coryphella gracilis (Alder & Hancock, 1844)+
Cuthona concinna (Alder & Hancock, 1844)+
Mollusca/Bivalvia
Nucula nucleus Linné, 1767+
Modiolus modiolus (juv.) (Linné, 1799)
Mytilus edulis (Linné, 1758)
Anomia ephippium (juv.) Linné, 1758•
Cerastoderma sp. Poli, 1795+
Spisula solida (Linné, 1758)+
Hiatella artica (Linné, 1767)
Hiatella gallicana (Pennant, 1777)•
Mya truncata Linné, 1758
Polychaeta (Errantia)
Harmothoe impar (Johnston, 1839)•
Sthenelais boa (Johnston, 1839)
Anaitides maculata (Linné, 1767)
Eumida sanguinea (Oerstedt, 1843)
Eulalia viridis (Linné, 1767)
Streptosyllis websteri Southern, 1914
Typosyllis armillaris (O. F. Müller, 1776)+
Syllides articulocirratus Gillandt, 1979•
Autolytus edwardsi Saint-Joseph, 1887
Autolytus prolifer (O. F. Müller,' 1776)
Procerea cornuta (Agassiz, 1862)
Nereis diversicolor O. F. Müller, 1776•
Nereis pelagica Linné, 1761
Polychaeta (Sedentaria)
Polydora ciliata (Johnston, 1838)
Polydora quadrilobata Jacobi, 1883+
Caulleriella bioculata (Keferstein, 1862)•
Cirratulus cirratus (O. F. Müller, 1776)+
Chaetozone setosa Malmgren, 1867+
Capitella capitata (Fabricius, 1780)+
Arenicola marina (Linné, 1758)•
Amphitrite figulus (Dalyell, 1853)
Nicolea zostericola (Oersted, 1844)
Lanice conchilega (Pallas, 1766)
Sabellaria alveolata (Linné, 1767)
Sabellaria spinulosa Leuckart, 1849•
Fabricia sabella (Ehrenberg, 1836)
Pomatoceros triqueter (Linné, 1767)
Circeis spirillum (Linné 1758)
Janua pagenstecheri Quatrefages, 1865
Spirorbis spirorbis (Linné, 1758)
Spirorbis tridentatus (Levinsen, 1883)
Oligochaeta
Oligochaeta sp.
Pantopoda
Nymphon rubrum Hodge, 1865
Achelia hispida Hodge, 1864
Pycnogonum littorale (Ström, 1762)•
Anoplodactylus angulatus (Dohrn, 1881)
Anoplodactylus petiolatus (Kroyer, 1884)
Crustacea/Cirripedia
Verruca stroemia (Müller, 1776)
Balanus crenatus Bruguière, 1789
Crustacea/Mysidaceae
Mysis relicta (Lovén)+
Crustacea/Amphipoda
Gammarellus homari (Fabricius, 1779)
Gammarellus angulosus (Rathke, 1843)
Gammarus (juv.) sp. Fabricius, 1775•
Melita palmata (Montagu, 1804)•
Calliopius laeviusculus (Kröyer, 1838)
Apherusa ovalipes Norman & Scott, 1906+
Apherusa jurinei (Milne & Edwards, 1830)
Apherusa bispinosa (Bate, 1857)
Dexamine spinosa (Montagu, 1813)
Dexamine thea Boeck, 1861
Orchomenella nana (Kröyer, 1846)
Ampelisca tenuicornis Lilljeborg, 1855+
Jassa falcata (Montagu, 1808)
Jassa marmorata Holmes, 1903
Corophium insidiosum Crawford, 1937
Caprella linearis (Linné, 1767)
Crustacea/Cumacea
Bodotria scorpioides (Montagu, 1804)•
Crustacea/Isopoda
Idotea granulosa Rathke, 1843
Idotea pelagica Leach, 1815•
Janira maculosa Leach, 1814
Crustacea/Natantia
Crangon crangon (Linné, 1758)+
Eualus occultus (Lebour, 1936)

Table 1 (Continued)

Macrofauna	
Crustacea/Anomura	*Ascidiella aspersa* (Müller, 1776)
Galathea intermedia Lilljeborg, 1851+	*Dendrodoa grossularia* (van Beneden, 1846)+
Galathea squamifera Leach, 1815	*Botryllus schlosseri* (Pallas, 1766)
Crustacea/Brachyura	*Botylloides leachi* (Savigny, 1816)+
Carcinus maenas (Linné, 1758)+	*Molgula citrina* Alder & Hancock, 1848+
Pilumnus hirtellus (Linné, 1761)	Pisces
Echinodermata	*Cyclopterus lumpus* (juv.) (Linné, 1758)+
Asterias rubens Linné, 1758	*Liparis liparis* (juv.) (Linné, 1758)+
Amphipholis squamata (Delle Chiaje, 1828)•	Spawn clutches
Ascidiae	*Lacuna divaricata*
Clavelina lepadiformis (Müller, 1776)	*Lacuna pallidula*
Sidnyum turbinatum Savigny, 1816	Opisthobranchia
Didemnum maculosum Milne Edwards, 1841	*Agonus cataphractus* (Linné, 1758)+

Table 2. The distribution of the most abundant macroflora and macrofauna species on *Laminaria digitata* 1987 on two different sites near Helgoland. Amounts of individuals (N: ◇) and colonies (%: □) were divided into three classes: ◇ □ 1–10/◆◪ 11–50/◆■ 51–100

Location		Sheltered									Exposed								
		Phylloid			Cauloid			Rhizoid			Phylloid			Cauloid			Rhizoid		
Month of sampling		M/A	J	S	M/A	J	S	M/A	J	S	M/A	J	S	M/A	J	S	M/A	J	S
Species \ Cover [%]		10	20	80	-	20	30	10	20	30	<10	<10	<10	<10	<10	<10	30	40	50
Flora	*Ulva spec.*	◇	◇	◇				◇	◇	◇						◇	◇	◇	◇
	Ectocarpus fasciolatus	◆		◇															
	Laminariocolax tomentos.	◆					◇	◇	◇		◇						◇		◇
	Litosiphon filiformis	◆		◇				◇			◇								
	Trailliella intricata			◇			◇	◇	◇	◇	◇					◇	◇	◇	◇
	Dermatolithon pustulatum							◇	◇	◇							◇	◇	◇
	Hildenbrandia rubra						◇	◇	◇	◇							◇	◇	◇
	Membranoptera alata							◇		◇						◇	◇	◇	◇
Fauna sessile	*Halichondria panicea*							◆	◆	◇							◇	◇	◆
	Obelia geniculata	□	◪	◪		□	□	□	■	◪							□	□	□
	Membranipora membranac.	□	□	◪		◪	◪		□	□	□	□	□						
	Electra pilosa	◪	□	■		◪	◪	□	■	■		□		□	◪		■	◪	◪
	Callopora lineata		□	□					□	□									
	Fabricia sabella								◇	◇							◇	◆	◆
	Spirorbis tridentatus																		
	Verruca stroemia																		
	Sidnyum turbinatum								□								□	□	□
	Botryllus schlosseri			◪						□									□
	Agonus cataphractus(eggs)							□	□	□							□	□	□
Fauna vagile	*Nicolea zostericola*			◇					◇	◇							◇	◇	◇
	Gibbula cineraria		◇	◇							◇	◇	◇						
	Rissoa parva	◇		◇				◇	◇	◇							◇	◇	◇
	Onoba aculeus																◇	◇	◇
	Lacuna divaricata			◇					◇	◇							◇	◇	◇
	Eulalia viridis							◇									◇	◇	◇
	Autolytus prolifer			◇						◆							◇		◇
	Nereis pelagica			◇					◇	◇							◇	◇	◇
	Jassa spp.			◇				◆	◆	◆							◆	◆	◆
	Corophium insidiosum	◇		◇				◇	◇	◇							◇	◇	◇
	Janira maculosum	◇							◇	◇							◇	◇	◇

Spawn clutches of *Lacuna divaricata* were found in March/April. On the *L. digitata* phylloid, only a few small colonies of *Membranipora membranacea* and spawn clutches of *Lacuna divaricata* were found.

At the sheltered site, phylloids were settled by patches of bryozoans, ascidians, hydrozoans (see Tables 2, 3).

Cauloid of *L. hyperborea* at the exposed site had a typical colonization characterized by *Membranipora membranacea, Electra pilosa, Membranoptera alata, Polysiphonia urceolata, Delesseria sanguinea* (Tables 2, 3).

In the "Südhafen", only bryozoan colonies were found on the cauloids of *L. hyperborea. L. digitata* cauloids on the NE-Reede were not settled by sessile species but a few colonies of *Electra pilosa* and *Membranipora membranacea* settled on the cauloids in the "Südhafen".

The highest abundance of species associated with the rhizoid was found on the "NE-Reede". In the "Südhafen", a similar but less diverse association was found (Tables 2, 3).

At both localities, *L. hyperborea* was usually associated with more species (125 fauna and 29 flora species) than *L. digitata* (83 fauna and 24 flora species) (Table 1).

An increasing amount of colonies and a more widespread distribution were found during the seven months for *Electra pilosa, Membranipora membranacea,* and *Obelia geniculata,* with a maximum in September. *Botryllus schlosseri* and *Ascidiella aspersa*

Table 3. The distribution of the most abundant macroflora and macrofauna species on *Laminaria hyperborea* 1987 on two different sites near Helgoland. Amounts of individuals (N: ◇) and colonies (%: □) were divided into three classes: ◇ □ 1–10/◈◪ 11–50/◆■ 51–100

Location		Sheltered									Exposed								
		Phylloid			Cauloid			Rhizoid			Phylloid			Cauloid			Rhizoid		
Month of sampling		M/A	J	S	M/A	J	S	M/A	J	S	M/A	J	S	M/A	J	S	M/A	J	S
Species \ Cover [%]		10	30	80	10	60	80	20	40	60	≈10	10	50	70	80	90	50	60	80
Flora	*Ulva spec.*	◇		◇	◇	◇	◇	◇	◇	◇				◇	◇	◇	◇	◇	◆
	Trailliella intricata	◇		◇	◇	◇	◇	◇	◇	◇				◇		◇	◇	◇	
	Dermatolithon pustulatum							◇	◇	◇				◇		◇	◇	◇	◇
	Hildenbrandia rubra	◇		◇	◇	◇	◇	◇	◇	◇	◇			◇	◇	◇	◇	◇	◇
	Ceramium rubrum	◇		◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇
	Membranoptera alata			◇	◇	◇	◇			◇	◇			◆	◆	◆	◇	◇	◇
	Polysiphonia urceolata	◇			◇	◇	◇		◇					◇	◇	◇	◇	◇	◇
Fauna sessile	*Leucosolenia complicata*				◇	◇	◇											◇	◇
	Halichondria panicea						◇	◇	◈	◇							◇	◈	◈
	Plumularia setacea															□		◪	◪
	Sertularella rugosa													□	□	□	□	□	□
	Obelia geniculata	□	◪	◪		□	□	□	□	□	□	◪	◪	◪	◪	◪	◪	◪	◪
	Celleporella hyalina	□	□	□	□	□	□	◪	◪	◪					□	□	◪	◪	◪
	Membranipora membranac.	□	◪	■	□	□	◪			□	◪	◪	■		□	□			
	Electra pilosa		□	◪	◪	◪	◪	□	◪	◪	□			◪	■	■	□	■	■
	Callopora lineata			□			□	□	◪	□							□	◪	□
	Spirorbis tridentatus	◇		◇		◇	◇		◇	◇									◇
	Ascidiella aspersa			◈															
	Botryllus schlosseri		□	□														□	
	Agonus catafractus[eggs]							□	□	□							◪	□	
Fauna vagile	*Metridium senile*	◇						◇		◇							◇	◇	◇
	Mytilus edulis							◇	◇	◇							◇	◇	◇
	Gibbula cineraria		◇	◇								◇	◇						
	Rissoa parva			◈			◆	◇	◈	◈				◇	◇	◈	◈	◈	◆
	Lacuna divaricata			◇					◇	◇					◇	◇	◇	◇	◇
	Eulalia viridis								◇	◇							◇	◇	◇
	Autolytus prolifer									◇				◇	◇	◇	◇	◇	◇
	Nereis pelagica								◇	◇						◇	◇	◇	◇
	Jassa spp.	◇	◇	◈			◇	◇	◈	◈		◇			◇	◈	◇	◈	◆
	Corophium insidiosum							◇	◇	◇					◇		◇	◇	◇

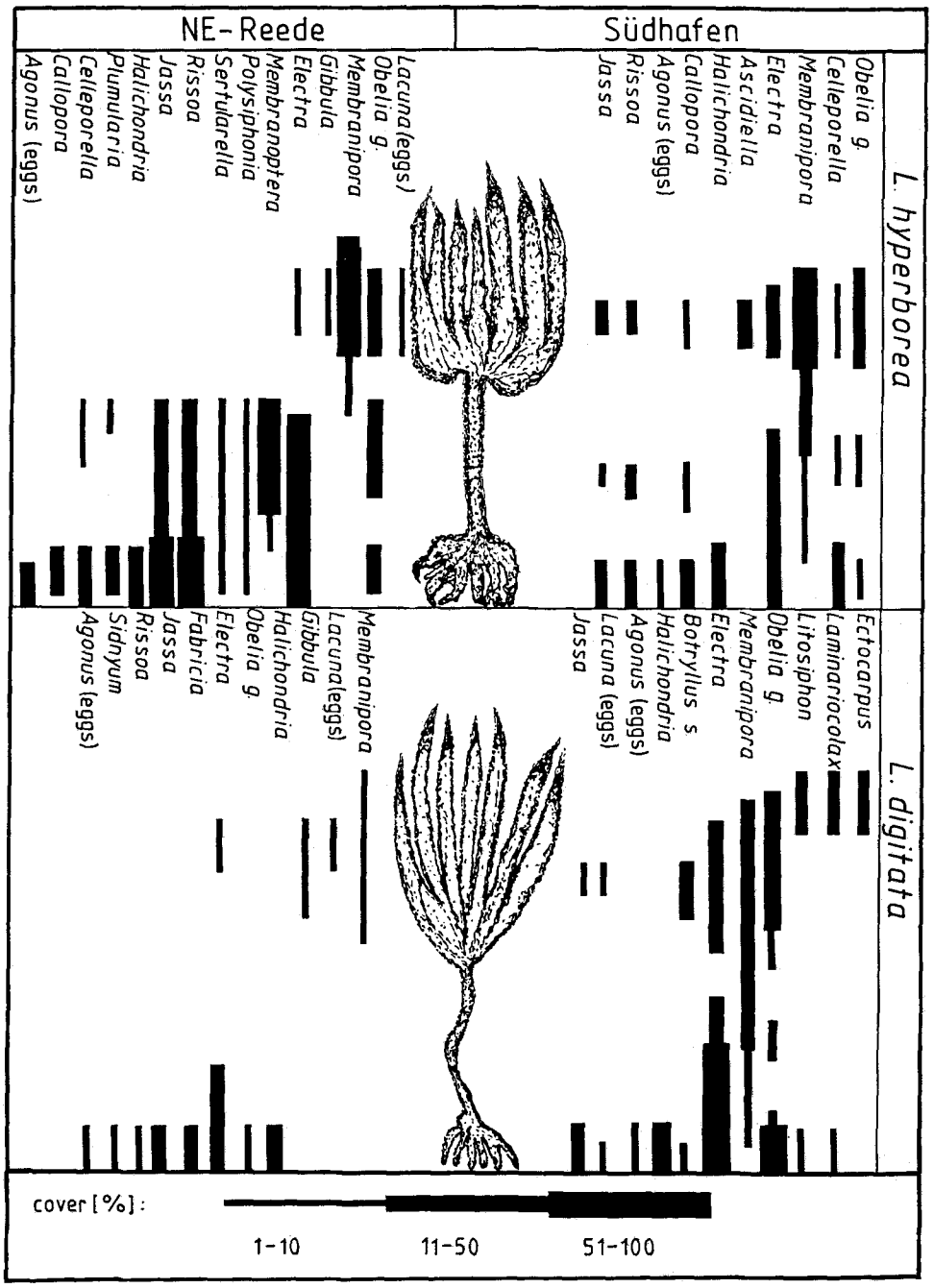

Fig. 2. The macrofauna associated with *Laminaria hyperborea* and *L. digitata* at Helgoland

appeared in July and increased up to September. *Callopora lineata* and *Celleporella hyalina* appeared during the study period and decreased in September. In general, the cover and species maximum was in July.

Annual phylloid development and loss of both *Laminaria* species influenced the patterns of cover and faunal associations. The seasonal change of the associations was more obvious on one-year old parts (phylloid) than on perennial parts (cauloid, rhizoid) of the kelp. In July, cover and diversity were lower on phylloids, especially on those at the exposed site (Tables 2, 3).

L. digitata cauloids showed a small amount of species, and a maximum cover of 30 % (flora and fauna) in September in the "Südhafen", while *L. hyperborea* had 80 % cover at the exposed station, and in September in the "Südhafen" (Tables 2, 3).

The cover of settling organisms on the rhizoid increased from March to September on both kelp species at both sites, in particular at the exposed locality, where up to 80 % of *L. hyperborea* was covered.

Primary settlers were in order of occurrence: *Membranipora membranacea, Electra pilosa,* and *Obelia geniculata.* Near the "collar"-region, especially *Membranipora membranacea* colonies spread widely and grew in the direction of the intercalar zone.

We first found *Membranipora membranacea* colonies in July on the phylloids of *L. hyperborea* (at both locations), whereas colonies on the phylloid of *L. digitata* were only found in September (only at the exposed location).

Due to the high amount of species and their abundance in the "Südhafen", there was a more intensive competition for space. *Membranipora membranacea* was always present, but most conspicuous in September. Competition for space showed the following ranking on the phylloid: *Membranipora membranacea, Electra pilosa, Callopora lineata, Celleporella hyalina. Obelia geniculata* overgrew other species without harming them.

Whenever *Botryllus schlosseri* and *Ascidiella aspersa* settled, they outcompeted most of the other potential competitors for space. Only *Membranipora membranacea* was able to overgrow *Botryllus schlosseri.*

On both *Laminaria* cauloids and at both localities, *Electra pilosa* was the dominant species. The Rhodophyceae on the cauloids of *L. hyperborea* on the "NE-Reede" were overgrown by *Electra pilosa. Membranipora membranacea* overgrew *Electra pilosa* at the top of the cauloids to 50 % in the "Südhafen" and to 30 % in the "NE-Reede".

The species diversity of the rhizoid community was higher than on other parts of the kelp. Typical competitors for space showed the following ranking *Halichondria panicea, Electra pilosa, Callopora lineata,* and *Celleporella hyalina.*

DISCUSSION

The attractiveness for settlement of *Laminaria hyperborea* (125 fauna and 29 flora species) is obviously higher than that of *L. digitata* (83 fauna and 24 flora species) around Helgoland. Figure 2 shows the typical fauna and flora association distributed on *L. digitata* and *L. hyperborea* at two different Helgoland sites. The study of the three parts of the kelp thallus (phylloid, cauloid, rhizoid) shows, in the Helgoland samples, a decrease of species density on the parts near the phylloid, especially at exposed stations compared with the sheltered regions.

The most attractive place for faunal settlement were the rhizoids, but there was no

homogeneous composition. The samples of *L. hyperborea* rhizoids are placed in two different groups by the cluster analysis (Fig. 3). One consisted of samples from the "Nordost-Reede", while the other consisted of those from the Südhafen. Within both groups, highest similarity occurred between the samples of July and September. Consequently, wave exposure seemed to play a more important role in community composition than seasonal influences (which also existed showing a low similarity between spring and summer samples).

Cluster results for *L. digitata* samples differed substantially from those of *L. hyperborea*. Highest similarity was measured in samples from the same dates, showing the more important effect of seasonal factors for the community composition. The reason therefore may be the lack of 26 species in *L. digitata* rhizoids, which showed a sensitivity to wave exposure or to other factors of the specific location. The absence of those species in *L. digitata* rhizoids may be explained by the smaller size of the rhizoids.

The composition of the associations found on the two kelps around Helgoland is similar to that found in different regions on other kelps such as *Laminaria*, *Macrocystis*,

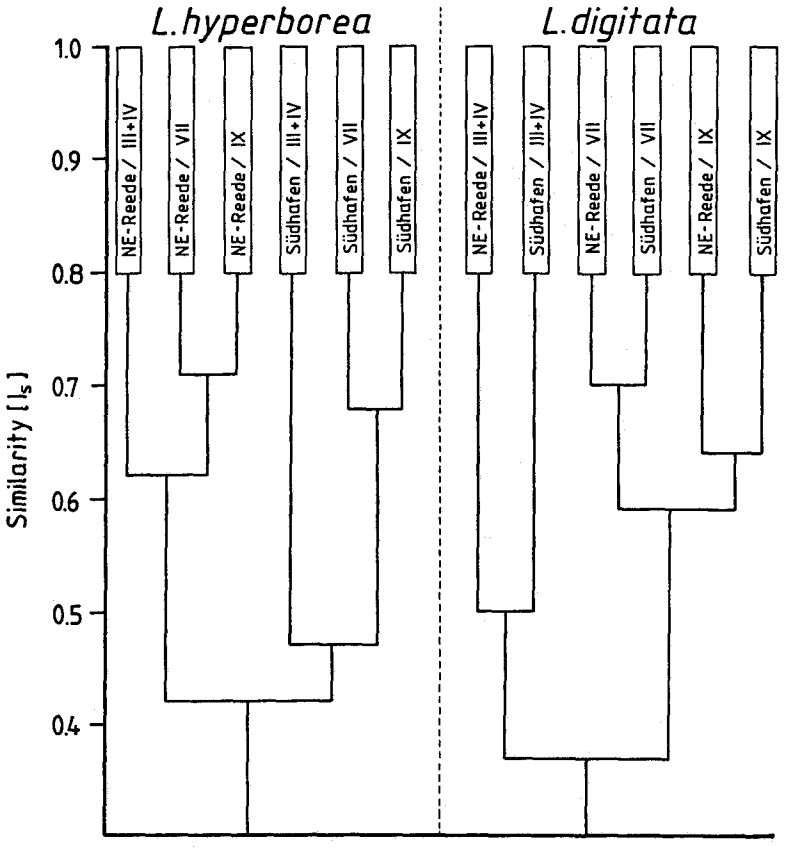

Fig. 3. Macrofaunal composition associated with the rhizoids of *Laminaria hyperborea* and *L. digitata* at the island of Helgoland. Similarity analysis using Sørensen index (see Braun-Blanquet, 1964) for a pairwise comparison for the samples. Indices were clustered by furthest neighbour method (Steinhausen & Langer, 1977)

and *Saccorhiza* (Kitching et al., 1934; Sloane et al., 1957; Norton, 1971). Most of the studies examined only one part of the kelp thallus (phylloid, cauloid or rhizoid) (Colman, 1940; Ebling et al., 1948; Ghelardi, 1971; Moore, 1973) or a detailed question (Wing & Clendenning, 1971; Stebbing, 1972; Norton, 1973; Dixon et al., 1981; Keough, 1986).

Norton (1971) found 89 fauna species associated with *Saccorhiza polyschides* near the Isle of Man. Janke (1986) dicovered 82 fauna species alone in the rhizoid of *L. digitata* around Helgoland from the shallow subtidal region. All these species, with the exception of *Clava multicornis*, were also found in this study.

Norton (1971) found a high reduction in the number of species towards the phylloid and at exposed sites, as we did in this study. At sheltered locations, an increase in the mobile fauna species was found on the phylloids when bryozoans and other sessile species settled there. This contrasts with the findings in exposed regions where the fronds were not covered with mobile forms when bryozoans were present. Wing & Clendenning (1971) found higher numbers of mobile animals on totally encrusted phylloids than on clean phylloid samples.

Most of the species found constantly associated with *S. polyschides* were also commonly found on *Laminaria* kelps near Helgoland (*Obelia geniculata, Electra pilosa, Celleporella hyalina, Callopora lineata, Gibbula cineraria, Nereis pelagica, Jassa* spp., *Ascidiella aspersa*). The distribution and abundance of this common species is similar to those on *Laminaria* kelps near Helgoland (Fig. 2), near Wembury (Kitching et al., 1934) and near Lough Ine (Sloane et al., 1957).

A very typical settler on the laminarians is *Membranipora membranacea*. This species shows a stronger affinity to *L. hyperborea* fronds than to *L. digitata* (Helgoland), and stronger to *L. digitata* than to *L. cloustoni* (Wembury) (Kitching et al., 1934). This bryozoan is rare on *L. digitata* near Helgoland and near Lough Ine (Sloane et al., 1957), but abundant on *L. hyperborea* (Helgoland), *S. polyschides* (Norton, 1971), and on *Macrocystis* (Yoshioka, 1982).

Membranipora membranacea does not settle only on the phylloid but also on the flat cauloids and frills of *S. polyschides* (Sloane et al., 1957). It was found mainly on the cauloids of *Laminaria* spp. in the "Südhafen".

The existence of a few sessile phytal forms depends on the kelp associations (*Membranipora membranacea, Sertularella rugosa* [obligate cauloid settler; Nishihira, 1967], *Spirorbis spirorbis*).

Most of the epifaunal species use the kelp as a place for settlement and not as a food resource. De Burgh & Fankboner (1978) showed in the case of *Nereocystis luetkeana*, labelled with radioactive carbon (C^{14}), that *Membranipora membranacea* absorbed the exudates from this kelp.

The cauloids of *L. hyperborea* are especially used as a habitat at the "NE-Reede". They present a favourite substrate for Rhodophyceae (see Lüning, 1985; Hiscock, 1985).

Moore (1973) investigated the crustacea of the rhizoid of *L. hyperborea* on the northeast coast of Britain. Amphipods represent and important part of the vagile fauna. Moore (1973) reported on the following species, which were also found during our investigation: *Idothea* sp., *Janira maculosa, Dexamine thea, Jassa* spp., *Caprella linearis, Apherusa* spp., *Gammarellus homari*.

The occurrence of *Nereis pelagica* and the sponge *Halichondria panicea* on the rhizoid (Hartmann-Schröder, 1971; Gillandt, 1979) was also found in the present study.

The appearance of new colonies of *Membranipora membranacea* was observed around Helgoland in July. Norton (1971) observed a new settlement of this species on *Saccorhiza polyschides* near the Isle of Man in May, and Seed & Harris (1980) found *Membranipora membranacea* between June to September near Strangford Lough (northern Ireland). It is remarkable that *Scrupocellaria reptans* as a primary settler on *Laminaria* spp. was not observed around Helgoland during this investigation. In other regions, this form is a typical kelp settler (Ebling et al., 1948; Norton, 1971; Stebbing, 1972).

The kelp region represents an important zone for the development of juvenile animals (Norton, 1971). Especially *Agonus cataphractus* lays its eggs in the rhizoid of *Laminaria* around Helgoland (Krüß, 1988).

The absence of juvenile Echinoidea *(Echinus esculentus, Psammechinus miliaris)* and the bryozoan *Scrupocellaria reptans* is conspicuous. The latter is found frequently on the phylloids of *Saccorhiza* (Ebling et al., 1948; Norton, 1971) and on *Laminaria* spp. in Eire (Stebbing, 1972).

Patina pellucida, a typical settler on *Laminaria* fronds (Fretter & Graham, 1976), was not found in this study. This gastropod has not been reported live around Helgoland since 1959 (Ziegelmeier, 1966), but fresh shells of this species are washed ashore at the "Düne" (see Fig. 1) every spring (Janke, 1987). On *Saccorhiza polyschides* (Norton, 1971) and on *L. digitata* in Strangford Lough (Seed & Harris, 1980), this gastropod is a very typical and abundant component of the fauna.

The associations of the two bull kelp species *L. digitata* and *L. hyperborea* near Helgoland show a similar pattern to those of other kelps from different regions, but they lack some typical dominant settlers.

Acknowledgements. The authors would like to thank the Director of the Biologische Anstalt Helgoland, Prof Dr. H.-P. Bulnheim, and the staff of the "Meeresstation" on the island Helgoland for providing space facilities and personal support. Our special thanks are due to the SCUBA divers for sampling the material, even under unfavourable conditions. We are grateful to Dr. M. Rieper-Kirchner for correcting an earlier draft of this manuscript.

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