Vol. 146: 135-143, 1997 | MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser | Published January 30

High prevalence of infection by endophytic brown algae in populations of *Laminaria* spp. (Phaeophyceae)

Elín Ellertsdóttir, Akira F. Peters*

Institut für Meereskunde, Abteilung Meeresbotanik and AG Marine Pathology, Düsternbrooker Weg 20, D-24105 Kiel, Germany

ABSTRACT: The occurrence of microscopic algae that are endophytes and potential pathogens of kelps was quantified during 1994 in wild populations of *Laminaria saccharina*, *L. hyperborea* and *L. digitata* at Helgoland, North Sea. Sampling was designed to enable analysis of the influence of 4 fixed factors: species, date, wave exposure, and depth. Microscopic examination of, in total, 1224 thalli showed that the prevalence of infection by endophytic algae was 85%, much higher than was inferred by gross lesions alone. One tenth of the hosts, mostly *L. saccharina*, showed severe morphological changes, such as distorted stipes or a crippled lamina. One third showed weaker symptoms of endophyte disease, such as dark spots on the lamina or warts on the stipe. In most infected thalli, the infection was not evident macroscopically. Prevalence was high throughout the year with a minimum in spring. At a more exposed site, prevalence was higher and disease symptoms stronger than at a sheltered locality. Disease symptoms were more severe in shallower than in deeper water. Endophytes, mostly brown algae, were repeatedly isolated and identified in laboratory cultures. Endophytes were not strictly host-specific, but *L. saccharina* was predominantly infected by *Laminarionema elsbetiae*, recently detected at Helgoland. This is the first epidemiological study comparing the prevalence and effects of kelp endophytes in different hosts at the same locality.

KEY WORDS: Disease · Kelp · Pathogen

INTRODUCTION

On temperate rocky shores, Laminariales form an important, often dominant component of the subtidal community, where the kelp forest provides the habitat for a great number of other organisms, for example Schultze et al. (1990) found 125 animal and 29 algal species on *Laminaria hyperborea* (Gunnerus) Foslie and 83 animal and 24 algal species on *L. digitata* (Hudson) Lamouroux. Kelps have been utilised and maricultured for human consumption and as a source of alginate. Diseases, understood here as continuing disturbances to an organism's normal structure or function such that it is altered in performance or economic value (definition slightly changed after Andrews 1976), of these ecologically and economically important marine plants are of interest to ecologists and kelp farmers and thus, various diseases of Laminariales have been studied. Pathologies of cultivated Laminariales were reviewed in Perez et al. (1992). Kelp diseases are presumed to be caused by changes in natural environment, pollution (Andrews 1976) and biotic agents, such as fungi (Kohlmeyer 1968, Schatz 1984, Apt 1988a), bacteria (Andrews 1976, Wu et al. 1983, Apt 1988a), and endophytic algae (Andrews 1977, Yoshida & Akiyama 1979, Apt 1988a, b). Apt (1988b) provided experimental evidence for the existence of an 'endophyte disease' in kelps: a brown algal endophyte (*Streblonema* sp.) is the causative agent of tumours in *Nereocystis luetkeana* (Mertens) Postels et Ruprecht. Mass infection of *Undaria* sp. by the endophytic brown alga *Gononema aecidioides* (Rosenvinge) Pedersen reduces its economic value

---

*Addressee for correspondence.
E-mail: afpeters@ifm.uni-kiel.de

(Yoshida & Akiyama 1979). Endophytic green algae may also be responsible for diseases of macroalgae, with details so far only studied in red algal hosts (Correa 1996, Sánchez et al. 1996 and references herein, Correa et al. 1997).

Only 4 epidemiological studies of endophyte prevalence in populations of Laminariales have been done. Andrews (1977) reported that in a population of *Nereocystis luetkeana* at San Juan Island, Washington State, USA, the infection rate by endophytes increased from 20% in June to 90% in August. In southern Norway, more than 20% of the population of *Laminaria hyperborea* showed dark spots on the lamina, presumably caused by an undescribed brown algal endophyte (Lein et al. 1991). Peters & Schaffelke (1996) found 87% of the population of *L. saccharina* (L.) Lamouroux in the brackish Kiel Fjord, western Baltic, to be infected by the brown alga *Gononema aecidioides*, and Schaffelke et al. (1996) reported a negative relationship between water depth and symptoms of endophyte disease. In other reports of infection of kelps by endophytes (e.g. Setchell & Gardner 1925, Dangeard 1931, Peters 1991), data on infection prevalence are lacking or vague. Data on endophyte prevalences are also scarce in other macroalga-endophyte pairs. They ranged from 20 to 80% in wild populations of the red alga *Mazzaella laminarioides* (Bory) Fredericq et Hommersand infected by green and blue-green endophytes (Correa & Sánchez 1996, Correa et al. 1997). Data on prevalences of red algal parasites in field populations of their hosts do not seem to exist, although the association of Rhodophyta with their often adelphoparasitic symbionts is otherwise very intensely studied (Goff 1982, Goff & Zuccarello 1994, Goff et al. 1996).

The high infection rates obtained in the small number of previous studies suggested endophytism is a common phenomenon in populations of Laminariales. The present work confirms this in the 3 species of *Laminaria* occurring at Helgoland. In addition, we use epidemiological data to infer the influence of season, wave exposure, water depth, and of the different host species on both prevalence of endophytes and severity of symptoms of the endophyte disease.

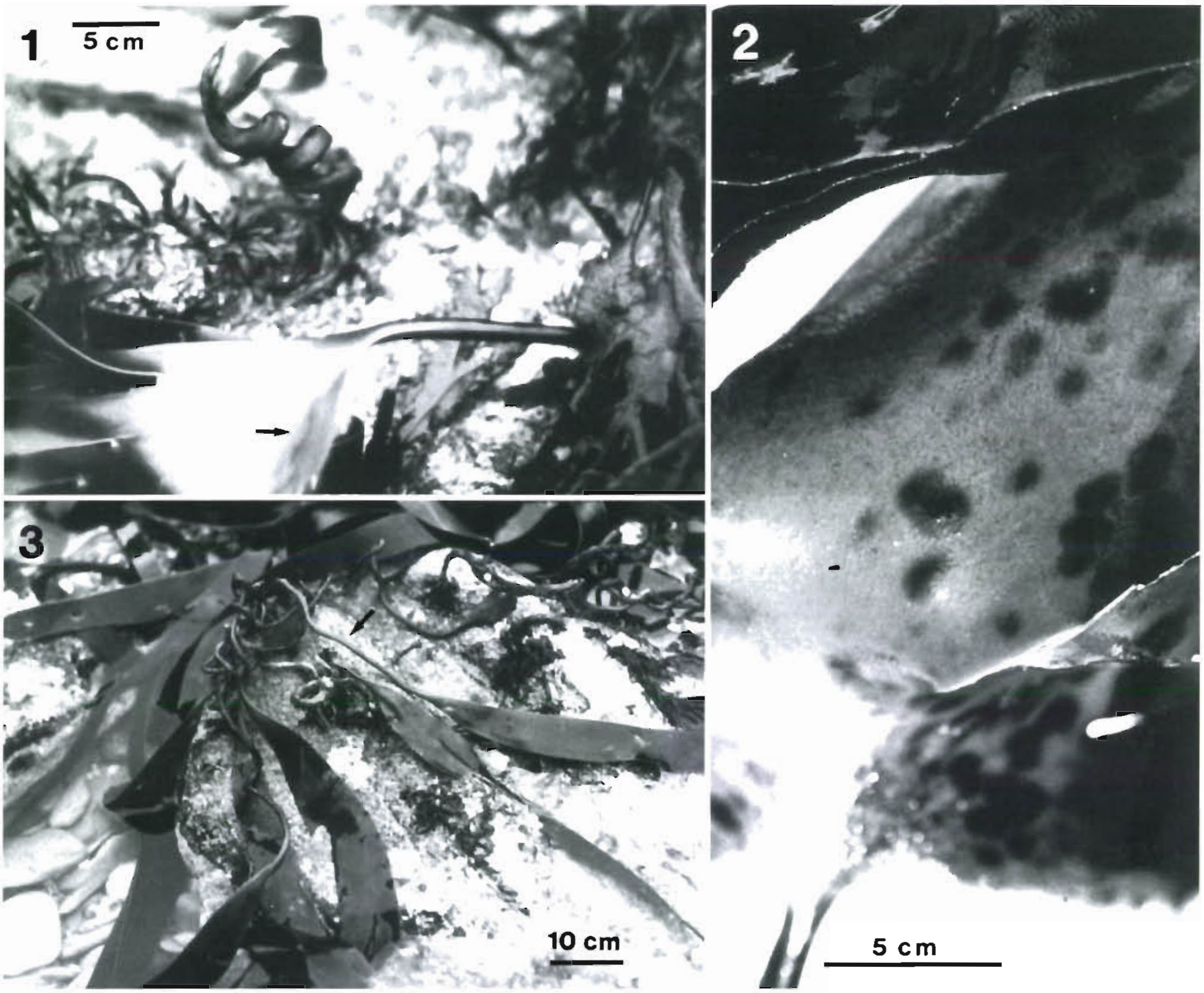
MATERIAL AND METHODS

Sampling. Collection of algae was done in 1994 at the island of Helgoland, North Sea, which is surrounded by a kelp forest consisting of 3 species of *Laminaria*. *L. digitata* dominates the upper sublittoral fringe from zero (average low water during spring tides) to 1.5 m depth, *L. hyperborea* occurs from 1 to 8 m, forming dense populations between 1.5 and 4 m, and *L. saccharina* grows patchily among the other species from zero to 3 m (Lüning 1970). The island was visited 4 times (10 to 15 February, 24 to 31 May, 15 to 25 August and 2 to 13 November) during periods of spring tides. Collection of individuals at the upper growth limit of every species was done from land, samples from greater depths were obtained by divers. Sampling was designed to enable analysis of the influence of the factors species, date, wave exposure and depth (Table 1). Individuals of the 3 *Laminaria* species were collected and not further subdivided by age, size class or other criteria, but thalli too young or too severely damaged to be identified were excluded. The 2 depths were chosen for every species to represent the upper and lower distributional limit of dense populations of the respective species (Lüning 1970, cf. above). For every combination of factors, we collected 3 independent samples (i.e. from different areas at the same site) of usually more than 10 individuals each. Collection in the field was haphazard. Randomization was achieved by random selection of 10 plants from each sample. Hence, there were 30 individuals per species, date, site and depth, in 3 subsamples of 10 plants each. The total number of thalli examined was 1224; bad weather precluded collection of the target number of 1440 (30 per sample × 3 species × 4 seasons × 2 sites × 2 depths), and in a few cases a subsample consisted of less than 10 individuals.

Detection of endophytes and determination of disease symptoms. Each thallus was classified into 1 of 3 morphological categories following Peters & Schaffelke (1996): (1) no visible signs of endophyte infection, (2) moderate alterations, such as dark spots on the lamina or small warts on the stipe, (3) heavily deformed thalli (Figs. 1 to 3). Only thalli of categories 2 and 3 are

Table 1. Sampling design. The 4 factors (species, date, site and depth) were fully crossed. The exposed site was at the open coast, the sheltered site inside the harbour. The levels of depth were the upper (u) and lower (l) limit of dense populations, which varied according to species

Species:	*Laminaria digitata, L. hyperborea,* and *L. saccharina*															
Date:	Feb 1994				May 1994				Aug 1994				Nov 1994			
Site:	Exposed		Sheltered		Exposed		Sheltered		Exposed		Sheltered		Exposed		Sheltered	
Depth:	u	l	u	l	u	l	u	l	u	l	u	l	u	l	u	l



Figs 1 to 3. *Laminaria digitata*, *L. hyperborea*, *L. saccharina*. Symptoms of endophyte disease in *Laminaria* spp. at Helgoland. Fig. 1. In foreground, thallus of *L. digitata* of disease category 2, i.e. morphologically normal plant with dark patch of *Laminariocolax tomentosoides* (arrow); in background, thallus of category 3, i.e. severely altered plant of *L. digitata* or *L. saccharina* with fully twisted stipe. Degeneration is too strong to allow determination to species. Fig. 2. *L. hyperborea*, spotted blade, but otherwise normal morphology, thus disease category 2. Fig. 3. A group of thalli of *L. saccharina*, with different severity of stipe twisting. Arrow indicates thallus which is morphologically almost unaltered. Such a plant falls into category 1 if endophytic filaments are detectable microscopically. Figs. 1 & 3 from February 1994, Fig. 2 from August 1994

regarded as 'diseased'. Distinction between categories 2 and 3 was arbitrary and had the following reason. While for the economical value of a kelp (e.g. use as food) the difference between a normal and an optically altered (e.g spotted) thallus may be relevant, the difference between a smooth and a deformed thallus seems to be more important for the hydrodynamic behaviour which is essential for survival in a wave-swept environment (Correa & Sánchez 1996). Hand sections were made of every thallus, either in altered parts or, in thalli without symptoms, in sectors likely to be infested. This was the distal blade portion in all hosts and also the stipe in *L. saccharina*. It was known from previous studies that green endophytes tend to be more frequent in the older thallus parts of their hosts (Correa et al. 1994, Correa & Sánchez 1996). Presence or absence but not density of endophyte filaments was determined in the sections under the light microscope. The microscopic endophytes grew in the interstice in the medulla or the inner cortex; they were pigmented and no staining was necessary to distinguish their cells from the unpigmented medullary cells of the host (cf. Fig. 2C in Lein et al. 1991 and Fig. 5 in Peters 1991). After microscopic examination, thalli of category 1 (no symptoms) were further subdivided into endophyte-free or endophyte-carrying plants.

Isolation of endophytes. Endophytic brown algae are very reduced morphologically, and identification to genus/species requires laboratory cultures to obtain reproductive structures. For every season and for both sites and both depths, a culture was started from the medullary tissue of at least 1 infected individual of each of the 3 host species. Additional isolates were made in 1995 and 1996. Isolation and general culture techniques followed Peters (1991). The endophytes were grown in unialgal culture at 14 ± 1°C and short days (8 h light:16 h dark) with 26 µmol m^{-2} s^{-1} photon fluence rate provided by white fluorescent tubes. Cultivated under these conditions, identification was usually possible within 1 to 2 mo.

Data analysis. Our sampling design (Table 1) allowed a statistical analysis of the data with 4 fixed factors: species with 3 levels, i.e. *Laminaria saccharina*, *L. hyperborea* and *L. digitata*; date with 4 levels, i.e. February, May, August and November; site with 2 levels, i.e. the more wave-exposed 'Nordostwatt' and the sheltered 'Südhafen'; and depth with 2 levels, i.e. the upper and lower growth limit of the respective species. The dependent variable was either discrete, i.e. the number of hosts in a subsample which contained endophyte filaments, or continuous, i.e. the percentage of infected individuals in a subsample falling into 1 of the 3 disease categories. From the 3 subsamples of each sample an average and a standard error were calculated. Chi-square tests were performed on the discrete values to test the H_0 of no difference in the number of infected thalli and non-infected thalli between species, seasons, sites or depths. More powerful statistical tests, such as ANOVA, were not possible on these data after transformation from discrete values into continuous percentages, since variances were not homogeneous. For the different disease categories H_0 stated that there was no difference in percentage of thalli belonging to each category between the different levels of the same factors as above. Arcsine-square-root transformed percentage values fulfilled the criterion of homogeneity of variances (test after Cochran, performed according to Sachs 1978) In some analyses, the symptom categories 2 and 3 were not distinguished and taken together as 'symptomatic thalli'. When a significant difference in a factor with more than 2 levels was obtained in the ANOVA, a Tukey-Kramer test was used to identify the responsible level. Statistical analyses were done with SUPER ANOVA (Abacus Concepts, Berkeley, California, USA) on a Macintosh IIsi.

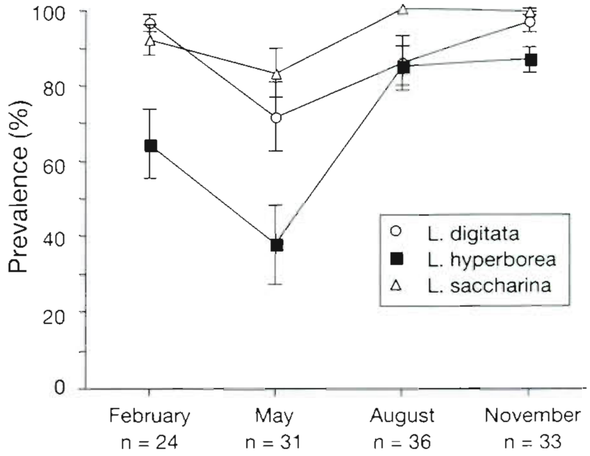


Fig. 4. Seasonal occurrence (±SE) of endophyte infection in the 3 *Laminaria* species of Helgoland in 1994. n, the number of subsamples of 10 individuals, is for all species together

RESULTS

General

Endophytic brown algal filaments were present in the medulla or the inner cortex in 85% of a total of 1224 examined thalli. Of these infected thalli, 59% had no visible morphological changes, but endophytes were observed upon microscopical examination. Roughly one third (30%) of infected thalli showed weak to moderate but visible thallus alterations and 11% severe deformations. All plants of morphological categories 2 and 3 had endophyte filaments in their tissue associated with the altered structures.

Season

There was a weak seasonality in endophyte prevalence during the year of research. All species together had a minimum in May (χ^2: $p < 0.05$). But even at its

Table 2. Results of analysis of variance. Dependent variable was proportion of symptomatic thalli (= sum of thalli in symptom categories 2 and 3; for definition of categories see 'Material and methods'). Values were arcsine-square-root transformed

Source	df	Sum of squares	Mean square	*F*	p
Month	3	0.575	0.192	0.904	0.4419
Site	1	10.081	10.081	47.534	0.0001
Depth	1	1.540	1.540	7.261	0.0082
Month × Site	3	0.664	0.221	1.044	0.3763
Month × Depth	3	0.794	0.265	1.248	0.2960
Site × Depth	1	0.007	0.007	0.031	0.8596
Site × Month × Depth	2	0.288	0.144	0.679	0.5093
Residual	108	22.905	0.212		

lowest value, *Laminaria hyperborea* still comprised 38% infected individuals. The highest prevalence of endophytes was in *L. saccharina* in August with 100% individuals infected (Fig. 4). The proportion of thalli with disease symptoms was not significantly different among months (Table 2).

Site

In general, the thalli had a higher endophyte prevalence at the more wave-exposed site (χ^2: $p < 0.05$). Broken down by species, the prevalence of endophyte infection was significantly higher at the more exposed site for *Laminaria saccharina* and *L. digitata* (χ^2: $p < 0.05$; Fig. 5). There was no such significance in the prevalence of *L. hyperborea*, but this species, like the other two, had significantly more symptomatic thalli at the more wave-exposed site (Fig. 6). The difference between the 2 sites was consistent over the course of the year (Table 2, Fig. 7).

Depth

According to H_0, there should be no difference in prevalence of endophytes or severity of disease symptoms between the upper and lower growth limit. For prevalence, this was in general true, only *Laminaria hyperborea* had a significantly greater number of thalli with endophytes at its upper growth limit (χ^2: $p < 0.05$; Fig. 8). In contrast, there were generally more symptomatic thalli at the upper than at the lower growth limits (Table 2; Fig 7).

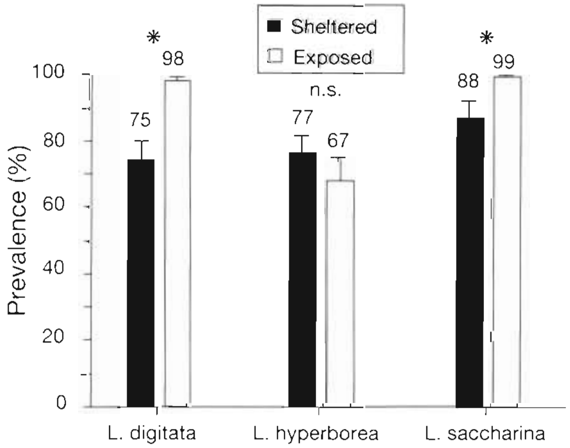


Fig. 5. Prevalence (SE) of endophyte infection in the 3 *Laminaria* species at 2 differently wave-exposed sites. Number of subsamples at exposed site: *L. saccharina* n = 24, *L. digitata* n = 24 and *L. hyperborea* n = 17; at sheltered site: *L. saccharina* n = 21, *L. digitata* n = 21 and *L. hyperborea* n = 17 Numbers above bars give means; n.s.: difference not significant; (✱) significant ($p < 0.05$)

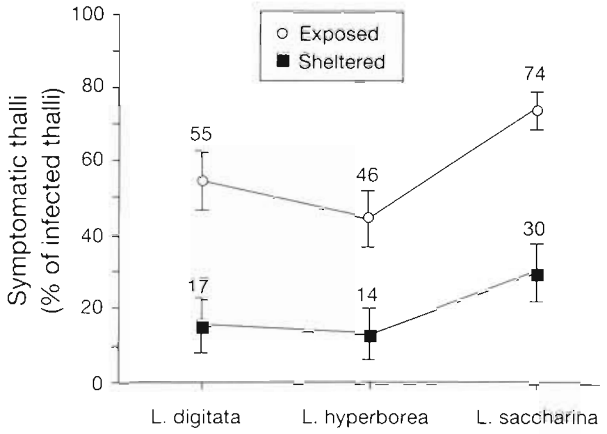


Fig. 6. Proportion (± SE) of symptomatic thalli (sum of thalli in symptom categories 2 and 3; for definition of categories see 'Material and methods') in the 3 *Laminaria* species at 2 sites with different wave exposure. Numbers of subsamples as for Fig. 5. Numbers above data points give means

Host species

Striking differences existed among the 3 host species both in endophyte prevalence and disease symptoms. *Laminaria saccharina* had the highest percentage of infected thalli (93 ± 12%), followed by *L. digitata* (86 ± 3%) and *L. hyperborea* (73 ± 4%). The difference between *L. saccharina* and *L. hyperborea* was significant. *L. saccharina* also had a significantly higher percentage of severe thallus deformations (Tukey-Kramer; $F = 22.9$, $p < 0.001$) than the other 2 species. There were no significant differences among the host species in the percentage of thalli with moderate alterations (Fig. 9).

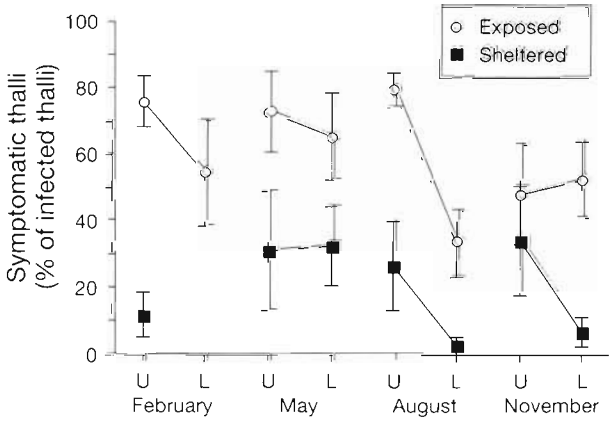


Fig. 7. Proportion (± SE) of symptomatic thalli, from 2 sites with different wave exposure, from upper (U) and lower (L) growth limits at 4 different dates. Bad weather precluded collection of thalli at lower growth limit of sheltered site in February

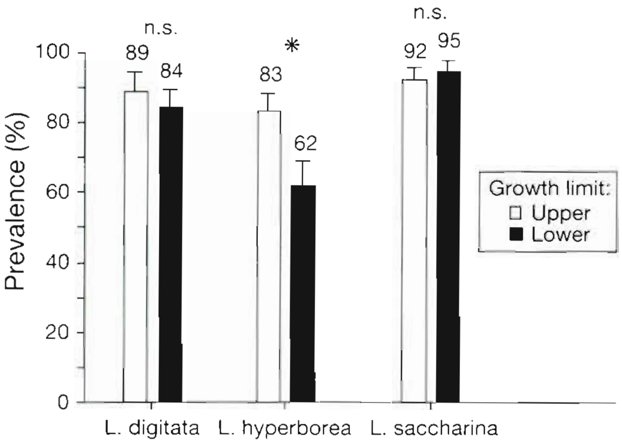


Fig. 8. Prevalence (SE) of kelp endophytes at different growth limits. Number of subsamples at upper growth limit: *Laminaria saccharina* n = 24, *L. digitata* n = 24 and *L. hyperborea* n = 16; at lower growth limit: *L. saccharina* n = 21, *L. digitata* n = 21 and *L. hyperborea* n = 18. Numbers above bars give means; n.s.: difference not significant; (*) significant ($p < 0.05$)

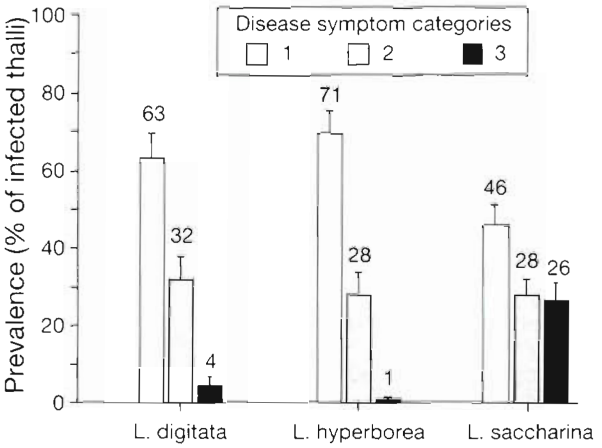


Fig. 9. Severity (SE) of endophyte disease symptoms in 3 *Laminaria* species at Helgoland. Category 1: light infection of kelp, only detectable under the microscope; category 2: moderate thallus alterations; category 3: severely deformed (crippled) thalli (details of categories in 'Material and Methods'). Number of subsamples: *L. saccharina* n = 45, and *L. digitata* n = 45 and *L. hyperborea* n = 34. Numbers above bars give means

Isolates and identification of endophytes

All alterations of host thalli were darker than the surrounding tissue, indicating presence of additional pigments. The most common endophytes isolated were brown algae, the most frequent taxa being *Laminarionema elsbetiae* Kawai et Tokuyama, *Laminariocolax tomentosoides* (Farlow) Kylin and an undescribed species henceforth referred to as *Streblonema* sp. (Table 3). Of isolates obtained from different infected thalli of *Laminaria saccharina*, 80% belonged to *Laminarionema elsbetiae*. It also occurred in *L. digitata* (17%) but was not isolated from *L. hyperborea*. *Laminariocolax tomentosoides* was found in *L. digitata* (25%) and less frequently in *L. hyperborea* (9%) and *L. saccharina* (3%). *Streblonema* sp. was only isolated from *L. hyperborea* (40%). In addition to these identified taxa, we isolated a number of brown algae not determined to species, e.g. *Ectocarpus*. In spring and summer isolates also contained green algae belonging to the genera *Bolbocoleon*, *Acrochaete* and *Enteromorpha* and a unicellular red alga of the family Porphyridiaceae.

DISCUSSION

Microscopic brown algae appear to be very common endophytes in natural populations of kelps. Their high prevalence (85%) in the kelps examined at Helgoland is as high as or exceeds previous records for other localities and for green endophytes in Rhodophyta (Andrews 1977, Lein et al. 1991, Correa & Sánchez 1996, Peters & Schaffelke 1996, Correa et al. 1997). This strongly suggests that phaeophycean endophytes play a role in the life of kelp sporophytes so far not considered by kelp ecologists. On one hand their relationship may be considered commensalistic, because there is no evidence that the endophytes studied are para-

Table 3. Isolates of endophytic algae made from *Laminaria* spp. at Helgoland. Σ: number of isolates = number of different host thalli used

	Laminaria saccharina	*Laminaria digitata*	*Laminaria hyperborea*
Laminarionema elsbetiae	25	6	0
Laminariocolax tomentosoides	1	9	3
Streblonema sp.	0	0	13
Ectocarpus sp.	1	5	4
Other brown microalgae	3	10	4
Green and red endophytes	1	6	8
Σ	31	36	32

sites that receive photosynthate from *Laminaria* spp. On the other hand there are good arguments that they are potential pathogens causing the observed colour and morphological changes in their hosts. A brown endophyte as causative agent of hyperplasia in kelps was demonstrated in another host-endophyte system by Apt (1988b), and thalli of *L. saccharina* infected in laboratory culture by *Laminarionema elsbetiae* developed disease symptoms that were not seen in control thalli (Ellertsdóttir 1995). In the present study, none of the thalli with dark spots or distorted thalli lacked endophytes, but more than half of the plants that contained endophytes did not show macroscopically visible disease symptoms. Mere presence of endophytes in any part of the host does not seem to be sufficient for disease symptoms to develop, and both endophyte density and distribution in the host may be important. Also, a lag phase between infection and appearance of a pathological disorder is usual in infectious diseases and has been reported by Peters & Schaffelke (1996) for the endophyte *Gononema aecidioides* in *L. saccharina* in the Western Baltic. However, we do not rule out the possibility that some of the pathogenic disorders observed were caused by other agents or by endophytes in combination with other factors. Schaffelke et al. (1996) found in a field experiment that UV light enhanced the severity of endophyte disease in *L. saccharina*, and Craigie & Correa (1996) demonstrated that complex interactions among biotic and abiotic factors were responsible for outbreak of diseases in commercial cultures of the red alga *Chondrus crispus* Stackhouse. In any case, previous epidemiological studies recording only the proportion of individuals with visible thallus alterations (Andrews 1977, Lein et al. 1991) probably underestimated the occurrence of endophytes.

The majority of endophytes isolated were filamentous brown algae, endophytic species belonging to other algal classes were rarely obtained, much in contrast to the red algal hosts *Chondrus crispus* and *Mazzaella laminarioides* in which green algae are very frequent endophytes (Correa et al. 1988, 1994). In our study, the most common endophyte, which preferred *Laminaria saccharina* as host but was also present at lower frequency in *Laminaria digitata*, was *Laminarionema elsbetiae* recently described from Japan (Kawai & Tokuyama 1995) and Helgoland (Peters & Ellertsdóttir 1996). In Japan *L. elsbetiae* occurs in *Laminaria japonica* Areschoug (Kawai & Tokuyama 1995). *L. elsbetiae* was not observed at Helgoland until recently and it is not known if it was previously overlooked at Helgoland or is a new invader of the island. Another brown algal endophyte that was isolated is *Laminariocolax tomentosoides*. It is an endophytic and epiphytic species preferring *Laminaria digitata* as host on the Isle of Man (Russell 1964). Only from *L. hyperborea* did we frequently isolate an endophyte which was present in conspicuous dark spots on the lamina. The species is so far undescribed and is probably identical to *Streblonema* sp. found in dark spots of *L. hyperborea* in southern Norway (Lein et al. 1991). *Ectocarpus*, isolated from all hosts in the present study, was the principal component of the epiflora of *L. digitata* on the Isle of Man (Russell 1983).

Prevalence of endophytes was high all year round, but all species had a minimum in spring. Winter and spring are the seasons of maximum growth in the kelps examined (Parke 1947, Kain 1963, Lüning 1979). In late winter the kelps may shed endophytes together with old portions of the blade. Peters & Ellertsdóttir (1996) noticed that the endophyte *Laminarionema elsbetiae* is fertile in spring and is thus supposed to spread in the host population in that season. Peters & Schaffelke (1996) reported that juvenile *Laminaria saccharina* in the Western Baltic were highly infected by endophytes after 2 to 3 mo. The kelp endophytes studied here grow in the interstice between host cells; vertical transmission of the infection such as in viruses (Müller 1991) to the gametophyte and following sporophyte generation is not possible.

A higher prevalence of endophyte infection and more severe disease symptoms were present at the more wave-exposed site. Apparently, the much stronger turbulence at greater exposure does not inhibit infection of new hosts. More intense shedding of distal parts at more exposed sites (Sjøtun 1993) may produce blade fragments that carry fertile endophytes over larger distances. However, additional factors like density, distribution and performance of hosts may have differed between the sites chosen. These factors, which can play an important role in the spreading of infective agents (Burdon & Chilvers 1982, Clay 1990), were not determined in our study.

There was no significant difference in the infection prevalence between depths but disease symptoms were significantly stronger in shallow water. The same was observed in Western Baltic *Laminaria saccharina* (Schaffelke et al. 1996). The endophytes isolated in the present study are pigmented and autotrophic, as evident from their capacity to grow in unialgal culture. We hypothesize that stronger light favours growth and development of the endophytes. The lower end of the vertical distribution of the hosts may thus act as a spatial refuge from endophyte disease.

Most conspicuous were the differences observed between *Laminaria saccharina* and the other 2 hosts. The prevalence of endophytes in *L. saccharina* was higher than in *L. digitata* and *L. hyperborea*. *L. saccharina* was also more seriously affected by the endophyte disease. One quarter of infected thalli in *L. saccharina* were crippled, in contrast to the other species which had less than 5% severely deformed thalli. We do not know if the 3 categories of disease symptoms chosen for classification are successive stages of the infection by endophytes and if a high number of endophytes necessarily results in severe thallus deformations. We hypothesize that the preference of *Laminarionema elsbetiae* for *L. saccharina* and its frequent occurrence in the stipe contribute to the stronger effect of the disease in *L. saccharina*.

Acknowledgements. Collection and examination of field thalli were performed during research visits to the Biologische Anstalt Helgoland. We thank Günther Thadday for kindly providing laboratory space and equipment, Cornelia Buchholz for helpful advice and Udo Schilling, Rolf Karez and many other divers of the scientific diving group at Helgoland for collecting lower subtidal individuals. Thanks are due to Thorsten Reusch for his advice how to design sampling and analyse the data. Furthermore, many thanks to Sarah Poynton and the reviewers for helpful comments on the manuscript. Financial support by Deutsche Forschungsgemeinschaft (Projekte 346/6) is gratefully acknowledged.

LITERATURE CITED

Andrews JH (1976) The pathology of marine algae. Biol Rev Camb Philos Soc 51:211-253

Andrews JH (1977) Observations on the pathology of seaweeds in the Pacific Northwest. Can J Bot 55:1019-1027

Apt KE (1988a) Galls and tumor-like growth on marine macroalgae. Dis Aquat Org 3:211-217

Apt KE (1988b) Etiology and development of hyperplasia induced by *Streblonema* sp. (Phaeophyta) on members of the Laminariales (Phaeophyta). J Phycol 24:28-34

Burden JJ, Chilvers GA (1982) Host density as a factor in plant disease ecology. Annu Rev Phytopathol 20:143-166

Clay K (1990) The impact of parasitic and mutualistic fungi on competitive interactions among plants. In: Grace JB, Tilman D (eds) Perspectives on plant competition. Academic Press, London, p 391-412

Correa JA (1996) Diseases in seaweeds: an introduction. Hydrobiologia 326/327:87-88

Correa JA, Buschmann A, Retamales C, Beltrán J (1997) Infectious disease of *Mazzaella laminarioides* (Rhodophyta): changes in infection prevalence and disease expression associated with latitude, season and within-site location. J Phycol 33:in press

Correa JA, Flores V, Garrido J (1994) Green patch disease in *Iridaea laminarioides* (Rhodophyta) caused by *Endophyton* sp. (Chlorophyta). Dis Aquat Org 19:203-213

Correa JA, Nielsen R, Grund DW (1988) Endophytic algae of *Chondrus crispus* (Rhodophyta). II. *Acrochaete heteroclada* sp. nov., *A. operculata* sp. nov., and *Phaeophila dendroides* (Chlorophyta). J Phycol 24:528-539

Correa JA, Sánchez PA (1996) Ecological aspects of algal infectious diseases. Hydrobiologia 326/327:89-95

Craigie JS, Correa JA (1996) Etiology of infectious diseases in cultivated *Chondrus crispus* (Gigartinales, Rhodophyta). Hydrobiologia 326/327:97-104

Dangeard P (1931) Sur un *Ectocarpus* parasite provoquant des tumeurs chez le *Laminaria flexicaulis* (*Ectocarpus deformans* nov sp.). C R Acad Sci Paris 192:57-60

Ellertsdóttir E (1995) Endophytische Algen in den *Laminaria*-Arten von Helgoland. Diploma thesis, University of Kiel

Goff LJ (1982) The biology of parasitic red algae. Prog Phycol Res 1:289-369

Goff LJ, Moon DA, Nyvall P, Stache B, Mangin K, Zuccarello G (1996) The evolution of parasitism in red algae. molecular comparisons of adelphoparasites and their hosts. J Phycol 32:297-312

Goff LJ, Zuccarello G (1994) The evolution of parasitism in red algae: cellular interactions of adelphoparasites and their hosts. J Phycol 30:695-720

Kain JM (1963) Aspects of the biology of *Laminaria hyperborea*. II. Age, weight and length. J Mar Biol Ass UK 43: 129-151

Kawai H, Tokuyama M (1995) *Laminarionema elsbetiae* gen. et sp. nov. (Ectocarpales, Phaeophyceae), a new endophyte in *Laminaria* sporophytes. Phycol Res 43: 185-190

Kohlmeyer J (1968) Revision and descriptions of algicolous marine fungi. Phytopathol Z 63:341-362

Lein TE, Sjøtun K, Wakili S (1991) Mass-occurrence of a brown filamentous endophyte in the lamina of the kelp *Laminaria hyperborea* (Gunnerus) Foslie along the southwestern coast of Norway. Sarsia 76:187-193

Lüning K (1970) Tauchuntersuchungen zur Vertikalverteilung der sublitoralen Helgoländer Algenvegetation. Helgoländer Wiss Meeresunters 21:271-291

Lüning K (1979) Growth strategies of three *Laminaria* species (Phaeophyceae) inhabiting different depth zones in the sublittoral region of Helgoland (North Sea). Mar Ecol Prog Ser 1:195-207

Müller DG (1991) Mendelian segregation of a virus genome during host meiosis in the marine brown alga *Ectocarpus siliculosus*. J Plant Physiol 137:739-743

Parke M (1947) Studies on British Laminariaceae. I. Growth in *Laminaria saccharina* (L.) Lamour. J Mar Biol Ass UK 17: 652-707

Perez R, Kaas R, Campello F, Arbault S, Barbaroux O (1992) La culture des algues marines dans le monde. IFREMER, Plouzané

Peters AF (1991) Field and culture studies of *Streblonema macrocystis* sp. nov. (Ectocarpales, Phaeophyceae) from Chile, a sexual endophyte of giant kelp. Phycologia 30: 365-377

Peters AF, Ellertsdóttir E (1996) New record of the kelp endophyte *Laminarionema elsbetiae* (Phaeophyceae, Ectocarpales) at Helgoland and its life history in culture. Nova Hedwigia 62:341-349

Peters AF, Schaffelke B (1996) *Streblonema* (Ectocarpales, Phaeophyceae) infection in the kelp *Laminaria saccharina* (Laminariales, Phaeophyceae) in the western Baltic. Hydrobiologia 326/327:111-116

Russell G (1964) *Laminariocolax tomentosoides* on the Isle of Man. J Mar Biol Ass UK 44:601-612

Russell G (1983) Formation of an ectocarpoid epiflora on blades of *Laminaria digitata*. Mar Ecol Prog Ser 11:181-187

Sachs I (1978) Angewandte Statistik. Statistische Methoden und ihre Anwendungen, 5th edn. Springer, Berlin

Sánchez P, Correa JA, García-Reina G (1996) Host-specificity of *Endophyton ramosum* (Chlorophyta), the causative agent of the green patch disease in *Mazzaella laminarioides* (Rhodophyta). Eur J Phycol 31:173-179

Schaffelke B, Peters AF, Reusch T (1996) Factors influencing depth distribution of soft bottom *Laminaria saccharina* (L.) Lamour in Kiel Fjord, Baltic Sea. Hydrobiologia 326/327: 117-123

Schatz S (1984) The *Laminaria-Phycomelaina* host-parasite association: seasonal patterns of infection, growth and carbon and nitrogen storage in the host. Helgol Meeresunters 37:623–631

Schultze K, Krüß KJA, Weidemann W (1990) The macrofauna and macroflora associated with *Laminaria digitata* and *L. hyperborea* at the island Helgoland (German Bight, North Sea). Helgol Meeresunters 44:39–51

Setchell WA, Gardner NL (1925) The marine algae of the Pacific coast of North America. III. Melanophyceae. Univ Calif Publ Bot 8:383–898

Sjøtun K (1993) Seasonal lamina growth in two age groups of *Laminaria saccharina* (L.) Lamour. in western Norway. Bot Mar 36:433–441

Wu CY, Chen D, Li J (1983) On the diseases of cultivated *Laminaria japonica*. In: Tseng CK (ed) Proceedings of the joint China-U.S. Phycology Symposium. Science Press, Beijing, p 211–220

Yoshida T, Akiyama K (1979) *Streblonema* (Phaeophyceae) infection in the frond of cultivated *Undaria* (Phaeophyceae). Proc 9th Intl Seaweed Symp, Santa Barbara, CA, p 219–223

This article was submitted to the editor

Manuscript first received: July 26, 1996
Revised version accepted: December 11, 1996