

# Effect of epiphytism on reproductive and vegetative lateral formation in the brown, intertidal seaweed *Ascophyllum nodosum* (Phaeophyceae)

Alexandra C. Kraberg\*† and Trevor A. Norton

Port Erin Marine Laboratory, University of Liverpool, Port Erin Isle of Man, British Isles IM9 6JA, UK

## SUMMARY

In the brown alga *Ascophyllum nodosum* (L) Le Jolis, a common species on sheltered Northern temperate rocky shores, gametes are produced in receptacles that emerge from small depressions (lateral pits) along the branched frond. These lateral pits are also the preferred settling site for the obligate epiphyte *Polysiphonia lanosa* (L) Tandy. Therefore, epiphytism can be expected to interfere with host reproductive output. The present study investigated the potential impact of the epiphyte on *A. nodosum* in two series of laboratory experiments that measured: (i) the direct shading of the host plant underneath an epiphyte canopy; and (ii) the development of receptacles in clean and epiphytised *A. nodosum* segments (excised from individual fronds) over a 6 month period. These experiments showed that light reaching emerged fronds underneath a dense epiphyte cover was reduced by 40%, and this was independent of the degree of desiccation the epiphyte experienced. Concurrently, in the growth study with epiphytised *A. nodosum* segments (segments with one clean and one epiphytised lateral pit) total receptacle biomass per epiphytised fragment was significantly reduced compared with clean segments (0.52 g and 1.25 g per gram of frond segment, respectively), although this effect was only significant in *A. nodosum* from sheltered shores. However, expressed as biomass per lateral pit, receptacle biomass in the remaining clean lateral pits in epiphytised segments was significantly increased in segments from both shores, demonstrating that *A. nodosum* can at least partially compensate for the loss of production resulting from epiphytism.

Key words: *Ascophyllum nodosum*, epiphytism, lateral growth, morphogenesis, reproduction, shading.

## INTRODUCTION

*Ascophyllum nodosum* (L) Le Jolis is a common intertidal brown seaweed in temperate latitudes that repro-

duces both sexually and vegetatively from small shoots at the base of a holdfast. The latter can survive and produce new shoots for decades. The shoots arising from the holdfast are initially unbranched but then develop laterals that produce reproductive structures (receptacles) from small depressions (hereafter called lateral pits, see Fig. 1) along the lateral branches (Baardseth 1970). The receptacles are initiated in the lateral pits approximately between May and July. Initially, all laterals generated in these pits are vegetative, but throughout the autumn and winter many of them become reproductive and gametes are released in the following spring. *Polysiphonia lanosa* (L) Tandy also frequently establishes as an epiphyte in the lateral pits of *A. nodosum* (Lobban & Baxter 1983). Newly settled epiphytes penetrate these pits and the underlying host tissue by means of a rhizoid, which can physically block these pits (Rawlence & Taylor 1972; Turner & Evans 1977) and prevent the emergence of lateral branches or receptacles.

An additional adverse effect of epiphytism can be direct shading of the host plant. Terry and Moss (1980) demonstrated that a reduction in overall irradiance could result in reduced lateral production and similar observations have been made in a related seaweed, *Fucus distichus* L. (Bird & McLachlan 1976). In addition, it has been suggested by several authors (e.g. Russell 1973; Mathieson *et al.* 1976) that the onset of reproduction might be triggered by photoperiod. This was again confirmed by Terry and Moss (1980), who established that short day photoperiods favour the production of reproductive over vegetative laterals in *A. nodosum*. Similar photoperiodic effects are also described by Uchida (1993) in *Sargassum horneri* (Turner) C. Agardh.

\* To whom correspondence should be addressed.

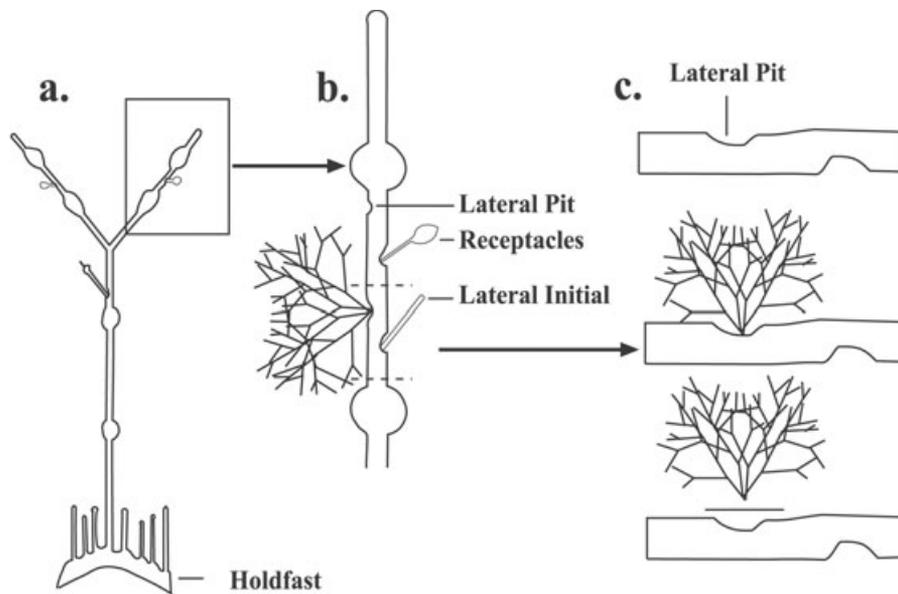
Email: akraberg@awi-bremerhaven.de

Communicating editor: K. Kogame.

† Present address: Alfred-Wegener Institute for Polar and Marine Research, Biological Station Helgoland, Kurpromenade 201, 27489 Helgoland, Germany.

Received 22 June 2005; accepted 15 May 2006.

doi: 10.1111/j.1440-1835.2006.00441.x



**Fig. 1.** Schematic drawing of an *Ascophyllum nodosum* frond showing the morphological features referred to in the text and indicating the areas of frond used in the experiments: (a) generalized *A. nodosum* frond; (b) detail of distal part of frond showing the area from which segments were excised (dotted lines); (c) three frond segment types used in the experiments.

The filamentous epiphyte *P. lanosa* is usually very patchily distributed on the fronds of *Ascophyllum*, but host plants bearing high epiphyte loads can be almost completely smothered (Lobban & Baxter 1983), resulting in a considerable reduction in irradiance reaching the host plant's frond surface (Sand-Jensen & Borum 1984; Sand-Jensen *et al.* 1985; Figueiredo *et al.* 2000). *A. nodosum* frequently occurs in very dense stands on sheltered shores and it is likely that plants on the surface of the canopy shade those beneath (Cousens 1985; Robertson 1987; Schroeter *et al.* 1995; Stengel & Dring 1998). Although the self-shading effects in *A. nodosum* have previously been studied, shading effects by the epiphyte have not yet been quantified.

One way to test a possible shading effect of the epiphyte on receptacle production and growth, is to conduct experiments involving the removal of the epiphyte from lateral pits, which should, if shading was an important factor, lead to a higher production of laterals and/or greater extension growth. This factor, if large enough, could exert significant costs on the host plant in terms of lost reproductive effort. The magnitude of each factor might also be expected to vary in populations on shores of different exposures, as it is known that plants on exposed shores often have a greater reproductive output with increasing exposure, but also carry higher epiphyte loads (Cousens 1982, 1985; Lobban & Baxter 1983). Therefore, the aim of the present paper is to investigate the relationship between infestation by the epiphyte *P. lanosa* and production of reproductive laterals by the host and to establish whether a reduction in irradiance or 'competition' for lateral pits or a combination of both have the potential to significantly decrease host reproduction.

## MATERIALS AND METHODS

### Sample collection

All experiments were carried out using plant material, collected on a sheltered shore on Fort Island (54°05'N, 4°37'W) or an exposed shore at Scarlett (54°04'N, 4°39'W), Isle of Man, British Isles. These shores will hereafter be referred to as sheltered and exposed shores, respectively. Samples were collected from the lower limit of the distribution of *A. nodosum*, where the highest epiphyte loads occurred. All plants were different genetic individuals and were sexually mature plants at least 1 m in length (Cousens 1985).

### Reproductive effort of *Ascophyllum nodosum* in the presence of *Polysiphonia lanosa*

The present study was carried out in April 2000 during the peak reproductive period of *A. nodosum*. Forty fronds carrying varying epiphyte loads were chosen. They were transported back to the laboratory in buckets of seawater to prevent drying and consequent gamete release and were stored at a constant temperature of 10°C until further processing. All receptacles and epiphyte clumps were removed from the fronds and their wet weight was measured after repeatedly blotting them between paper towelling until no more moisture appeared on the paper. Dry weights were obtained by drying tissues in an oven at 60°C until constant weight. Total reproductive effort was calculated as the receptacle weight as a proportion of total tissue biomass per frond (Mathieson & Guo 1992; Åberg 1996).

## Measurement of light levels underneath a dense canopy of *Polysiphonia lanosa*

Individual clumps of *P. lanosa* were excised from the host plant. They were attached in a straight line to a transparent Perspex sheet to create an experimental 'frond'. Clumps were attached by passing their bases through small holes bored into the Perspex sheet. A ruler was then attached to the edge of the sheet so that measurements with a light meter could be made at precise intervals. The experiment was carried out using three *Polysiphonia* clumps spaced 40 mm apart. The clumps were large enough for adjacent clumps to lightly touch. Measurements were made from 40 mm in front of the first epiphyte clump to 40 mm beyond the third clump, giving the experimental frond a total length of 160 mm.

A white fluorescent tube (Philips 58 W/35) was placed 500 mm above the clumps, providing the same irradiance all along the experimental frond. The irradiance was measured in air using a LI-250 light meter (LI-COR), with the probe facing upwards, through the canopy, from approximately 10 mm below the Perspex sheet. To obtain light measurements the probe was passed along the three clumps at a rate of approximately 10 mm per second. During this time 15 readings were obtained. The measurements were repeated five times and were made in the absence of the epiphyte (control) and at 5 degrees of desiccation: 1, 2, 4, 6 and 8 h.

## Growth of laterals from epiphytised and clean *Ascophyllum nodosum* segments

The present study was run in the laboratory between June and December 2000, using segments of *A. nodosum* that had been excised from the second youngest internode of a frond. The fronds were collected in June, the key period for lateral initiation, so that effects of epiphyte removal on lateral growth could be investigated. Three treatments were set up: segments with two clean lateral pits, segments with one clean and one epiphytised pit and segments with one clean pit and one pit from which the epiphyte had been removed (Fig. 1c).

Each treatment was applied to excised frond segments from an exposed shore and a sheltered shore (i.e. six treatments in total). A total of 30 segments were excised for each treatment, resulting in a total of 180 segments. The number of replicates in the sheltered treatment, from which epiphytes had been removed, only contained 4 groups, due to mortality of segments in one container within the first month of the experiment. As lateral development had already started in the other replicates, these segments were not replaced.

Each excised segment had two lateral pits. Segments from epiphytised fronds were chosen so that one lateral pit was epiphytised, whereas the other was completely clean and bore lateral initials. The segments were usually 10 mm in length. However, as epiphytised fronds often had a wider diameter than clean ones, smaller segments were sometimes excised for the epiphyte treatments to gain segments of comparable size between treatments. Prior to carrying out experiments, all segments were examined under a binocular microscope to ensure that clean looking lateral pits were actually un-epiphytised and that no *Polysiphonia* germ-lings were present. In epiphytised segments, *P. lanosa* clumps were also cleaned of contaminating green algae and small grazers. For each treatment, five 0.5 L plastic containers, each containing six segments, were set up. Prior to the start of the experiment the initial length and number of lateral initials per lateral pit were recorded for each of the segments.

Following the culture and lighting conditions of Terry and Moss (1980), frond segments were maintained in a culture cabinet in filtered seawater without nutrient supplements at 10°C and a short day 8:16 h photoperiod under white light (Philips 58 W/35 white fluorescent tubes, approximately 40  $\mu\text{mol}/\text{m}^2/\text{s}$ ). Tanks were rotated periodically within the culture cabinet to compensate for possible variations in irradiance. At the end of the study the dry weights of vegetative and receptacle tissue were determined for each segment.

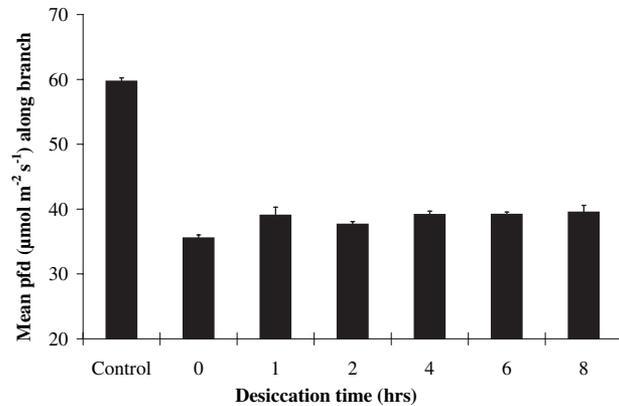
## Statistical analysis

Differences in lateral length and weight per lateral pit among and within treatments were analyzed using either nested or repeated measures analysis of variance (ANOVA) procedures on the basis of the general linear model (GLM) using the GLM module in Statistica version 6 (StatSoft, Tulsa, USA). This model allows analyses not only of multiple predictor variables but also different types of variables (e.g. categorical and continuous variables). Prior to each analysis data were tested for homogeneity of variance using Cochran's *C*-test. Where variances were heterogeneous, data were log transformed (Underwood 1981) or, in the case of percentage data, arcsin transformed. Following the ANOVA, a Student–Newman Keuls (SNK) procedure was carried out, where appropriate, to further examine differences between treatments.

## RESULTS

### Measurement of light levels underneath a dense canopy of *Polysiphonia lanosa*

The light measurements in the laboratory caused a 40% reduction in the photon flux density under a dense



**Fig. 2.** Light penetration through a canopy of *Polysiphonia lanosa* at varying degrees of desiccation of the epiphyte,  $n = 5$ , error bars  $\pm 1$  standard error.

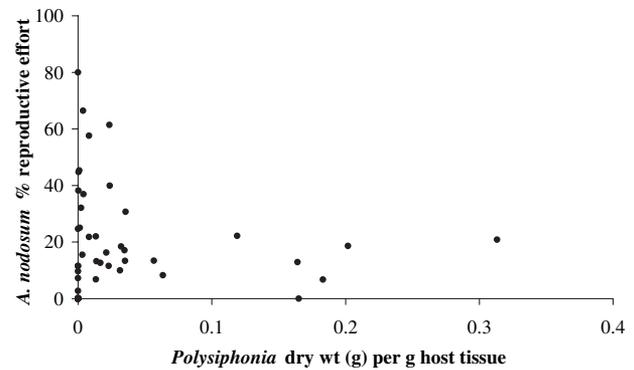
cover of *P. lanosa* compared with control measurements. Desiccation only caused very slight changes in light penetration; that is, the maximum degree of shading was reached soon after exposure and is likely to remain at this level until re-immersion (Fig. 2). These findings were confirmed by a one-way repeated measures ANOVA and post hoc test ( $P < 0.0001$ , SNK procedure: control  $>$  0–8 h and 2 h = 4 h = 6 h = 8 h).

### Reproductive effort of *Ascophyllum nodosum* in the presence of *Polysiphonia lanosa*

A linear regression analysis carried out on the transformed data from epiphytised and clean fronds of *A. nodosum* from Fort Island revealed a statistically significant negative linear relationship between the dry weight of *P. lanosa* per gram of vegetative tissue of the host plant and the reproductive effort of *A. nodosum* fronds ( $F_{1,38} = 5.617$ ,  $P = 0.023$ ,  $y = -0.36x - 3.494$ , transformed data not presented graphically). The untransformed data showed that for clean fronds or those with very low epiphyte loads the reproductive efforts ranged from between 10 and 68% but reproductive effort was generally low at epiphyte loads of above 0.05 g epiphyte tissue per gram of *A. nodosum* tissue (Fig. 3).

### Morphological differences between clean and epiphytised segments

Within each site, the width of the fronds and the starting numbers of lateral initials per lateral pit were significantly higher in epiphytised than in clean fronds (sheltered site:  $F_{2,124} = 12.534$ ,  $P < 0.0001$ ; exposed site:  $F_{2,194} = 19.159$ ,  $P = 0.0001$ ). This is a possible confounding factor but one that could not be avoided. However, because no analyses were planned for the



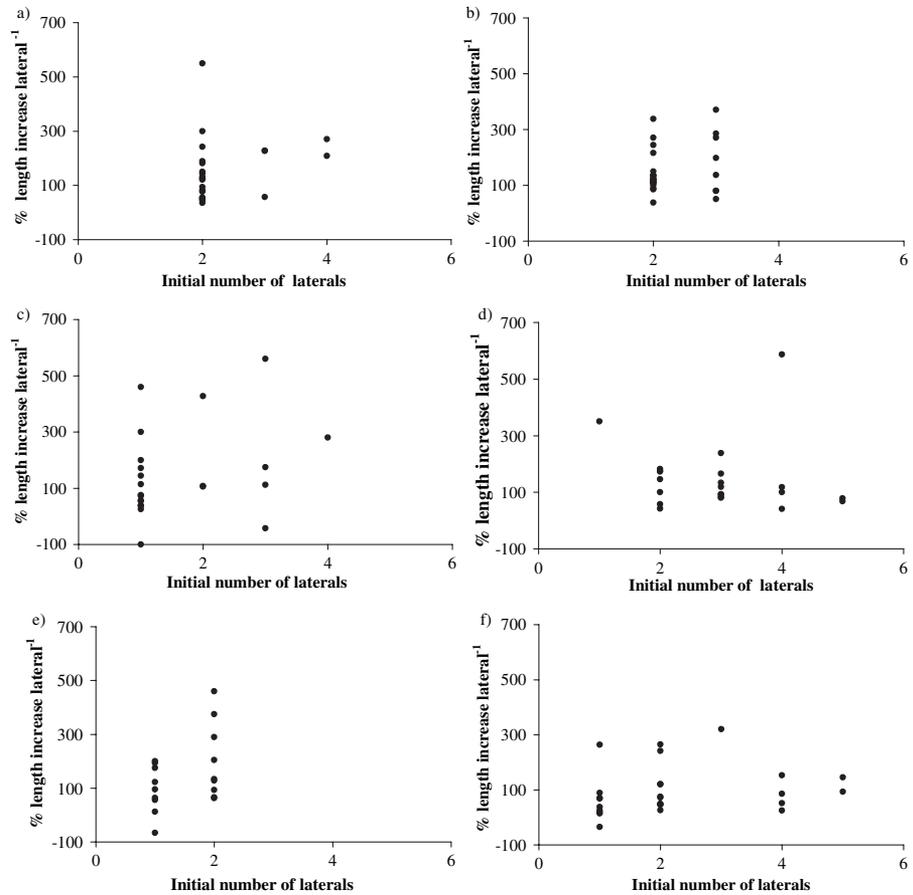
**Fig. 3.** The relationship between reproductive effort of fronds of *A. nodosum* (g dry weight receptacle mass per total frond biomass) and their epiphyte load (g dry weight per gram host tissue). Data shown are not transformed,  $n = 40$ .

growth of new laterals from lateral pits but solely for the development of existing lateral initials, this was deemed to be tolerable. Despite the initial differences in lateral numbers per lateral pit, no significant differences occurred between initial number of lateral initials and average growth in length of individual laterals in any of the treatments over the course of the experiment (Fig. 4). Therefore, differences in initial lateral numbers per lateral pit between treatments were assumed not to interfere with the analysis of length growth and, most importantly, lateral differentiation into vegetative and reproductive laterals, which was the main focus of the study (Fig. 4).

### Lateral branch differentiation on clean lateral pits

The development of receptacles, judged from the thickening of the tip of laterals in the lateral pits and formation of conceptacles, began within a month of the start of the experiment. In all treatments a small proportion of the laterals emerging from lateral pits remained vegetative during the course of the study. The proportion of these laterals appeared higher in the segments from the exposed than the sheltered site, irrespective of whether the segments were epiphytised or not (Table 1). Within the samples from the exposed shore, clean segments produced the highest proportion of vegetative laterals (18.87%). In the treatments with plants from the sheltered shore, the highest proportion of vegetative laterals occurred in epiphytised plants (12.5%). The length of receptacles on segments from both sites had also increased considerably by the end of the study. In both sites the length of laterals at the end of the experiment was slightly higher in clean than in epiphytised plants (Fig. 5a,b). However, the ANOVA showed that this difference was only significant for segments from the sheltered site (sheltered site:

**Fig. 4.** The relationship between initial numbers of laterals and average length increase per lateral. (a,b) clean segments, (c,d) epiphytised segments, (e,f) segments from which epiphytes had been removed (a, c and e = sheltered shore; b, d and f = exposed shore).



**Table 1.** Development of receptacles and vegetative laterals in segments from the sheltered site at Fort Island and the exposed site at Scarlett Point

Treatment	No of initial lateral buds		% vegetative shoots of total at end of study	% epiphytised lateral pits with lateral formation
	Initial	Final		
Sheltered clean	69	67	10.45	0
Sheltered + epi	40	40	12.5	5
Sheltered ex epi	28	28	3.45	7.14
Exposed clean	68	69	18.87	0
Exposed + epi	68	69	14.49	0
Exposed ex epi	63	64	10.94	0

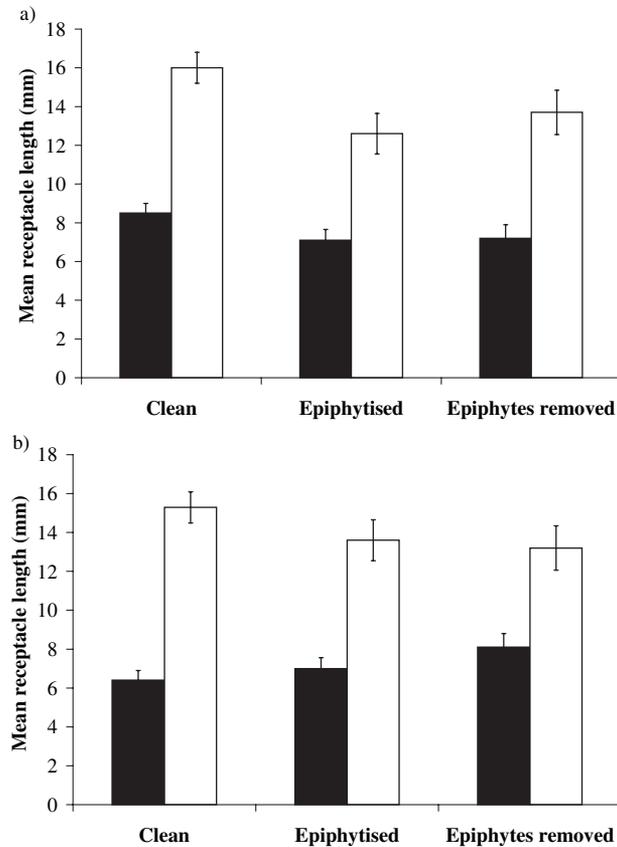
For both sites 'clean' refers to unepiphytised segments, '+epi' to epiphytised segments and 'ex epi' to segments from which epiphytes had been removed.

$F_{2,122} = 3.671$ ,  $P = 0.028$ ; exposed site:  $F_{2,162} = 1.256$ ,  $P = 0.288$ ).

### Receptacle dry weights in clean and epiphytised segments

Receptacle biomass expressed as g dry weight per g of host tissue showed that in both sites clean segments carried a significantly higher receptacle mass than epiphytised segments (sheltered shore:  $F_{2,49} = 25.061$ ,  $P = 0.0001$ , exposed shore:  $F_{2,55} = 5.399$ ,  $P = 0.007$  see also Fig. 6). This effect was slightly more pro-

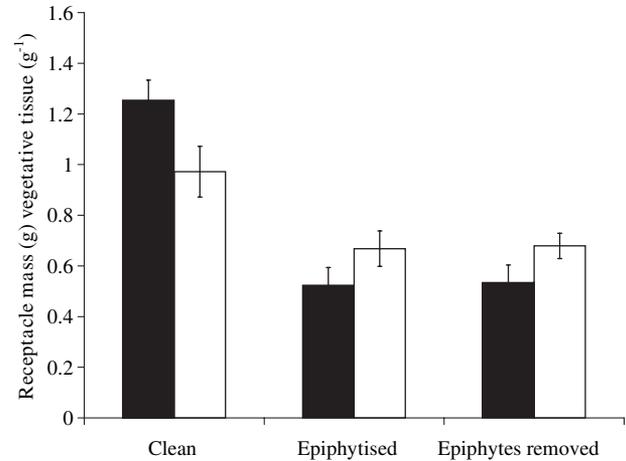
nounced in plant segments from the sheltered than the exposed shore. However, expressed as receptacle dry mass per lateral pit, dry weights in epiphytised plants with only one lateral pit available for receptacle production were significantly higher than in clean fronds. Differences between treatments were again significant for both exposures. In addition, receptacle dry weight per lateral pit was also significantly higher in segments with one epiphytised lateral pit than in segments from which epiphytes had been removed (sheltered shore:  $F_{2,50} = 4.65$ ,  $P = 0.014$ , exposed shore:  $F_{2,60} = 27.005$ ,  $P < 0.0001$ ; also see Fig. 7).



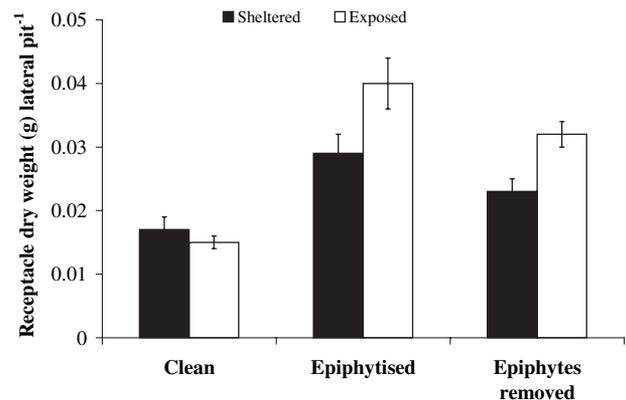
**Fig. 5.** The mean length of laterals on clean lateral pits in the three types of *Ascophyllum nodosum* segments from (a) Sheltered site and (b) Exposed site in June (solid bars) and December (open bars).  $n = 30$  ( $n = 24$  for segments from sheltered site with epiphytes removed), error bars are  $\pm 1$  standard error.

## DISCUSSION

In the present study, shading was investigated as one possible factor by which the epiphyte *P. lanosa* can adversely affect reproduction in its host plant, *A. nodosum*. Several authors report effects of reduced irradiance and changed photoperiods on growth and in some cases morphogenesis in different aquatic plants, but these studies do not specifically mention effects on sexual reproduction (Critchley 1983; Moore & Wetzel 2000). Fitzpatrick and Kirkman (1995), for instance, describe a decrease in the shoot numbers and leaf growth rates in the sea grass *Posidonia australis* Hooker 1858. Hwang and Dring (2002) reveal an effect of photoperiod on frond development in *Sargassum muticum* (Yendo) Fensholt, whereas Cousens (1985) demonstrate that the longer, older fronds on top of an *A. nodosum* canopy make the greatest contribution to the reproductive output. Significantly, it is also these fronds that normally carry the highest epiphyte loads. In such fronds host reproduction is, therefore, likely to be considerably impaired.



**Fig. 6.** Dry weight of receptacle tissue (g) in each treatment, expressed per gram of vegetative tissue: closed bars = sheltered site, open bars = exposed site;  $n = 30$  ( $n = 24$  for segments from sheltered site with epiphytes removed), error bars are  $\pm 1$  standard error.



**Fig. 7.** Total receptacle dry weight per lateral pit in clean and epiphytised segments in December 2000: closed bars = sheltered site, open bars = exposed site;  $n = 30$  (24 for segments from sheltered site with epiphytes removed). Error bars are  $\pm 1$  standard error.

Substantial decreases in total irradiance reaching the surface of the host plant could also be demonstrated in the present study. However, this does not necessarily mean that shading was the main determinant of the decrease in reproduction found in heavily epiphytised fronds on the shore. Importantly, there was no significant difference in the extension growth of laterals between epiphytised segments and those from which epiphytes had been removed, indicating that the presence of the epiphyte did not exert a negative influence on the development of existing lateral initials.

One possible reason for the apparent absence of any adverse impact of the epiphyte on the growth and

development in the lateral pits adjacent to the epiphytised ones is that the laterals, once initiated, are fully photosynthetic and, therefore, are able to fix their own carbon from a very early stage, without being reliant on neighboring host tissues. The only difference between treatments was a generally higher proportion of laterals remaining vegetative in plant segments from the exposed shore compared to the sheltered shore. Such a pattern does not indicate an effect of the epiphyte as such but might point towards a generally different survival strategy of *A. nodosum* on shores of different exposure. It is consistent with observations by previous authors that the proportion of laterals becoming reproductive increases with decreasing exposure in *A. nodosum* (Cousens 1986).

It might be argued that removal of the epiphytes could not have led to production of new laterals, because the number of laterals per lateral pits had already been determined prior to the start of the experiment (i.e. the resources had already been allocated) (Geber *et al.* 1997; Watson *et al.* 1997). This would be a fruitful subject for further investigation. It has in the past been difficult to carry out such experiments with large modular seaweeds, although segments of smaller algae have been cultured (Komatsu *et al.* 1997). The present study has not only confirmed the results by Terry and Moss (1980), but has also shown that it is possible to maintain the epiphyte in a healthy state for a comparable period of time together with the host plant. Therefore, studies with such small segments are a viable option for carrying out laboratory studies on large modular seaweeds not normally amenable to laboratory culture.

Taking into account the above results it appears likely that it is not an indirect irradiance effect that reduces current reproduction, but the physical blockage or even destruction of epiphytised lateral pits (rather than adverse effects on neighboring pits) that is the main factor reducing the reproductive effort of *A. nodosum*. According to Rawlence and Taylor (1972) the host tissue surrounding the penetrating rhizoid of *P. lanosa* degenerates and in some cases completely disappears. If the tissue destroyed by the penetrating rhizoid includes the meristematic region of the lateral pits (Moss 1970), they are likely to permanently lose the ability to produce laterals and, therefore, reproductive bodies. This could explain why on the shore the most severely epiphytised plants often do not consist of more than the epiphytised main axis and one or two laterals.

Perhaps most importantly however, although epiphytised lateral pits do not produce any lateral branches themselves, either vegetative or reproductive, clean lateral pits on the same epiphytised internodes produce more receptacles per pit than lateral pits on completely clean internodes. This is inconsistent with adverse

effects of shading on the number or length of apical shoots and lateral branches described in earlier studies, and shows that *A. nodosum* seems to be able to compensate to some extent for the loss of lateral pits by increasing production of receptacles from those remaining.

That *A. nodosum* is able to increase production of receptacle biomass from clean lateral pits when adjacent pits are blocked, indicates that the cost of epiphytism in terms of lost reproductive output in the host might be considerably lower than estimates from the mere presence of *P. lanosa* would indicate. However, because receptacles and vegetative laterals are produced from the same lateral pits, blockage of these pits means inhibition of lateral production in general. This would, therefore, not only affect current but also future reproduction as further sites for the production of laterals become reduced and also by preventing the growth of vegetative laterals, which would produce new lateral pits. Such a cost assessment would depend on the actual incidence of *P. lanosa* in a given *A. nodosum* population. The shape of the curve in Figure 2, shows clearly that beyond a certain threshold epiphyte load, reproductive effort would be permanently low. Therefore, although *A. nodosum* might be able to tolerate low to medium epiphyte loads, reproductive inhibition is likely to occur at high incidences of *P. lanosa*. On exposed shores epiphyte loads are often higher and host biomass lower than on sheltered shores (Cousens 1985) and it might be in these populations that the effect of the epiphyte on host reproduction will be most pronounced.

## ACKNOWLEDGMENTS

The authors would like to thank the technicians of the Port Erin Marine Laboratory who provided support during various parts of the project, particularly in maintaining the culture facility.

## REFERENCES

- Åberg, P. 1996. Patterns of reproductive effort in the brown alga *Ascophyllum nodosum*. *Mar. Ecol. Prog. Ser.* **138**: 199–297.
- Baardseth, E. 1970. Synopsis on biological data on knobbed wrack, *Ascophyllum nodosum* (Linnaeus) Le Jolis. *FAO Fish. Synop.* **38**: (Rev. 1), 41 pp.
- Bird, N. L. and McLachlan, J. 1976. Control of formation of receptacles in *Fucus distichus* L. subsp. *distichus* (Phaeophyceae, Fucales). *Phycologia* **15**: 79–84.
- Cousens, R. 1982. The effect of exposure to wave action on the morphology and pigmentation of *Ascophyllum nodosum* (L.) Le Jolis in South-Eastern Canada. *Bot. Mar.* **25**: 191–195.

- Cousens, R. 1985. Frond size distributions and the effect of the algal canopy on the behaviour of *Ascophyllum nodosum*. *J. Exp. Mar. Biol. Ecol.* **92**: 231–49.
- Cousens, R. 1986. Quantitative reproduction and reproductive effort by stands of the brown alga *Ascophyllum nodosum*. *Estuar. Coast. Shelf Sci.* **22**: 495–507.
- Critchley, A. T. 1983. Experimental observations on variability of leaf and air vesicle shape of *Sargassum muticum*. *J. Mar. Biol. Assoc. UK* **63**: 825–31.
- Figueiredo, M. A. De O., Kain, J. M. and Norton, T. A. 2000. Responses of crustose corallines to epiphyte and canopy cover. *J. Phycol.* **36**: 17–24.
- Fitzpatrick, J. and Kirkman, H. 1995. Effects of prolonged shading stress on growth and survival of the seagrass *Posidonia australis* in Jervis Bay, New South Wales. *Mar. Ecol. Prog. Ser.* **127**: 279–89.
- Geber, M. A., Watson, M. A. and de Kroon, H. 1997. Development and resource allocation in perennial plants. The significance of organ preformation. In Bazzaz, F. A. and Grace, J. (Eds) *Plant Resource Allocation*. Academic Press, London, pp. 113–41.
- Hwang, E. K. and Dring, M. J. 2002. Quantitative photoperiodic control of erect thallus production in *Sargassum muticum*. *Bot. Mar.* **45**: 471–475.
- Komatsu, T., Meinesz, A. and Buckles, D. 1997. Temperature and light responses of the alga *Caulerpa taxifolia* introduced into the Mediterranean Sea. *Mar. Ecol. Prog. Ser.* **146**: 145–53.
- Lobban, C. S. and Baxter, D. M. 1983. Distribution of the red algal epiphyte *Polysiphonia lanosa* on its algal host *Ascophyllum nodosum* in the Bay of Fundy, Canada. *Bot. Mar.* **26**: 533–538.
- Mathieson, A. C. and Guo, Z. 1992. Patterns of furoid reproductive biomass allocation. *Brit. Phycol. J.* **27**: 271–92.
- Mathieson, A. C., Shipman, J. W., O'Shea, J. R. and Hasevlat, R. C. 1976. Seasonal growth and reproduction of estuarine furoid algae in New England. *J. Exp. Mar. Biol. Ecol.* **25**: 273–84.
- Moore, K. A. and Wetzel, R. L. 2000. Seasonal variations in eel grass (*Zostera marina* L.) responses to nutrient enrichment and reduced light availability in experimental ecosystems. *J. Exp. Mar. Biol. Ecol.* **244**: 1–28.
- Moss, B. 1970. Meristem and growth control in *Ascophyllum nodosum* (L.) Le Jol. *New Phytol.* **69**: 253–60.
- Rawlence, D. J. and Taylor, A. R. A. 1972. A light and electron microscopic study of the rhizoid development in *Polysiphonia lanosa* (L.) Tandy. *J. Phycol.* **8**: 15–24.
- Robertson, B. L. 1987. Reproductive ecology and canopy structure of *Fucus spiralis* L. *Bot. Mar.* **30**: 475–482.
- Russell, G. 1973. The Phaeophyta: a synopsis of some recent developments. *Oceanogr. Mar. Biol. Ann. Rev.* **11**: 45–88.
- Sand-Jensen, K. and Borum, J. 1984. Epiphyte shading and its effect on photosynthesis and diel metabolism of *Lobelia dortmanna* L. during the spring bloom in a Danish Lake. *Aquat. Bot.* **20**: 109–19.
- Sand-Jensen, K., Revsbech, N. P. and Barker-Joergensen, B. 1985. Microprofiles of oxygen in epiphyte communities on submerged macrophytes. *Mar. Biol.* **89**: 55–62.
- Schroeter, S. C., Dean, T. A., Thies, K. and Dixon, J. D. 1995. Effects of shading by adults on the growth blade stage *Macrocystis pyrifera* (Phaeophyta) during and after the 1982–84 El Niño. *J. Phycol.* **31**: 697–702.
- Stengel, D. B. and Dring, M. J. 1998. Seasonal variation in the pigment content and photosynthesis of different thallus regions of *Ascophyllum nodosum* (Fucales, Phaeophyta) in relation to position in the canopy. *Phycologia* **37**: 259–68.
- Terry, L. A. and Moss, B. L. 1980. The effect of photoperiod on receptacle initiation in *Ascophyllum nodosum* (L.) Le Jol. *Brit. Phycol. J.* **15**: 291–301.
- Turner, C. H. C. and Evans, L. V. 1977. Physiological studies on the relationship between *Ascophyllum nodosum* and *Polysiphonia lanosa*. *New Phytol.* **79**: 363–71.
- Uchida, T. 1993. The life cycle of *Sargassum horneri* (Phaeophyta) in laboratory culture. *J. Phycol.* **29**: 231–5.
- Underwood, A. J. 1981. Techniques of analysis of variance in experimental marine biology and ecology. *Oceanogr. Mar. Biol. Annu. Rev.* **19**: 519, 605.
- Watson, M. A., Hay, M. J. M. and Newton, P. C. D. 1997. Developmental phenology and the timing of determination of meristem fates: evolved pathways that modulate the expression of fitness in clonal plants. In De Kroon, H. and Van Groenendael, J. (Eds) *Clonality in Plants*. Backhuys Academic Publications, Leiden, pp. 31–53.