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Seasonal growth and recruitment of *Himanthalia elongata* (Fucales, Phaeophycota) in different habitats on the Irish west coast

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Vegetative and reproductive growth of individually marked plants of the brown alga *Himanthalia elongata* was monitored over 2.5 years at two sites with different wave exposures on the Irish west coast. Macro-recruits were first visible to the unaided eye in February/March. About 65% of all buttons produced receptacles during autumn of the same year, whereas others remained sterile. Growth of receptacles started between late August and late November, when vegetative plants were 9–14 months old, but no further plants became reproductive after December. At both sites, length increase of receptacles was greatest between February and April, but only longitudinal growth occurred and no more new dichotomies were produced. At the more wave-exposed site, growth was fastest in plants growing in red algal turfs and slowest in plants on open rock. Growth rates were maximal when seawater temperatures were 10–12 °C in early spring but decreased from May onwards with the maturation of receptacles aged 7–9 months in June. Release of viable gametes started in June and continued throughout the autumn and winter, until all plants disappeared from the population in February. Plant density was highest in March after the appearance of macro-recruits in the population, and declined during summer when the number of buttons decreased. Percentage plant cover was highest in June immediately before the onset of gamete release and this was followed by the decay and disintegration of receptacles. Since both survival and growth of young buttons was highest in red algal turfs and lowest on exposed rocks, the distribution of *H. elongata* on semi-exposed shores in Ireland may be limited by the availability of suitable micro-habitats for recruitment, and reduced by the early loss of fertile, adult plants from exposed sites.

Key words: biennial life-history, distribution, Fucales, *Himanthalia elongata*, *in situ* growth, micro-habitat, recruitment, seasonality, wave exposure.

Introduction

In most members of the order Fucales (Phaeophycota), the proportion of reproductive to vegetative biomass ranges between 10% and 50% (Brenchley *et al.*, 1996), and is typically in the range of 20–30% (Cousens, 1986; Bäck *et al.*, 1991). By contrast, the only extant representative of the fuclean family Himanthaliaceae, *Himanthalia elongata* (L.) S. F. Gray, has a unique life-cycle and growth strategy, with up to 98% of the total biomass invested in reproductive rather than vegetative tissue (Brenchley *et al.*, 1996). Whereas in other Fucales energy resources for the reproductive tissue are at least partially supplied by the vegetative thallus, receptacles of *H. elongata* are mostly self-supportive in their carbon assimilation and nutrient uptake (Brenchley *et al.*, 1996, 1997). The mature vegetative thalli of *H. elongata* are peltate ('buttons'), about 2–3 cm in height, and typically produce two thong-like receptacles in the autumn, although one, three and

four thongs per button have occasionally been observed (Gibb, 1937). Unlike other members of the Fucales, *H. elongata* is not a perennial plant, and investigations of the size and age structure of populations in the Irish Sea by Gibb (1937) and, more recently, by Russell (1990) suggested a biennial life-cycle, although some plants grew vegetatively for 2 years before becoming reproductive in their third year (Russell, 1990).

In most Fucales, such as *Fucus* spp. and *Ascophyllum nodosum*, growth is apical (Moss, 1969), although longitudinal extension growth and secondary thickening have also been observed in older, non-apical parts of vegetative thalli of *A. nodosum* (David, 1943). Growth of most members of the Fucales is strongly seasonal (Mathieson *et al.*, 1976; Niemeck & Mathieson, 1976; Stengel & Dring, 1997) and reproduction is thought to be triggered by temperature and photoperiod (Sundene, 1973; McLachlan, 1974; Ang, 1991). After gamete release, vegetative meristems produce new vegetative tissue for several years. By contrast, reproductive growth of *H. elongata* is limited to one reproductive season by the presence of only one apical meristem per receptacle; this has determinate

growth and is lost by the time of gamete release in summer (Moss, 1969). During spring, most of the elongation is due to growth of surface cells and stretching of internal cells (Naylor, 1951; Moss, 1969).

Himantalia elongata is limited to semi-exposed shores of the north-eastern Atlantic (Moss *et al.*, 1973; Lüning, 1990) and usually occurs near the low water mark of spring tides, but in some locations it also grows subtidally (Moss *et al.*, 1973). Zygotes were able to grow on a variety of geological substrata in north-eastern England, but *H. elongata* was less abundant at sites with high silt loadings, possibly due to a reduction of zygote germination by light-limitation (Moss *et al.*, 1973). On the west coast of Ireland, *H. elongata* forms a zone between *Fucus serratus* and *Laminaria* spp., and is locally very common on semi-exposed shores, but is absent from or present only in small numbers on exposed shores (Brennan, 1950).

As the food value of *H. elongata* is high (Indergaard & Minsaas, 1991; Lahaye, 1991; Rouxel & Crouan, 1995), commercial harvesting from the west coast of Ireland, similar to that in northern France, is under way on a small scale, and is likely to expand quickly. Since the structure of local populations is still poorly understood, an investigation into the characteristics of vegetative and reproductive growth at sites on the Irish west coast was undertaken. The aims of the present work were to assess the seasonality of vegetative and reproductive growth in individual plants of *H. elongata*, and to monitor the annual fluctuation in growth rate and seasonal changes in plant density and biomass. In addition, the effects of different substrata and wave exposure on growth and survival of vegetative and reproductive stages were investigated.

Materials and methods

Study sites

Field work was carried out on two separate populations of *Himantalia elongata* in Galway Bay, at Finavarra, Co. Clare (53°9'20"N; 09°7'10"W), and at Spiddal, Co. Galway (53°14'20"N; 9°18'40"W). The site at Spiddal was more exposed to wave action than the site at Finavarra, and could be divided into three habitats: (1) a rockpool with an average depth of about 40 cm, (2) the rockpool edge covered by red algal turfs (mainly *Rhodothamniella floridula* (Dillwyn) J. Feldmann *ex* T. Christensen, *Osmundea pinnatifida* (Hudson) Stackhouse, *Mastocarpus stellatus* (Stackhouse) Guiry and *Chondrus crispus* Stackhouse) and some plants of *Fucus serratus*, and, finally, (3) open granite rock surface, mostly free from other vegetation apart from scarce plants of *F. serratus*. At Finavarra, *H. elongata* grew either in areas of flat limestone under shallow drifting sand or on limestone outcrops covered in red algae such as *Corallina officinalis* L., *M. stellatus* and *O. pinnatifida*, similar to those at the edge of the rockpool at Spiddal.

Growth and mortality of vegetative plants in situ

Artificial substrata (9 concrete blocks, 22 cm × 44 cm × 11 cm) were placed amongst the population at Finavarra in November 1995. The numbers of all visible 'macro-recruits' (terminology of Ang, 1991) on the upper surface of each block were monitored monthly between June 1996 and July 1997. Densities of recruits are expressed as number per block (upper surface 968 cm²: no recruits were found on the vertical sides of the blocks) and were not extrapolated to an area of the site, since in the population at Finavarra recruitment was patchy and appeared to be limited by substratum availability. Therefore, the absolute density observed on artificial substrata, if expressed on an area basis, would not necessarily represent the density found in the population as a whole, although relative changes were representative of the natural situation.

Measurements of reproductive growth in situ

To monitor growth rates of plants of *H. elongata* *in situ*, individual plants in both natural populations (Finavarra and Spiddal) were marked using PVC tape fastened with cable ties around the base of the vegetative buttons. Lost plants or labels were replaced to maintain a minimum number of 26 marked plants in each of the three habitats in the population at Spiddal and a total of 100 in the population at Finavarra. At Spiddal, the increase in button diameter, and length of receptacles and number of branches were monitored at 2- or 4-weekly intervals during spring low tides between October 1995 and May 1996, and at Finavarra between February 1995 and July 1997.

Inter-dichotomy growth in situ and in the laboratory

Non-apical growth of young, immature receptacles was monitored *in situ* and in the laboratory. In the natural population at Finavarra, two points in the young receptacles at 50 and 100 mm from the vegetative buttons were marked by nylon line threaded through the tissue in February 1995. This did not appear to damage the receptacle nor visibly affect its growth. Distances between the two markers and between the markers and the base of the receptacles were measured at regular intervals over a period of 3 months (February–May 1995). For laboratory experiments, 16 plants with receptacles 20–25 cm in length were collected from the population at Finavarra in February 1997. All but one of the receptacles were removed from each plant, then one branch of each dichotomy was removed. The remaining single branch, which had the positions of the dichotomies still visible, was measured. Distances between dichotomies were measured to an accuracy of 0.5 mm at 2-weekly intervals for 14 weeks. Growth was expressed as relative growth rates ($RGR = \{\ln(\text{length}_2) - \ln(\text{length}_1)\} / \{\text{time}_2 - \text{time}_1\}$).

In the laboratory, receptacles were grown at a photon irradiance of $40 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Thorn, cool-white fluorescent tubes, 36 W, Pluslux 4000, UK) in a 16:8 h (light:dark) regime at 10°C in enriched seawater (half-strength Von Stosch; modified after Guiry & Cunningham, 1984) in 10-l glass flasks, and media were changed weekly.

Seasonal change in plant density and percentage plant cover

The density of *H. elongata* at Finavarra was monitored in 90 quadrats, 1000 cm^2 in size, positioned by random coordinates in an area of $20 \text{ m} \times 50 \text{ m}$, delimiting the population studied, on a monthly basis between June 1996 and July 1997. In each quadrat, all mature fertile plants, sterile vegetative buttons and macro-recruits were counted. In the same quadrats, percentage algal cover was estimated. Changes in percentage algal cover and in number of algae were analysed by ANOVA after arcsin and $\sqrt{(x + 0.5)}$ transformations respectively.

Results

Vegetative growth

The first macro-recruits became visible in the population at Finavarra in March 1996, and their number was monitored on the artificial substrata from June onwards. During summer, an average of about 45 buttons was present on each block, but this number decreased rapidly during autumn and winter (Fig. 1a). An average density of about 20 buttons per block was counted by the end of November 1996 and the density continued to decrease during winter and spring. In early summer 1997, only about 4 or 5 buttons per block were counted (Fig. 1a). In March 1997, the density of recruits of the next generation on the same blocks was over 1500 per block, but decreased rapidly during April and May. The density remained at about 250 buttons per block during summer 1997, in contrast to about 45 buttons per block during the same months of the previous year (Fig. 1a). Button density decreased linearly with increasing diameter for buttons when they grew larger than 12 mm (Fig. 1b), although no relationship existed between the density and diameter for recruits with average diameters below 10 mm.

In both natural populations at Spiddal and Finavarra, diameters of young recruits increased during spring and summer, and reached average sizes of 10–25 mm by August, although some buttons had diameters of only 3–7 mm (data not shown). During winter of 1995/6, diameters of buttons from Finavarra and from all three micro-habitats in Spiddal continued to increase significantly to a maximum size of about 28 mm in late November and December (two-way ANOVA, $p < 0.05$; Fig. 2a). Mean diameter of buttons growing in the rockpool and on the open rock surface at Spiddal decreased significantly between December and January (two-way ANOVA, $p < 0.05$), whereas the mean diameter of

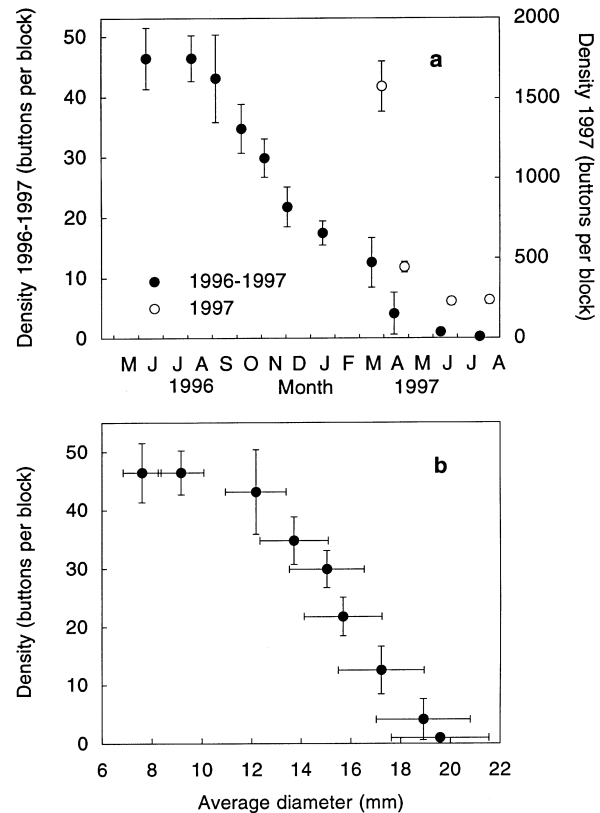


Fig. 1. *Himanthalia elongata*. (a) Density of recruits on artificial substrata (number of buttons per block; area = 968 cm^2) in the population at Finavarra between June 1996 and July 1997 and new recruits between March 1997 and July 1997. (b) Density of recruits versus diameter between June 1996 and July 1997 (details as in a). For two sampling occasions (January and June 1997) for which data are included in (a), no values for diameters were available in (b). Values are averages for nine blocks; error bars are standard deviations.

buttons growing in algal turfs continued to increase until March 1996 (no more measurements were taken at Finavarra after February). Except during November and December, buttons growing in the algal turf at Spiddal were significantly larger than those in the rockpool or on the open, exposed rock surface, but were similar in size to those at Finavarra. The probability of vegetative plants producing receptacles between early September and November increased with plant diameter (Fig. 2b; data from Finavarra are pooled over five sampling occasions between 2 September and 9 November 1995). By November, 99 of 100 marked buttons with a diameter greater than 15 mm had produced receptacles.

Reproductive growth

In both populations, the first vegetative buttons produced receptacles in early autumn, and first measurable ($> 2 \text{ mm}$) reproductive growth was recorded in September 1995 and 1996 (Fig. 3a; data for Finavarra). Average length of receptacles increased little during autumn and winter, but increased rapidly between February and May (Fig. 3a). Maximum average lengths were reached in July

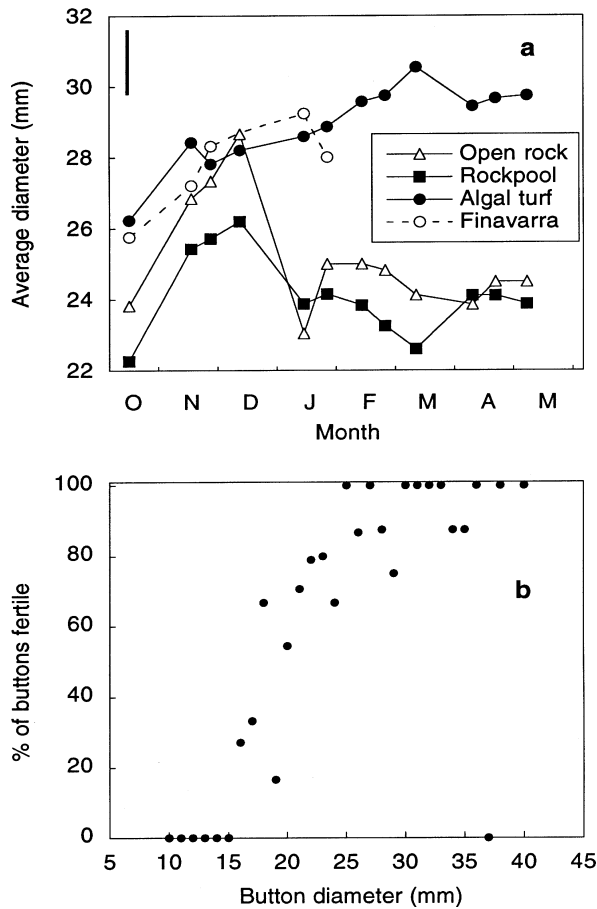


Fig. 2. *Himanthalia elongata*. (a) Average diameter of buttons from three different micro-habitats (rockpool, open rock surface and in algal turf, $n = 26$ in each) at Spiddal between October 1995 and May 1996, and average diameters of all buttons in the population at Finavarra between October 1995 and February 1996 ($n = 100$). Error bar represents least significant difference at $p = 0.05$. (b) Percentage of buttons of different sizes producing receptacles in autumn 1995 (data for Finavarra are pooled over five sampling occasions between 2 September and 2 November 1995).

and August, and mean length decreased during the following autumn and winter due to necrosis after gamete release and breakage of branches. Increased variation in plant length during late summer, autumn and winter was indicated by the wider confidence limits (Fig. 3a). Maximum length was similar over the 3 years of sampling, but was reached earlier in 1995 (August) than in 1996 (September) (two-way ANOVA, $p < 0.05$; Fig. 3a). All mature plants had disappeared from the population at Finavarra by March in 1996 and by April in 1997.

In 1996, in plants from all three micro-habitats at Spiddal, maximal increase in length occurred between March and April, and the increase levelled off in late April/May (Fig. 3b) – therefore earlier than in plants at Finavarra (Fig. 3a). Maximum receptacle length at Spiddal occurred in May and was lower in plants in all habitats than in plants at Finavarra (Fig. 3b, cf. Fig. 3a). Plants growing in the algal turf at Spiddal had the longest receptacles and plants on open, exposed rock had the shortest (two-way ANOVA, $p < 0.05$).

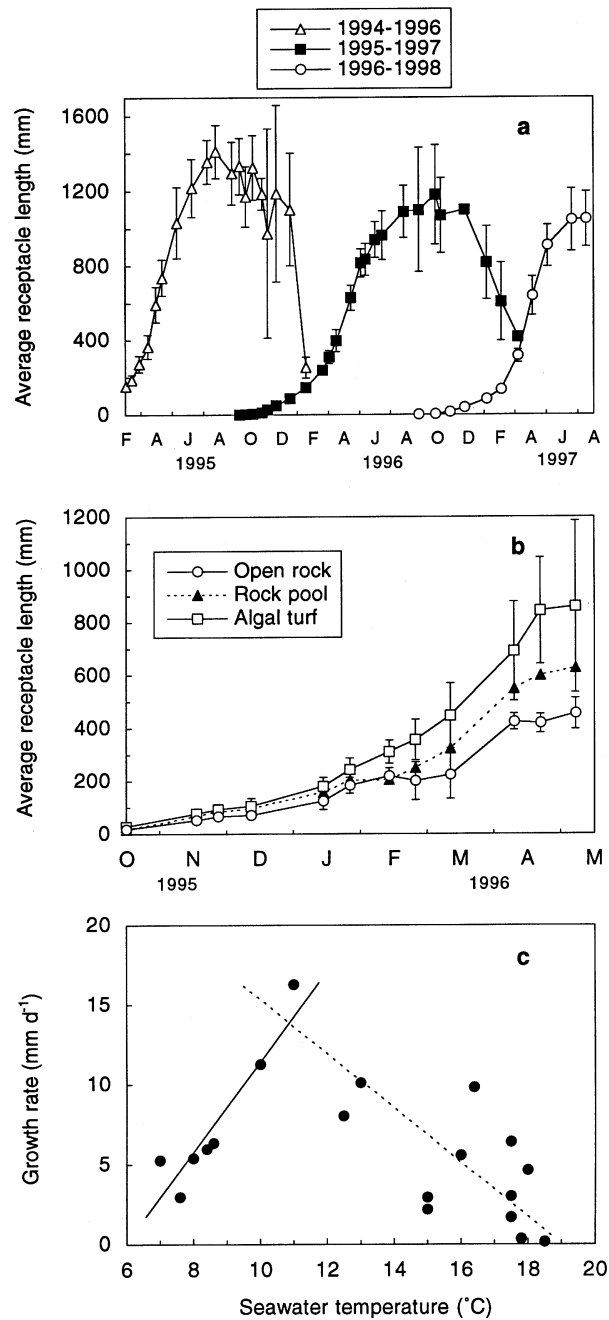


Fig. 3. *Himanthalia elongata*. (a) Length of receptacles (mm) at Finavarra between February 1995 and July 1997. (b) Length of receptacles (mm) from three micro-habitats at Spiddal between October 1995 and May 1996; for clarity, no error bars are fitted to data for plants in the rockpool. (c) Absolute length increase (mm d^{-1}) of receptacles from Finavarra versus seawater temperature. Only data from the active growing season between September and May (1995, 1996 and 1997; $n = 35\text{--}100$) are included. Error bars in (a) and (b) are 95% confidence limits (CL). n for (a) and (b) as in Fig. 2b.

Absolute increase in length of young, non-fertile receptacles from Finavarra measured during the active growing seasons (September to May, when it could be assumed that no breakage occurred, cf. Fig. 3a) was positively correlated with seawater temperature up to about 12 °C ($p < 0.01$, $r = 0.943$, d.f. = 5; Fig. 3c). Maximum rates of 16 mm d^{-1} were measured at tempera-

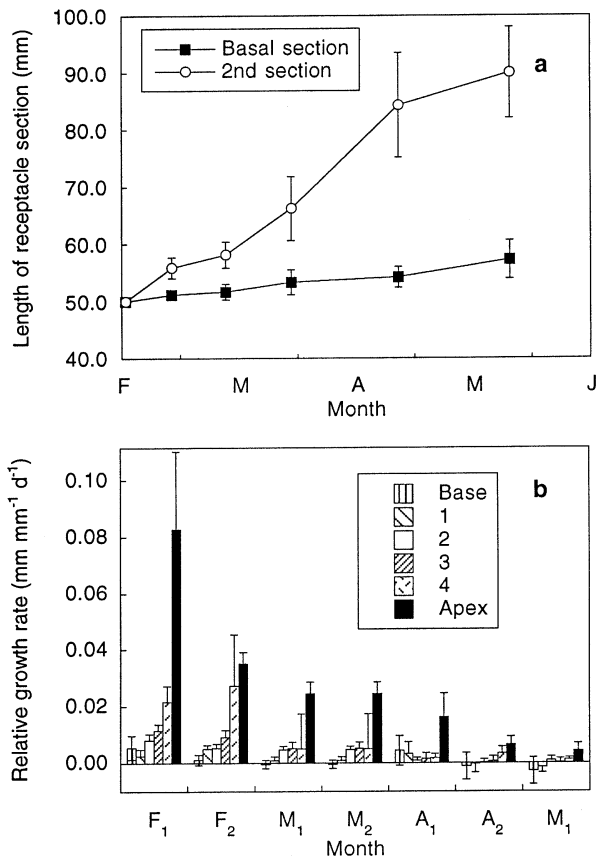


Fig. 4. *Himantalia elongata*. (a) Non-apical reproductive growth *in situ*: lengths of receptacle sections between two markers inserted originally 50 and 100 mm from the base of the receptacles in the population at Finavarra between February 1995 and May 1995, $n = 35$. (b) Relative growth rates (calculated from length measurements) of different thallus sections between dichotomies of plants collected from Finavarra in January 1997 and grown in the laboratory at 10 °C, 20 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for 14 weeks between February (F) and May (M) 1997; subscripts indicate 2-weekly intervals in each month; 'Base' is the section between the receptacle base and the first dichotomy, '1', the section between the first and second dichotomies, etc.; $n = 16$. Error bars are 95% CL.

tures of 10–12 °C, but length increase was correlated negatively with a further increase in temperature ($p < 0.05$, $r = -0.598$, d.f. = 12) as measured in May and later in summer (see Fig. 5a).

At Finavarra, no significant increase in length was detected in the basal, originally 50-mm-long section of the receptacle, defined by markers, between the beginning of February and the end of May 1995 (Fig. 4a). By contrast, lengths of receptacle sections originally between 50 mm and 100 mm from the base of the receptacle increased significantly during the same time.

In laboratory experiments conducted between February and May 1997, relative growth rates (RGR) of different receptacle sections increased with distance from the base (Fig. 4b). RGR of basal sections decreased in late February, and those of all sections by the end of the experiment. RGR of apical sections were significantly ($p < 0.05$) higher than those of all other sections at all times, but also

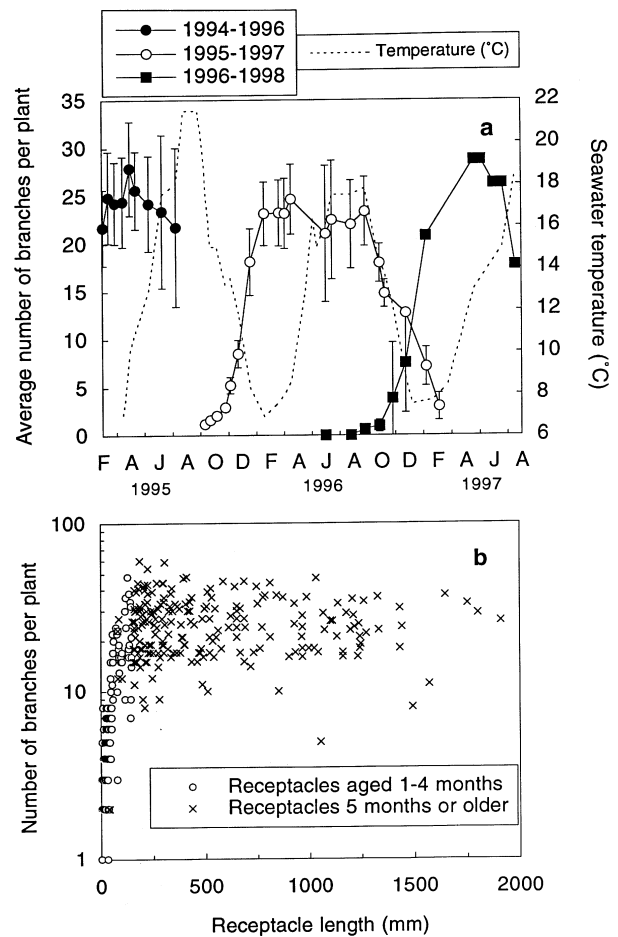


Fig. 5. *Himantalia elongata*. (a) Average number of branches per plant in the population at Finavarra and seawater temperature (dotted line) between February 1995 and August 1997. (b) Log number of branches per plant versus length for receptacles of different ages from Finavarra over three growth seasons between September and May 1995, 1996 and 1997.

decreased significantly ($p < 0.05$) within the duration of the experiment (two-way ANOVA).

Simultaneously with the increase in receptacle length in field plants, the average number of branches increased from September onwards (Fig. 5a, data for Finavarra). Most new dichotomies were produced in winter between November and January, and the number of branches was constant at about 25 per plant from late February/early March (Fig. 5a) to August/September. Thereafter, the average number of branches decreased. This coincided with the decrease in plant length at this time of the year (Fig. 3a) until, in March 1996, all mature plants were lost.

There was a positive linear relationship between the logarithm of the number of branches and receptacle length until average lengths reached about 200 mm (ANOVA of regression analysis, $p < 0.0001$, $F = 1572.85$, d.f. = 580; Fig. 5b), which occurred around January (cf. Fig. 3a), but no further increase in the number of branches was observed in receptacles older than 4 months. A few individual plants had up to 50 or 60 branches, but 25–30 branches were most common.

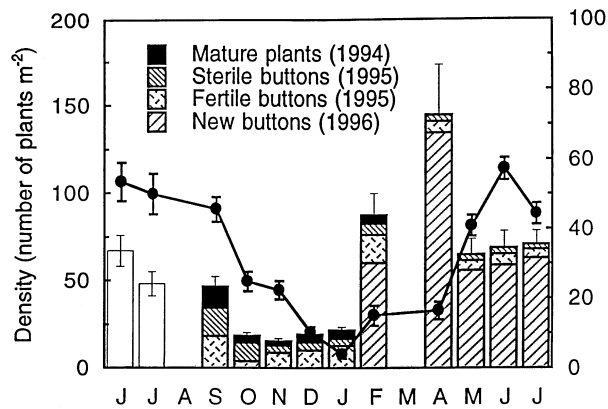


Fig. 6. *Himanthalia elongata*. Average number of plants of different reproductive stages (sterile buttons, fertile buttons, immature and mature receptacles; columns) and percentage plant cover (line; scale on right) in 90 randomly chosen 100 cm² quadrats in the population at Finavarra between June 1996 and July 1997. No distinction was made between different categories of plants in June and July 1996 (first two columns) and values represent total density. No data are available for August 1996 and March 1997. Error bars are 95% CL for total density and percentage cover.

Density of plants of different reproductive stages and percentage plant cover

The seasonal changes in plant density of different categories of plants (mature plants, sterile buttons, fertile buttons, new buttons of different generations) and changes in percentage plant cover in the population at Finavarra between June 1996 and July 1997 are illustrated in Fig. 6. In June and July 1996, fertile, receptacle-bearing plants of the 1994–7 generation ('1994') and young, sterile buttons of the 1994–7 generation and of the 1995–8 generation ('1995') were present, but no distinction was made between the different categories in Fig. 6.

Total plant density (including all categories) decreased from about 70 per square metre in summer 1996 to about 50 during autumn and winter. There was a large increase in plant density between February and April 1997, followed by a sharp decline between April and May 1997.

During summer 1996, a few sterile buttons of the 1994 generation had persisted in the population and some of these old buttons of the 1994 generation produced primordia for receptacles. However, none of these appeared to develop into receptacles, although development was occasionally observed in other locations. Buttons of the 1994 and 1995 generations could readily be distinguished by their colour and the degree of decay (Stengel, personal observation). About half the buttons of the 1995 generation had produced receptacles by September ('fertile buttons') (Fig. 6). The observed decrease in plant density between September and October 1996 was due to a loss of mature plants of the 1994 generation and also to a reduction in the number of fertile buttons, while the number of sterile buttons decreased only slightly.

The decrease in plant density in October 1996 was due to a significant (one-way ANOVA, $p < 0.05$) reduction in

the number of old, receptacle-bearing plants of the previous generation ('1994'), but no further plants were lost during winter and no significant changes occurred in any category.

In February 1997, a large number of new, sterile buttons of the next generation ('1996') ('macro-recruits', which had been present as 'micro-recruits' during winter; Ang, 1991) became visible, while the average number of mature plants of the 1994 generation and of young, receptacle-bearing plants of the 1995 generation remained similar.

Algal density was highest in April 1997 (no data available for March), after the appearance of further new macro-recruits ('1996'), but decreased significantly (one-way ANOVA, $p < 0.001$) with the density of these recruits between April and May (Fig. 6). All old, mature plants of the 1994 generation had disappeared by April.

During the following months, from May to July 1997, the average number of all plant groups remained similar. The total number of plants present in June 1997 was similar to that observed in June 1996.

The percentage plant cover decreased significantly during late summer (one-way ANOVA, $p < 0.05$) from June 1996, and remained low during autumn and winter. Minimum percentage cover was observed in January (whereas minimal algal density occurred in November 1997), but increased from February, coinciding with the elongation of receptacles at this time of the year (Fig. 3), and reached another peak in June. Algal cover increased during April and May, but decreased from July onwards (Fig. 6).

Discussion

The present investigation suggests that, although the seasonal pattern of vegetative growth of *Himanthalia elongata* was similar at the two sites on the Irish west coast, the success of recruitment and the survival of adult plants were linked to the degree of exposure and type of micro-habitat available for recruitment.

As was observed by Creed (1995) on the Isle of Man, the early settlement of germlings appeared clumped at both sites. At Finavarra, the density of recruits of *H. elongata* found on the artificial substrata was considerably greater in spring 1997 than in spring 1996, which was probably due to the fact that in November 1995, when the blocks were initially placed in the population, most gametes had been shed already, and only those released between late November and February settled on the blocks.

At both sites, the mortality of buttons increased with button diameter during spring and summer. At Spiddal, mortality of young recruits was highest on the open rock surface. Optimum growth of young buttons occurred in dense red algal turfs, which appeared to protect the recruits from wave action, and from desiccation in early summer (Stengel, personal observation).

The majority of buttons produced receptacles between

late August and November during their first year, but about 35% continued to grow vegetatively during winter (cf. Fig. 6). In contrast to previous observations by Russell (1990) on the Isle of Man, the onset of reproductive growth in the populations at Spiddal and Finavarra was related to the diameter of the buttons in autumn, and only those with a minimum diameter of about 15 mm produced receptacles. However, the onset of reproductive growth also appeared to be controlled by environmental conditions, most likely temperature and/or photoperiod, in addition to button diameter, since only buttons which reached this minimum size before December became reproductive. Some of the buttons which failed to produce receptacles in their first year may have become reproductive during the autumn of the following season. However, this could not be confirmed from the present data. Most of them were badly damaged by epiflora and epifauna and died (data not shown), so that, in addition to wave exposure, the survival of vegetative plants may also be related to biotic factors. In exposed habitats, such as at Spiddal, the frequent shedding of 'skin' from vegetative plants may have damaged the button and resulted in a decrease in button diameter, after the protective, slimy film on its surface was destroyed (Russell & Veltkamp, 1984; Kitching, 1987). Diameters of fertile, receptacle-bearing buttons decreased during the year and whole plants were lost, probably because of the deterioration of the buttons, observations similar to those made by Brenchley *et al.* (1996).

At both sites on the Irish west coast, the seasonal pattern of reproductive growth was similar to that of plants on the Isle of Man (Gibb, 1937). The onset of exclusively elongation growth in early spring coincided with an increase in daylength and sea temperatures, as well as irradiances. Highest growth rates of receptacles occurred in March and April at *in situ* water temperatures of 10–12 °C. Similar optimum temperatures for reproductive longitudinal growth of *H. elongata* were found in the laboratory (Stengel & Guiry, unpublished data). Growth rates were slightly lower than those measured for low intertidal (*Fucus serratus*) or subtidal (*Laminaria* spp.) brown macroalgae in the North Atlantic (Fortes & Lüning, 1981). *Himantalia* may be adapted to produce optimum growth when favourable conditions occur in early spring – maximum growth rates of up to 16 mm d⁻¹ were measured then. After the production of a large number of branches during winter, without the investment in longitudinal growth during the first winter, young photosynthetic tissue was available for rapid growth in more favourable conditions in spring to ensure successful maturation of receptacles and subsequent gamete release from June onwards. The possibility of a photoperiodic control of reproductive growth, similar to that demonstrated for other brown algae (e.g. Lüning, 1986), cannot be discounted and requires further study.

Interdichotomy, non-apical growth of young receptacles was observed *in situ*, during winter and spring as well as in culture, and decreased with the maturation of

receptacles. Although the decrease in longitudinal growth in the laboratory could also have been due to potentially sub-optimal artificial culture conditions, all plants remained healthy until the end of the experiment and no adverse effects of cultivation were observed. The daylength of 16:8 h (light:dark) in culture was similar to conditions in the field in May, by which time growth rates of field plants had decreased (the culture temperature of 10 °C had been chosen since it was the optimum temperature for reproductive growth). It is possible, therefore, that the cessation of growth was caused by long-day conditions, although further, more detailed experiments need to be undertaken to confirm this hypothesis.

The beginning of gamete release in June in plants from Finavarra and Spiddal (as indicated by the breakage of receptacles; data shown for Finavarra, Fig. 3) occurred at water temperatures of 16–18 °C at both sites. Gamete release in *H. elongata*, therefore, may have been triggered by temperature, but also coincided with the onset of long days. Preliminary laboratory data indicated that gamete release occurred at temperatures between 10 and 20 °C, both in light and darkness. Recently, Serrão *et al.* (1996) and Pearson *et al.* (1998) demonstrated that the release of gametes of other members of the Fucales growing on exposed shores is related to water motion. On the Irish west coast, viable gametes were released until all mature plants were lost from the population (in Spiddal by December; in Finavarra by February). The difference in the persistence of adult plants in the field was probably caused by the difference in the degree of wave exposure between the two sites. On the Isle of Man, adult plants were present until February (Gibb, 1937), as at Finavarra, but only until October in an exposed site in Scotland (Brenchley *et al.*, 1996). The early loss of fertile, gamete-releasing plants during autumn decreased the probability of the establishment of the next generation of recruits, since a larger number of recruits appeared to settle after November.

At the more sheltered site, Finavarra, both average receptacle length and the degree of branching were greater than at the more exposed site, and the relationship between receptacle length and the number of branches was constant over the 3 years of the study. Further, non-quantitative observations from other sites on the Irish coast suggested that plant size varies considerably among sites. Longer, repeatedly branched reproductive plants appeared to be more common at sites with strong currents but little wave exposure (Stengel, personal observation), which concurs with observations from the south coast of Ireland (Kitching & Ebling, 1967). Smaller plants with fewer, narrower receptacles occurred at more wave-exposed sites (Stengel, personal observation). Such morphological differences between individual plants from exposed and more sheltered habitats have previously been reported for other members of the order Fucales (Lewis, 1964; Russell, 1978; Norton *et al.*, 1982). Also, plants of *Laminaria longicuris* in New England were longer and

narrower at wave-exposed than at sheltered sites (Gerard & Mann, 1979).

There was no consistent relationship between the percentage plant cover and the total number of plants in the individual quadrats over the year. This was partly because receptacles of mature plants were not completely contained within the quadrat in which the holdfast was situated. Also, the large number of recruits that became visible in spring and summer had no impact on the percentage cover but greatly increased average plant density. In late spring and early summer, plant cover increased with the elongation of receptacles, while this did not affect plant density. During autumn and winter, both plant cover and density decreased with the loss of mature, reproductive plants and breakage of parts of receptacles after gamete release, while the number of vegetative plants also decreased. The total number of plants reached a sharp peak in February/March with the appearance of macro-recruits, but then decreased again due to the high mortality of recruits in spring and summer.

In populations of *H. elongata* at Finavarra and Spiddal, three 'generations' of plants were present during autumn and winter, viz. (1) plants bearing mature receptacles, and sterile buttons of the same generation which had not produced receptacles, (2) plants of the next generation bearing immature receptacles and, again, sterile buttons of that generation, and (3) new recruits. During spring and summer, only two 'generations' were present, viz. generation 2 with maturing receptacles and generation 3 recruits. Except for a few buttons that produced receptacles in the second instead of the first year, no exchange of gametes occurred between these two generations (2 and 3) since the maturation of plants before gametes were released usually took 2 years. Consequently, two potentially genetically independent populations were present at any time within one site. Although environmental conditions within one site are probably similar over several years, short-term disturbances such as high temperatures during spring tides or winter storms may be responsible for a loss of recruits that would not be detectable until the following year. Such disturbances may have caused the fluctuations in population size and distribution observed by Russell (1990). Although the highest biomass occurred between May and July, commercial harvesting of receptacles should be delayed until gametes are shed in summer. Alternatively, due to the predominantly biennial life-history of the species, more extensive harvesting might take place every 3 years to allow recovery and exchange of gametes between different generations.

The biennial life-history of *H. elongata* is unique amongst the Fucales and has important implications for the success of recruitment. In other members of the order, the success of recruitment is largely dependent on the presence of an adult plant canopy (e.g. *Pelvetia fastigiata* (J. Agardh) De Toni; Brawley & Johnson, 1991), and young recruits are protected from environmental stress by adult plants all year round. By contrast, early growth of recruits

of *H. elongata* occurs during late winter and spring in the absence of a protective parent canopy, before receptacles of the following generation elongate in late spring.

The lack of a protective adult canopy in winter and early spring places more emphasis on the nature of the micro-habitat for the success of recruitment. It has been suggested that, in Britain, the distribution of *H. elongata* was limited to habitats with clear water and, possibly, also with particular substrata, since the germination of zygotes of *H. elongata* is inhibited by low-light conditions in waters with high silt contents (Moss *et al.*, 1973). Early growth of recruits, however, does not appear to be negatively affected by low-light conditions since, in the present work, highest growth rates of recruits occurred in dense algal turfs. Within the more exposed site at Spiddal, survival of recruits was also highest in such protective algal turfs. At exposed sites, the early loss of fertile, mature plants in autumn limits the period of potential gamete release and, therefore, reduces the probability of successful recruitment. In addition, the limited distribution of protective algal turfs on the west coast (e.g. Lewis, 1964) could explain the presence of *H. elongata* on semi-exposed shores but its absence from very exposed shores in Ireland.

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