

Factors determining the upper limits of intertidal canopy-forming algae

S. J. Hawkins¹ and R. G. Hartnoll²

¹ Department of Zoology, University of Manchester, Manchester M13 9PL, United Kingdom

² Department of Marine Biology, University of Liverpool, Port Erin, Isle of Man, United Kingdom

ABSTRACT: The causes of zonation of canopy-forming algae have been investigated by canopy removal experiments, combined with observations at the upper limits of various species on certain British shores during the exceptionally hot weather of summer 1983. *Fucus vesiculosus*, *F. serratus* and *Laminaria digitata* all extended their range upshore when the species zoned above were experimentally removed, indicating that competition can be directly responsible for setting upper limits of low- and mid-shore canopy algae. Removal of species zoned immediately below permitted down-shore extension of *Pelvetia canaliculata*, *F. spiralis*, *F. vesiculosus*, *F. serratus* and *Himantalia elongata*, confirming the setting of lower limits of these species by competition. Amongst canopy-forming species, *P. canaliculata*, *F. spiralis*, *L. saccharina*, *L. digitata* and the 'button' stage of *H. elongata* showed signs of damage during summer 1983. There were no signs of damage to *F. vesiculosus*, *F. serratus* and *Ascophyllum nodosum*. Some species of low-shore, turf-forming understorey and encrusting red algae seemed more vulnerable to hot weather than the canopy-forming species. *Corallina officinalis* and 'lithothamnia' suffered extensive damage during summer 1983.

INTRODUCTION

It is generally accepted that the lower limits of the zones of intertidal plants and sessile animals are set by biological interactions such as competition for space, grazing and predation. However, until recently it was believed that physical 'emersion' factors, particularly heat and desiccation, were directly responsible for setting their upper limits (e.g. Connell, 1972; Carefoot, 1977; Underwood, 1979; Lubchenco, 1980; but see Hawkins and Hartnoll, 1983a for review of the role of grazing in setting upper limits). In this study, various manipulative experiments on algal-dominated areas of shore on the Isle of Man further tested whether the lower limits of fucoids were set by competition with the species zoned immediately below. More importantly, by means of additional experiments we investigated whether competition for space determined the upper limits of fucoids and *Laminaria digitata*.

Assessment of the importance of physical factors in setting the upper limits of intertidal algae was helped during 1983 by the hottest summer in the British Isles for 7 yr (meteorological records are presented in the appendix). Careful searches were made on the Isle of Man and in South-west England for damage or death of algae at their upper limits on the shore. If physical

factors were directly setting these limits, then some extension up the shore would be expected during 1977–1982, followed by die-back caused by unusually hot weather in 1983.

Algal nomenclature follows Parke and Dixon (1976). 'Lithothamnia' is used as a collective name for all encrusting calcareous algae.

METHODS

The moderately-sheltered shore just south of the Albert Pier, Port St Mary, and the sheltered shore at Langness were both used for experiments. At Langness the fucoid zonation from top to bottom of the shore is *Pelvetia canaliculata*, *Fucus spiralis*, a very narrow *F. vesiculosus* band, *Ascophyllum nodosum* and *F. serratus*. At Port St Mary the sequence is *F. spiralis*, *F. vesiculosus* and *F. serratus*. A more exposed part of Kallow Point, where *F. serratus* directly abutted *Laminaria digitata*, was used for other experiments. Details of these shores are given in Southward (1953), Bruce et al. (1963) and Hawkins (1979). Lewis (1964) outlines general patterns of zonation on British shores.

Details of experiments are summarized in Tables 1 and 2. Areas of canopy were removed either above or

below the zone of the species under test for extension of range. These experiments were usually started so as to coincide with the expected appearance of sporelings of the test species, based on the experience of previous monitoring and grazing exclusion experiments (Hawkins, 1981a, b; Hawkins and Hartnoll, 1983b). Usually the canopy was removed just once by cutting the plant at or just above the holdfast. Repeated selective removals were generally not possible as furoid sporelings cannot be distinguished easily from each other until quite large. However, selective removal was possible in experiments involving competition between *Fucus serratus* and *Laminaria digitata*. In each experiment an untouched control area was designated nearby.

To avoid edge effects a 0.5 m to 1 m wide 'buffer zone' was cleared around the 2 × 2 m areas used for the larger species (*Fucus vesiculosus* at the bottom of its range, *F. serratus*, *Ascophyllum nodosum* and *Laminaria digitata*). With the smaller plants of *F. spiralis* and *F. vesiculosus* at the top of its range, smaller areas of 1 × 1 m were sufficient, though care was taken to remove adjacent plants whose fronds could sweep into the treatment area.

Throughout the period 1977–1983 evidence for damage or death of algae at their upper limits was looked for on the Isle of Man. From 1980 to 1983 observations were also made at various locations (listed in Table 3) in South-west England. In 1983, particularly careful searches were made on various shores in both areas during the hot weather of July and August. Damage to populations of each species was assessed on a subjective scale: no sign of bleaching or damage; bleaching and death of occasional plants in population; extensive bleaching and death of many plants.

RESULTS

Initial canopy compositions of each experiment are given in Tables 1 and 2. Further details of fauna and understory algae can be found in Hawkins (1979).

Changes following canopy removal are summarized in Tables 1 and 2. *Fucus spiralis*, *F. vesiculosus* and *F. serratus* were all able to extend their range downshore after removal of the species zoned immediately below (Table 1). *F. serratus* and *Laminaria digitata* appeared further up the shore than normal in Experiments 4c and 5 respectively, even though these experiments were set up with the aim of inducing downshore extension in other species. *F. vesiculosus* and *L. digitata* were also enabled to extend higher up the shore by the removal of the species zoned above them (Table 2). No change in canopy composition was observed in any control area.

The meteorological data indicates that though June

1983 was duller than average, July 1983 was exceptionally hot, exceeding the summers of 1975 and 1976. In South-west England, August 1983 was much hotter than preceding years and approached the exceptional summer of 1976 – the latter being the hottest since recordings began at R.A.F. Mountbatten during the First World War. Generally, conditions were not so hot and sunny on the Isle of Man during 1983 as in South and South-west England. Most importantly, however, hot and sunny conditions coincided with low water springs during both July and August 1983 in all localities studied. Continuous hot and sunny weather also coincided with the neap tide periods of late July and early August.

Table 3 summarizes observations on the effects of the hot summer of 1983, together with observations in other years. Amongst the canopy algae, *Laminaria digitata* was the only species to show signs of drought bleaching in most years on the Isle of Man, and considerable damage was observed in 1983 both around Plymouth and on the Isle of Man. *L. saccharina* showed some signs of drought bleaching in 1983 in the Plymouth area and the Isle of Man. Whilst no effects were noted in 1983 on the adult plants of *Himantalia*, the 'button' stage showed signs of bleaching in the Plymouth area. *Pelvetia canaliculata* and *Fucus spiralis* both appeared damaged in 1983 only. *Ascophyllum nodosum*, *F. vesiculosus* and *F. serratus* never showed any signs of damage at any of the localities studied.

Red algae, found in the sublittoral fringe or forming an understory beneath *Ascophyllum* and *Fucus serratus* in the lower eulittoral, seemed more prone to drought damage (Table 3) than low- and mid-shore canopy algae. During July 1983, damage was particularly apparent in *Corallina officinalis* and 'lithothamnia', especially plants at the rim of evaporating mid-tide rock pools. Occasionally, damaged plants of *Palmaria palmata*, *Laurencia pinnatifida* and *Gigartina stellata* were seen during 1983. All the species showing susceptibility to hot dry weather also died when protective canopies of *Ascophyllum* and *F. serratus* were removed (Tables 1 and 2; see Hawkins, 1979; Hawkins and Harkin, in press, for further details). 'Lithothamnia' were also noticed to extend higher up the shore under *Fucus* patches induced by grazer-removal experiments on the Isle of Man (Hawkins, 1979, 1981a, b) and following kills of limpets caused by the 'Torrey Canyon' clean-up using toxic dispersants (Southward and Southward, 1978).

Ephemeral algae high in the littoral fringe were bleached completely and died back in the summers of most years (Table 3; Hawkins and Hartnoll, 1983b).

Many other species of intertidal algae, not listed in Table 3, seemed unaffected by the unusually hot weather of 1983.

Table 1. Details of design and summary of results of experiments testing the setting of lower limits by competition

Experiment no. and date	Site	Initial canopy	Size	Design	Hypothesis	Results	
						Canopy	Understorey
(1) Apr 1978	Langness	100 % <i>F. spiralis</i> immediately below <i>Pelvetia</i>	1 m ²	Cleared once	<i>F. spiralis</i> limits downshore extension of <i>Pelvetia</i>	Some <i>Pelvetia</i> (max. 10 % cover) appeared but swamped by recolonizing <i>F. spiralis</i>	No understorey – some growth of green algae upon canopy removal. No change in control
(2) Nov 1977	Langness	100 % <i>F. vesiculosus</i> immediately below <i>F. spiralis</i>	1 m ²	Cleared once	<i>F. vesiculosus</i> limits downshore extension of <i>F. spiralis</i>	<i>F. vesiculosus</i> recolonized rapidly but no <i>F. spiralis</i> observed	No understorey – some growth of green algae. No change in control
(3) Nov 1977	Port St Mary sheltered	100 % <i>F. vesiculosus</i> immediately below <i>F. spiralis</i>	1 m ²	Cleared once	<i>F. vesiculosus</i> limits downshore extension of <i>F. spiralis</i>	40–50 % <i>F. spiralis</i> established one year later, eventually swamped by <i>F. vesiculosus</i>	No understorey – some growth of green algae. No change in control
(4a) Nov 1978	Langness	90 % <i>Ascophyllum</i> , and 10 % <i>F. vesiculosus</i> zoned below 100 %	2 × 2 m	All cleared once	<i>Ascophyllum</i> limits downshore extension of <i>F. vesiculosus</i>	(a) <i>F. vesiculosus</i> achieved 80 % cover after 1 y	In all replicates understorey algae such as 'Lithothamnia' and <i>Corallina</i> died in spring and summer. No change in controls
b Apr 1978		<i>F. vesiculosus</i>	2 × 2 m			(b) <i>F. vesiculosus</i> achieved 80 % cover after 1 y	
c Aug 1978			3 × 2 m			(c) <i>F. vesiculosus</i> achieved 80 % cover; some <i>F. serratus</i> (10 % cover) extended upwards after 1 y	
(5) Aug 1977 See Hawkins & Harkin (in press) for further details	Port St Mary exposed	100 % <i>F. serratus</i> some way from a patchy <i>F. vesiculosus</i> / barnacle zone	2 × 2 m	Cleared once	<i>F. serratus</i> limits downshore extension of <i>F. vesiculosus</i>	No <i>F. vesiculosus</i> found. <i>Laminaria</i> <i>digitata</i> sporelings survived, reaching 0.5 m long and 5 % cover. Though bleached in summer, plants survived 1 y later. <i>Laminaria</i> sporelings in control did not grow	'Lithothamnia' died, rapid growth of <i>Enteromorpha</i> and <i>Palmaria</i> . No change in control
(6) Oct 1978	Port St Mary sheltered	80 % <i>Laminaria</i> , 20 % <i>F. serratus</i>	2 × 8 m	<i>Lamina- ria</i> re- peatedly removed	<i>L. digitata</i> limits downshore extension of <i>F. serratus</i>	<i>F. serratus</i> and <i>Himantalia</i> extended range downshore. <i>F. serratus</i> forming 100 % cover where previously 20 % after 1 y	Even though canopy removal in autumn, 'Lithothamnia' died. No change in control

DISCUSSION

The long-standing hypotheses that competition can set the lower limits of canopy forming algae in the inter-tidal (e.g. reviews by Southward, 1958; Lewis, 1964) have more recently been experimentally confirmed by other workers (e.g. Menge, 1975; Lub-

chenco, 1980; Schonbeck and Norton, 1980) and now ourselves (see also Hawkins and Harkin, in press). *Ascophyllum*, however, still remains enigmatic. Very few viable sporelings of *Ascophyllum* are found on the shore (Burrows, 1947; Hawkins, 1979; Schonbeck and Norton, 1980) making it an unsuitable subject for manipulative experiments. It recolonizes its own zone

Table 2. Details of design and summary of results of experiments testing the setting of upper limits by competition

Experiment no. and date	Site	Initial canopy	Size	Design	Hypothesis	Results	
						Canopy	Understorey
(7) Apr 1978, replicates a & b	Langness	100 % <i>F. spiralis</i> immediately above <i>F. vesiculosus</i>	1 m ²	Cleared once	<i>F. spiralis</i> limits upshore extension of <i>F. vesiculosus</i>	(a) 1 plant of <i>F. vesiculosus</i> established and survived 1 y (b) 5–10 % cover of <i>F. vesiculosus</i> became established and survived 1 y	<i>Catenella</i> died, some green algae appeared. No change in <i>Catenella</i> in control
(8) Nov 1978	Port St Mary sheltered	100 % <i>F. vesiculosus</i> immediately above <i>F. serratus</i>	2 × 2 m	Cleared once	<i>F. vesiculosus</i> limits upshore extension of <i>F. serratus</i>	20 % cover of <i>F. serratus</i> sporelings 6 m later 10–15 % after 1 y	'Lithothamnia' and few <i>L. digitata</i> sporelings died, no change in control
(9) Nov 1978	Port St Mary exposed	95 % <i>F. serratus</i> and 5 % <i>L. digitata</i> zoned above 50 % <i>L. digitata</i> and 50 % <i>F. serratus</i>	2 × 1 m	Cleared once	<i>F. serratus</i> limits upshore extension of <i>L. digitata</i>	20 % <i>L. digitata</i> in May, 6 m later, some bleaching in summer but survived and achieved 25 % cover after 1 y	'Lithothamnia' died, but not in control

very slowly (Burrows, 1947; Hawkins, 1979; Boaden and Dring, 1980) and sporelings were never found in various *Fucus serratus* removals (not all detailed here, but see Hawkins, 1979). The factors setting the lower limit of *Ascophyllum* remain unclear. Greater water movement and depth may be directly unfavourable to it, preventing formation of dense monospecific stands of large plants. Indirectly, greater water movement may increase *Patella* numbers and hence grazing pressure, and also enhance sweeping by *F. serratus*; both may prevent establishment of *Ascophyllum* sporelings.

More interestingly, our work shows that on sheltered shores, the upper limits of *Fucus serratus* and *F. vesiculosus* are set directly by competition with the species zoned immediately above. The upper limits of *Laminaria digitata* can be directly set by competition acting on sporelings; though extremes of both hot (our study) and cold weather (Todd and Lewis, 1984) can also cause kills of adult plants at their upper limit. Extreme physical stress, however, does definitely set the upper limits of the high-shore canopy forming algae *Pelvetia canaliculata* and *F. spiralis*. The upper limits of both these species at Port St Mary, Isle of Man were raised during the cool damp summers of 1978–1982 (S. J. Hawkins, unpubl.), whereas in 1983 there was die-back of both these species at several

localities. Schonbeck and Norton (1978) similarly reported trimming back of zones of *Pelvetia* and *F. spiralis* during hot weather in 1975 and 1976. In contrast to us, however, they reported die-back of *Ascophyllum* at its upper limit, which we did not observe in 1983. They also found no deaths of *F. serratus* at their upper limit.

Other work, primarily concerned with grazing, has also shown that upper limits of some mid and low shores species are not set directly by physical factors (for review see Hawkins and Hartnoll, 1983a). In particular a mixture of *Fucus* species, with *F. serratus* far above its normal zone, can be seen after limpet removal (Burrows and Lodge, 1950; Hawkins, 1981b). *Laminaria digitata* and *Himantalia elongata* were found much higher up the shore as a consequence of limpet kills following the Torrey Canyon (Southward and Southward, 1978). Colonization of new substrata is also informative. All 3 species of *Fucus* were found side by side on 2 yr old blocks on Plymouth Breakwater (Hawkins and Southward, unpubl.). In contrast, only *F. vesiculosus* in small patches was found at similar shore levels on older blocks (> 20 yr) and on the Breakwater itself (> 150 yr). Mixed zonation was also found on new harbour works at Port Erin, Isle of Man (Hawkins, 1979) and at Hunterston, Scotland (Clokier and Boney, 1980). During succession, several years are needed

Table 3. Effects of drought on intertidal algae at their upper limits. (- no effects; + signs of damage or death; ++ severe damage; / no observations)

Species	Location					
	Isle of Man		Plymouth	N. Devon & N. Cornwall	Swanage	
	1977-82	1983	1983	1983	1980-82	1983
Littoral fringe species						
<i>Blidingia minima</i>	+	+	+	+	+	+
<i>Enteromorpha</i> spp.	+	+	+	+	+	+
<i>Porphyra</i> spp.	+	+	+	+	+	+
<i>Prasiola stipitata</i>	+	+	+	+	+	+
<i>Ulothrix/Urospora</i>	+	+	/	/	+	+
Eulittoral canopy species						
<i>Pelvetia canaliculata</i>	-	+	+	/	/	/
<i>Fucus spiralis</i>	-	+	+	/	-	+
<i>F. vesiculosus</i>	-	-	-	-	-	-
<i>Ascophyllum nodosum</i>	-	-	-	/	/	/
<i>Himantalia elongata</i>	-	-	+ 'Buttons'	-	-	-
<i>F. serratus</i>	-	-	-	-	-	-
Sublittoral fringe canopy species						
<i>Laminaria digitata</i>	+	++	++	/	-	+
<i>L. saccharina</i>	-	+	+	/	/	/
<i>Polyschides sacchoriza</i>	/	/	-	/	/	/
<i>L. hyperborea</i>	-	-	-	/	/	/
Sublittoral fringe and low-shore turf and mid-shore understorey species						
<i>Laurencia pinnatifida</i>	-	+	+	-	-	-
<i>Gigartina stellata</i>	-	+	+	-	-	+
<i>Chondrus crispus</i>	-	-	-	-	-	-
<i>Corallina officinalis</i>	+	++	++	++	-	++
'Lithothamnia'	+	++	++	++	+	++
<i>Palmaria palmata</i>	-	-	+	/	/	/

before grazing or competition (sometimes acting together) sort out zonation patterns.

Consideration of the factors setting upper limits of low-shore turf-forming algae or encrustations is more problematic. They are often found higher up the shore under canopies or on shaded rocks, and Dayton (1975) considered them in that situation as an 'obligate understorey' since they invariably die when their protective canopy is removed. Not surprisingly, many of these species on open lower-shore rock showed signs of damage or death at their upper limits during 1983. Desiccation can be considered responsible for the death of species such as *Corallina officinalis*, *Chondrus crispus* and *Gigartina stellata* as very shallow pools or trickles of water can result in extension much higher up the shore than on well-drained surfaces. On the Isle of Cumbrae in Scotland porous sandstone probably enables *Chondrus* and *Gigartina* to extend much higher upshore than is usual (S.J.H. pers. obs.). Some of the more delicate reds, such as *Lomentaria*, may be true 'shade plants' in that they are damaged by high light intensities rather than desiccation. These 2 factors are hard to separate and need further investiga-

tion. Several turf-forming species extended higher up on an exposed shore following limpet kills after the Torrey Canyon oil spill (Southward and Southward, 1978). Various turf algae have also been induced by experimental grazer removal to grow higher up the shore during the winter and damp summers on more moderately exposed shores on the Isle of Man (*Palmaria palmata*, *Ceramium* sp.; Hawkins, 1979, 1981b) and at Swanage (*Ceramium* sp., *Laurencia pinnatifida*, *Cladostephus*; S.J.H. pers. obs.). Together these observations suggest that except in occasional extreme conditions, grazing rather than physical restrictions sets the upper limit of such species.

Littoral fringe algae usually die-back every summer (see also Hawkins and Hartnoll, 1983b). They leave what appears to be bare rock, though it is likely that some species (perhaps members of *Blidingia* and *Enteromorpha*) may be able to regrow from the microscopic remains of bases. Other species, such as those of *Porphyra* and *Ulothrix*, may be completely killed off; though they probably recruit from alternate stages in their life histories (Lubchenco and Cubit, 1980) that occur lower on the shore during the summer, which are

either burrowing ('*Conchocoelis*' phase of *Porphyra*) or prostrate (*Ulothrix*).

Low-water springs occur in the middle of the day (1000 to 1300 h) at the sites on the north coasts of Devon and Cornwall, and around Plymouth. In contrast, on the Isle of Man they are in the early morning and evening (0500 to 0800 and 1700 to 2000 h) and at Swanage in the late afternoon and very early morning (1500 to 1800 and 0300 to 0600 h). Comparisons between the Isle of Man and South-West England are

difficult to make because of latitudinal differences in summer conditions (see Lewis, 1964 and appendix) – differences which were apparent in 1983. The weather in 1983 at Swanage, however, was very similar to that at Plymouth. So it is interesting to note that drought damage, particularly in *Laminaria digitata*, was less marked at Swanage. This confirms the long-standing hypothesis of Lewis (1964) that the timing of low water springs can be a factor affecting the distribution and abundance of low shore species.

APPENDIX: Summary of mean monthly maximum air temperatures °C (Tmax) and total sunshine hours (Sh) during Jun, Jul and Aug 1975 to 1983. Deviations from 30 yr average given in brackets. I_T is an index of temperature anomaly derived by summing the differences of the 30 yr average from the observed figure for Jun, Jul, Aug. I_S is an index of total sunshine hours anomaly derived by summing the differences of the 30 yr average from the observed figure for Jun, Jul, Aug

	Ronaldsway								Ilfracombe							
	Jun		Jul		Aug		I_T	I_S	Jun		Jul		Aug		I_T	I_S
	Tmax.	Sh	Tmax.	Sh	Tmax.	Sh			Tmax.	Sh	Tmax.	Sh	Tmax.	Sh		
1975	17.2 (+1.1)	303 (+89)	18.5 (+1.2)	187 (-4)	19.3 (+2.0)	202 (+23)	+5.8	+108	18.5 (+1.3)	301 (+75)	20.0 (+1.4)	235 (+25)	20.7 (+1.7)	152 (-40)	+4.4	+60
1976	16.3 (+0.2)	199 (-15)	19.5 (+2.2)	228 (+37)	20.7 (+3.4)	273 (+94)	+9.5	+116	19.0 (+1.8)	235 (+9)	21.6 (+3.0)	260 (+50)	22.1 (+3.1)	333 (+141)	+7.9	+200
1977	15.6 (-0.5)	232 (+18)	18.4 (+1.1)	211 (+20)	18.0 (+0.7)	228 (+49)	-0.9	+87	15.4 (-1.8)	179 (-47)	19.1 (+0.5)	234 (+24)	19.1 (+0.1)	196 (+4)	-1.2	-19
1978	15.5 (-0.6)	169 (-35)	16.2 (-0.9)	175 (-16)	16.3 (-1.0)	129 (-50)	-2.3	-101	16.8 (-0.4)	199 (-27)	17.1 (-1.5)	147 (-63)	18.7 (-0.3)	186 (-6)	-2.2	-96
1979	15.3 (-0.8)	212 (-2)	16.6 (-0.3)	139 (-52)	15.9 (-1.4)	184 (+5)	-1.2	-49	16.7 (-0.5)	181 (-45)	18.7 (+0.1)	212 (+2)	18.2 (-0.8)	133 (-59)	-1.2	-102
1980	15.1 (-1.0)	177 (-37)	16.6 (-0.7)	179 (-12)	16.7 (-0.6)	127 (-52)	+0.5	-101	16.7 (-0.5)	176 (-50)	17.7 (-0.9)	166 (-44)	19.0 (0.0)	146 (-46)	-1.4	-140
1981	14.5 (-1.6)	183 (-31)	16.6 (-0.7)	156 (-35)	17.4 (+0.1)	174 (-5)	+0.6	-71	16.2 (-1.0)	163 (-63)	17.6 (-1.0)	152 (-56)	19.3 (+0.3)	203 (+11)	-2.3	-108
1982	16.4 (+0.3)	187 (-27)	18.8 (+1.5)	196 (+5)	17.6 (+0.3)	180 (+1)	+0.9	-21	18.3 (+1.1)	171 (-54)	19.2 (+0.6)	170 (-40)	18.5 (-0.5)	115 (-77)	+1.2	-171
1983	15.8 (-0.3)	196 (-18)	20.4 (+3.1)	224 (+33)	19.4 (+2.1)	209 (+30)	+8.5	+45	17.2 (0.0)	162 (-64)	22.1 (+3.5)	299 (+89)	21.3 (+2.3)	262 (+70)	+5.8	+95
30 yr average 1951–80	16.1	214	17.3	191	17.3	179			17.2	226	18.6	210	19.0	192		
	Plymouth								Swanage							
	Jun		Jul		Aug		I_T	I_S	Jun		Jul		Aug		I_T	I_S
	Tmax.	Sh	Tmax.	Sh	Tmax.	Sh			Tmax.	Sh	Tmax.	Sh	Tmax.	Sh		
1975	19.3 (+2.2)	331 (+109)	20.3 (+1.2)	244 (+31)	21.3 (+2.2)	193 (-3)	+5.6	+137	19.2 (+1.4)	332 (+98)	20.5 (+0.8)	263 (+26)	21.3 (+1.6)	243 (+29)	+3.8	+153
1976	20.2 (+2.6)	255 (+33)	21.8 (+2.7)	260 (+47)	23.3 (+4.2)	308 (+112)	+9.3	+192	20.6 (+2.8)	275 (+35)	22.6 (+2.9)	303 (+66)	22.0 (+2.3)	309 (+95)	+8.0	+196
1977	15.7 (-1.9)	163 (-59)	19.8 (+0.7)	223 (+10)	19.2 (+0.1)	212 (-16)	-1.1	-65	15.3 (-2.5)	165 (-75)	19.2 (-0.5)	224 (-13)	19.0 (+0.7)	178 (-36)	-2.3	-124
1978	17.1 (-0.5)	216 (-8)	17.4 (-1.7)	145 (-84)	18.8 (-0.3)	220 (+24)	-2.5	-68	17.0 (-0.8)	214 (-26)	18.1 (-1.6)	156 (-83)	18.7 (-1.0)	221 (+7)	-3.4	-100
1979	16.4 (-1.2)	172 (-52)	19.9 (+0.8)	237 (+24)	18.1 (-1.0)	194 (+2)	-1.4	-26	16.7 (-1.1)	181 (-59)	20.3 (+0.6)	249 (+12)	18.4 (-1.3)	213 (-1)	-1.8	-48
1980	16.8 (-0.8)	175 (-48)	17.5 (+1.4)	177 (-36)	18.8 (-0.3)	167 (-29)	+0.3	-123	17.0 (-0.8)	219 (-21)	17.6 (-2.1)	177 (-60)	18.9 (-0.8)	186 (-28)	-3.7	-109
1981	16.3 (-1.3)	197 (-26)	18.9 (-0.2)	164 (-49)	20.8 (+1.7)	241 (+45)	+0.7	-31	16.4 (-1.4)	181 (-59)	19.5 (-0.2)	185 (-52)	20.6 (+0.9)	237 (+23)	-0.7	-88
1982	17.9 (+0.3)	203 (-20)	20.1 (+1.0)	165 (-48)	18.5 (-0.6)	155 (-41)	+0.7	-109	18.0 (+0.2)	230 (-10)	20.0 (+0.3)	212 (-25)	19.5 (-0.2)	199 (-15)	+0.3	-50
1983	17.8 (+0.2)	180 (-43)	24.0 (+4.9)	290 (+77)	22.3 (+3.2)	280 (+84)	+8.3	+188	17.8 (0.0)	210 (-30)	22.9 (+3.2)	287 (+50)	21.3 (+1.6)	260 (+46)	+4.8	+66
30 yr average 1951–80	17.6	222	19.1	213	19.1	196			17.8	240	19.7	237	19.7	214		

In summary, littoral fringe algae and upper eulittoral canopy algae have their upper limits set directly by physical factors. Biological interactions such as grazing on more exposed shores and competition on sheltered shores can set the upper limit of mid and low-shore canopy forming species. 'Obligate understory' species, primarily reds, can also have their upper limit set by physical factors acting directly. Low-shore laminarians can have their upper limit set on the short-term directly by competition or grazing but any extension can get trimmed back during exceptionally hot (or cold – see Todd and Lewis, 1984) weather. Further work must be done on *Ascophyllum*.

Acknowledgements. S. J. Hawkins was primarily supported by an N.E.R.C. Studentship, though some fieldwork between 1980 and 1983 was funded by an N.E.R.C. Fellowship and Research Grant (GR3/4412) plus grants from the Manchester University Staff travel fund. Professor E. Naylor (Port Erin) and Professor E. J. Denton (Plymouth) provided laboratory space. We are most grateful to Drs. A. J. Southward, G. T. Boalch and Professor T. A. Norton for general encouragement and for improving earlier drafts. We thank the meteorological offices and personnel at Bracknell, R.A.F. Mountbatten, Ronaldsway Airport and Swanage for supplying information. R.G.H. wishes to thank the University of Liverpool Research Fund for support.

LITERATURE CITED

- Boaden, P. J. S., Dring, M. T. (1980). A quantitative evaluation of the effects of *Ascophyllum* harvesting on the littoral ecosystem. *Helgoländer Meeresunters.* 33: 700–710
- Bruce, J. R., Colman, J. S., Jones, N. S. (1963). Marine fauna of the Isle of Man. L.M.B.C. Mem. typ. Br. mar. Pl. Anim. 36, Liverpool University Press
- Burrows, E. M. (1947). A biological investigation of the behaviour of *Ascophyllum nodosum*. Ph. D. thesis, University of London
- Burrows, E. M., Lodge, S. M. (1950). Note on the inter-relationships of *Patella*, *Balanus* and *Fucus* on a semi-exposed coast. *Rep. mar. biol. Stn Port Erin* 62: 30–34
- Carefoot, T. (1977). Pacific seashores. A guide to intertidal ecology. J. J. Douglas, Vancouver
- Clokie, J. J. P., Boney, A. D. (1980). The assessment of changes in intertidal ecosystems following major reclamation work: framework for interpretation of algal-dominated biota and the use and misuse of data. In: Price, J. H., Irvine, D. E. G., Farnham, W. F. (ed.) Systematics association, Spec. Vol. N. 17(b) The shore environment, Vol. 2, Ecosystems. Academic Press, London, p. 609–675
- Connell, J. H. (1972). Community interactions on marine rocky intertidal shores. *Ann. Rev. Ecol. System.* 3: 169–192
- Dayton, P. K. (1975). Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecol. Monogr.* 45: 137–159
- Hawkins, S. J. (1979). Field studies on Manx rocky shore communities. Ph. D. thesis, Liverpool University
- Hawkins, S. J. (1981a). The influence of *Patella* grazing on the furoid/barnacle mosaic on moderately exposed rocky shores. *Kieler Meeresforsch.* 5: 537–543
- Hawkins, S. J. (1981b). The influence of season and barnacles on the algal colonisation of *Patella vulgata* exclusion areas. *J. mar. biol. Ass. U.K.* 61: 1–15
- Hawkins, S. J., Harkin, E. (in submission). The effects of experimental canopy removal in rocky low-shore and shallow sub-tidal communities (submitted to *Botanica mar.*)
- Hawkins, S. J., Hartnoll, R. G. (1983a). Grazing of intertidal algae by marine invertebrates. *Oceanogr. mar. Biol. A. Rev.* 21: 195–282
- Hawkins, S. J., Hartnoll, R. G. (1983b). Changes in a rocky shore community: an evaluation of monitoring. *Mar. environ. Res.* 9: 131–181
- Lewis, J. R. (1964) The ecology of rocky shores. English Universities Press, London
- Lubchenco, J. (1980). Algal zonation in the New England rocky intertidal community: an experimental analysis. *Ecology* 61: 333–344
- Lubchenco, J., Cubitt, J. (1980). Heteromorphic life histories of certain marine algae as adaptations to variations in herbivory. *Ecology* 61: 676–687
- Menge, J. L. (1975). Effect of herbivores on community structure of the New England rocky intertidal region: distribution, abundance and diversity of algae. Ph. D. thesis, Harvard University, Cambridge, Mass.
- Parke, M., Dixon, P. S. (1976). Check-list of British marine algae: third revision. *J. mar. biol. Ass. U.K.* 56: 527–594
- Schonbeck, M. W., Norton, T. A. (1978). Factors controlling the upper limits of furoid algae. *J. exp. mar. Biol. Ecol.* 31: 303–313
- Schonbeck, M. W., Norton, T. A. (1980). Factors controlling the lower limits of furoid algae on the shore. *J. exp. mar. Biol. Ecol.* 43: 131–150
- Southward, A. J. (1953). The ecology of some rocky shores in the south of the Isle of Man. *Proc. Trans. Liverpool biol. Soc.* 59: 1–50
- Southward, A. J. (1958). The zonation of plants and animals on rocky sea shores. *Biol. Rev.* 33: 137–177
- Southward, A. J., Southward, E. C. (1978) Recolonization of rocky shores in Cornwall after use of toxic dispersants to clean up the Torrey Canyon spill. *J. Fish. Res. Bd Can.* 35: 682–706
- Todd, C. D., Lewis, J. R. (1984) Effects of low air temperature on *Laminaria digitata* (L.) in south-western Scotland. *Mar. Ecol. Prog. Ser.* 16: 199–201
- Underwood, A. J. (1979) The ecology of intertidal gastropods. *Adv. mar. Biol.* 16: 1–109