THE BIOLOGY OF *CHTHAMALUS STELLATUS* (POLI)

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(Text-figs. 1–4)

Introduction

Chthamalus stellatus (Poli) is a littoral barnacle, very similar both in habitat and in external appearance to another shore barnacle, *Balanus balanoides*. Actually with practice the two species can nearly always be distinguished *in situ* on the rocks (see Moore, 1936, p. 704). Although these two species appear to occupy similar ecological niches on the shore, their geographical distributions are different, since *Chthamalus* replaces *Balanus balanoides* progressively towards the south and west of the British Isles, and eastwards in the English Channel. In this paper an attempt is made to bring together what is known of the biology of *Chthamalus stellatus*, and to make a comparison between this species and *Balanus balanoides*.

Material and Methods

The observations reported in this paper are of very scattered origin, and concern the geographical distribution, relationships with other organisms, and growth rate of the barnacle *Chthamalus stellatus*.

For the investigation of the geographical distribution of *Chthamalus*, records of its presence or absence around the coasts of the British Isles were made by both authors, and also by a number of people who kindly sent material for examination. Except when observers were familiar with the differences between *Chthamalus* and *Balanus balanoides*, such material was always examined personally by one of the authors, and no records of absence were accepted from doubtful sources. The results of this collection of data are described and discussed on pp. 527–31, and summarized in Table I.

Notes on the general relationships of *Chthamalus*, and counts of its density, were made both on the Dorset coast and in the neighbourhood of Loch Sween by J. A. Kitching. Corresponding observations were made in Devon and Cornwall and in the north and west of Scotland by H. B. Moore, with the assistance, in Scotland, of Mr G. M. Spooner. The methods of counting and

Table I

Locality no. (see map)	Name of locality	Abundance of *Chthamalus*	Observer, or reference to previous record	Date of field observations
1	Nybster, Caithness	Only 2 found in 15 min. search; *Chthamalus* confined to extreme top of barnacle zone	H. B. Moore	28. vi. 36
2	Dunnet Hd., Caithness	Only 6 seen in 10 min. search; *Chthamalus* confined to top 20 cm. of barnacle zone	H. B. Moore	27. vi. 36
3	Skullomie, Sutherland	Up to 120 per m.^{2}; confined to top 50 cm. of barnacle zone	H. B. Moore	27. vi. 36
4	Geodha Chobhair, Sutherland	Up to 2200 per m.^{2}; confined to top 140 cm. (*ca.*) of barnacle zone	H. B. Moore	24. vi. 36
5	Bay of Stoer, Sutherland	Up to 3800 per m.^{2}	H. B. Moore	22. vi. 36
6	Seana Chamas, Ross	Present	H. B. Moore	20. vi. 36
7	Sgòir Beag, Vatternish, Skye	Abundant; occupying 50–100 cm. at top of barnacle zone	H. B. Moore	15. vi. 36
8	Scurrival Point, Barra, Outer Hebrides	Present	*Mrs N. McMillan	13. vii. 37
9	Breivig Bay, Barra, Outer Hebrides	Present	*Mrs N. McMillan	6. vii. 37
10	Òb Allt an Daraich, Skye	Up to 2400 per m.^{2}	H. B. Moore	11. vi. 36
11	Port na Cullaidh, Elgol, Skye	Up to 3200 per m.^{2}	H. B. Moore	18. vi. 36
12	Ardmore Pt., Mull	Plentiful	Kitching (1935)	5. viii. 34
13	Staffa	Plentiful	Kitching (1935)	14. viii. 34
14	Fionphort, Mull	Scarce	Kitching (1935)	6. viii. 34
15	Sound of Mull, near Loch Aline	Scarce	Kitching (1935)	2. viii. 34
16	Loch Buie, Mull	Plentiful	Kitching (1935)	7. viii. 34
17	South end of Kerrera, Firth of Lorne	Scarce	Kitching (1935)	1. viii. 34
18	Ardnoe Pt., near Crinan	Rather sparse	Kitching (1935)	24. vi. 34
19	Mouth of West Loch Tarbert, Jura	Rather sparse	J. A. Kitching	26. viii. 36
20	Farland Pt., Cumbrae	Up to 480 per m.^{2}	H. B. Moore	5. vii. 35
21	Whiting Bay, Arran	A very few present	H. B. Moore	10. vii. 35
22	Macrihanish, Kintyre	Scarce	Kitching (1935)	27. viii. 34
23	Mull of Kintyre	Absent	Kitching (1935)	27. viii. 34
24	Port Stewart, Co. Londonderry	Present	*Mrs N. McMillan	26. ix. 36
25	Saltpan Rock, 1–2 miles south of Moville, Co. Donegal	Present	*Mrs N. McMillan	28. iii. 37
26	Malin Hd., Co. Donegal	Present	*Mrs N. McMillan	29. iii. 37
27	Horn Hd., Co. Donegal	Present	†Dr J. W. S. Pringle	—. viii. 36
28	Bundoran, Co. Donegal	Present	*Dr R. Lloyd Praeger	8. v. 37
29	Achill I. (west corner), Co. Mayo	Abundant; no *Balanus balanoides* present	Mr D. A. Webb	—. vii. 37
30	Achillbeg I., Co. Mayo	Abundant; about equal in numbers with *B. balanoides*	Mr D. A. Webb	—. vii. 37
31	Dukes, Dingle Bay, Co. Kerry	Present	Dr W. R. G. Atkins	—. ix. 36
32	Rossbehy, Dingle Bay, Co. Kerry	Fairly plentiful	J. A. Kitching	21. vii. 38
33	Castlecove, Co. Kerry	Abundant	*Dr S. Kemp	24. viii. 36
34	Dunmanus Bay, Co. Cork	Abundant	Miss E. M. Moore	—. viii. 36
35	Barley Cove, Co. Cork	Abundant	Miss E. M. Moore	—. viii. 36
36	Middle Calf I., Schull, Co. Cork	Present	*Miss E. M. Moore	24. viii. 36
37	Castle I., Schull, Co. Cork	Present	*Miss E. M. Moore	24. viii. 36
38	Lough Ine, Co. Cork	Present	*Miss E. M. Moore	—. viii. 36
39	Oysterhaven, Co. Cork	Abundant	H. B. Moore	10. vii. 37
40	Fountainstown, Co. Cork	Abundant	H. B. Moore	15. vii. 37
41	Ardmore, Co. Waterford	Abundant	H. B. Moore	8. vii. 37
42	Stradbally, Co. Waterford	Abundant	H. B. Moore	8. vii. 37
43	Greenore Pt., Co. Wexford	Abundant	J. A. Kitching	1. vii. 38
44	Wicklow, Co. Wicklow	Only 2 seen in about 10 m. of shore	H. B. Moore	6. vii. 37
45	Bray Hd., Co. Wicklow	Present; less than 1 per m.^{2}	H. B. Moore	6. vii. 37
46	Ireland's Eye, Co. Dublin	Sparse; only on most wave-beaten rocks	J. A. Kitching	25. vii. 38
47	Greenisland, Co. Antrim	Absent	Mrs N. McMillan	—. viii. 36
48	White Hd., Co. Antrim	Absent	Mrs N. McMillan	—. xii. 36
49	Island Magee, Co. Antrim	Absent	Mrs N. McMillan	29. ix. 36
50	Kirk Michael, I. of Man	Absent	H. B. Moore	—. —. 32
51	‡Port Erin, I. of Man	Absent	H. B. Moore	—. —. 34
52	Langness, I. of Man	Absent	H. B. Moore	—. —. 34
53	Leasowe Embankment, Wirral, Cheshire	Absent	Mrs N. McMillan	18. vi. 37
54	Penrhyn Bay, Llandudno	Absent	Mr D. P. Wilson	3. vii. 35
55	Penmon Pt., Anglesey	Absent	Mr D. P. Wilson	—. ix. 36
56	Bay near Rhosneigr, Anglesey	Absent	Mr D. P. Wilson	—. vii. 37
57	Rhosneigr, Anglesey	Present but very rare	*Mr D. P. Wilson	—. vii. 37
58	Porth Oer, Carnarvon	Present	*Mrs N. McMillan	16. v. 37
59	Bardsey I.	Present	Kidd, Pyefinch & Butler (1935)	—. —. 33

* Specimens examined by H. B. Moore.
† Specimens examined by J. A. Kitching.
‡ An early record by Marrat (1886) is of very doubtful value.

Locality no. (see map)	Name of locality	Abundance of *Chthamalus*	Observer, or reference to previous record	Date of field observations
60	Black Rock, near Criccieth, Carnarvon	Present	*Mrs N. McMillan	16. v. 37
61	Aberystwyth	Present	Walton (1915)	—. —. 15
62	Llangranog, South Cardigan	Present	†Mrs N. McMillan	18. iv. 38
63	Nash Pt., Glamorgan	Plentiful	†Mr G. E. H. Foxon	—. v. 38
64	Clevedon, Somerset	Absent	J. A. Kitching	11. iv. 38
65	Blue Anchor Bay, Somerset	Absent	H. B. Moore	10. xi. 35
66	Lee Bay, North Devon	Abundant	H. B. Moore	31. x. 35
67	Hartland Pt.	Abundant	H. B. Moore	5. viii. 35
68	Millook Haven, North Cornwall	Abundant	H. B. Moore	2. ix. 34
69	Treyarnon	Abundant; up to 70,000 per m.²	H. B. Moore	26. vii. 36
70	Holywell Bay	Abundant	H. B. Moore	26. viii. 36
71	St Ives	Abundant; commoner than *B. balanoides*	H. B. Moore	24. vii. 35
72	Cape Cornwall	Abundant; up to 47,000 per m.²; in very wave-exposed places no *B. balanoides* present	H. B. Moore	6. viii. 36
73	Tresco, Scilly Is.	Abundant	*Mr G. M. Spooner	22. iv. 36
74	Porth Mellin (Mullion Cove)	Abundant	H. B. Moore	28. xii. 35
75	Charlestown, South Cornwall	Abundant	H. B. Moore	28. x. 34
76	Gara Pt., Yealm	Abundant	H. B. Moore	6. iv. 35
77	Black Cove	Abundant	H. B. Moore	21. iv. 35
78	Start Pt.	Abundant	H. B. Moore	21. iv. 35
79	Hope's Nase	Abundant	H. B. Moore	22. iv. 35
80	Dawlish Warren	Abundant	H. B. Moore	31. i. 37
81	Lyme Regis	Fairly abundant	H. B. Moore	21. x. 35
82	Redcliff Pt., Weymouth	Present in a very narrow zone	H. B. Moore	11. i. 36
83	Durlston Pt.	Present	J. A. Kitching	29. vii. 36
84	Old Harry Rocks, near Swanage	Absent	J. A. Kitching	30. vii. 36
85	Freshwater Bay, I. of Wight	Absent	Fischer-Piette (1936)	13. iii. 34
86	St Catherine's Pt., I. of Wight	Absent	Fischer-Piette (1936)	27. ix. 32
87	Culver Cliff, I. of Wight	Absent	Fischer-Piette (1936)	12. iii. 34
88	Newhaven	Absent	Fischer-Piette (1936)	13. v. 33
89	Hythe	Absent	Mr P. R. Crimp	—. ix. 37
90	Dover	Absent	J. A. Kitching	—. iv. 34
91	Flamborough Hd.	Absent	Mr J. H. Fraser	—. x. 36
92	Robin Hood's Bay	Absent	Mr R. Bassindale	—. —. 36
93	Tees Mouth	Absent	Mr R. Bassindale	—. —. 36
94	Bass Rock, Firth of Forth	Absent	H. B. Moore	4. vii. 36
95	Isle of May, Firth of Forth	Absent	J. A. Kitching	8. v. 37
96	St Andrews	Absent	Miss K. M. G. Flemming	—. ii. 38
97	Aberdeen	Absent	Mr A. Milne	—.—. 36
98	Helmsdale, Sutherland	Absent	H. B. Moore	28. vi. 36
99	Bruneval, Normandy	Absent	Fischer-Piette (1932)	6. ii. 31
100	Cap de la Hève	Absent	Fischer-Piette (1932)	30. vi. 27
101	Arromanches	Absent	Fischer-Piette (1932)	7. ii. 32
102	Grandcamp-les-Bains	Absent	Fischer-Piette (1932)	28. vii. 30
103	Pointe de Barfleur	Absent	Fischer-Piette (1932)	31. vii. 27
104	Cap Levi	Absent	Fischer-Piette (1932)	18. vii. 31
105	Cap de la Hague	Absent	Fischer-Piette (1932)	31. vii. 27
106	Flamanville	Absent	Fischer-Piette (1932)	30. iv. 30
107	Carteret	Up to 100 per m.²	Fischer-Piette (1932)	30. iv. 30
108	Ile Lihou, Guernsey	Very few; about 1 per m.²	Fischer-Piette (1932)	30. v. 31
109	La Corbière, Jersey	A very few	Fischer-Piette (1932)	20. iv. 30
110	Saint Germain-sur-Ay	A few	Fischer-Piette (1932)	28. iv. 30
111	Granville	Scarce	Fischer-Piette (1932)	4. ix. 26
112	Cancale, pointe du Grouin	Abundant in upper part of shore	Fischer-Piette (1932)	29. vi. 30
113	Cap Fréhel	Abundant	Fischer-Piette (1932)	12. vii. 32
114	Pointe de Pordic	Abundant	Fischer-Piette (1932)	23. ii. 32
115	Bréhat	Abundant	Fischer-Piette (1932)	21. iv. 32
116	Ploumanach	Abundant in places	Fischer-Piette (1932)	27. ix. 31
117	Ile d'Ouessant	Abundant	Fischer-Piette (1936)	11–15. ii. 33

* Specimens examined by H. B. Moore. † Specimens examined by J. A. Kitching.

of determining the tissue weights of the *Chthamalus* were those already used by Moore (1935, p. 264; 1936, p. 703) in similar work on *Balanus balanoides*.

Finally, observations on the growth rate were made by H. B. Moore on a rock at Drake's Island, Plymouth Sound. For this purpose patches of *Chthamalus* at three different levels were photographed for future recognition, and the individuals were measured *in situ* at intervals. These results are shown graphically in Fig. 4, and discussed on pp. 536–8.

Larval History and Settlement of Spat

Developing larvae were found by Bassindale (1936) in the mantle cavity of *Chthamalus* at Plymouth from July to September. In cultures these larvae reached the sixth naupliar stage in 2–3 weeks, and they would presumably have reached the cypris stage soon after had they lived. Settlement of spat took place at Plymouth during the late autumn and winter. Hatton & Fischer-Piette (1932) have given the first dates of settlement at St Malo in 1931 and 1932 as September 14 and 24 respectively, and according to Hatton (1938) settlement continues for 5 months.

The naupliar stages have been illustrated by Bassindale (1936). The larva is very much smaller than that of *Balanus balanoides*. The sixth stage nauplius has a length of only 0·49 mm., as compared with the 1·15 mm. attained by *Balanus balanoides* at this stage. Also the newly settled young of *Chthamalus* is much smaller than that of *Balanus balanoides*.

The following figures have been given by Hatton (1938), and partly by Hatton & Fischer-Piette (1932), for the population density of *Chthamalus* spat (per 1/100 sq. m.) from counts made in January or February, when settlement was complete:

	High wave exposure		Slight wave exposure	
Level	1931	1932	1931	1932
Just above high water of neap tides	21	21	48	60
Just below high water of neap tides	270	205	39	42
Mid-tide level	1830	1610	8	19
Low water of neap tides	8	5	0	0

They show that the density of settlement was greatest at the highest wave exposure, and suggest also a shift of the optimal level for settlement of the spat from about mid-tide level at the higher wave exposure to high water of neap tides at the more sheltered locality. There was no settlement in a position of extreme shelter (Hatton & Fischer-Piette, 1932).

Zonation, and Interrelations with *Balanus balanoides*

Lower limit of vertical distribution

For *Chthamalus*, as for *Balanus balanoides*, the lower limit of distribution on the shore is very variable and difficult to determine. However, it may be stated that *Chthamalus* rarely if ever occurs below low water of spring tides. It is hard to see why it should not do so in a favourable situation, since Fischer (1928) has shown that it can survive a continuous immersion of 12 months under natural conditions. It is not possible to say whether it is excluded by some physical factor, such as excessive immersion (see below), or by competition with sublittoral organisms such as coralline algae or other rock-encrusting forms. The adverse factor, whatever it may be, might only operate at some particular stage in the life history of the *Chthamalus*, e.g. on newly attached larvae. It is quite possibly the same factor which prevents *Balanus balanoides* from extending below low water of spring tides.

Actually the lower limit of *Chthamalus* is in many districts far above low water of spring tides, and it may be above high water of neap tides (Fig. 1). No doubt the same factors which locally restrict *Balanus balanoides* also

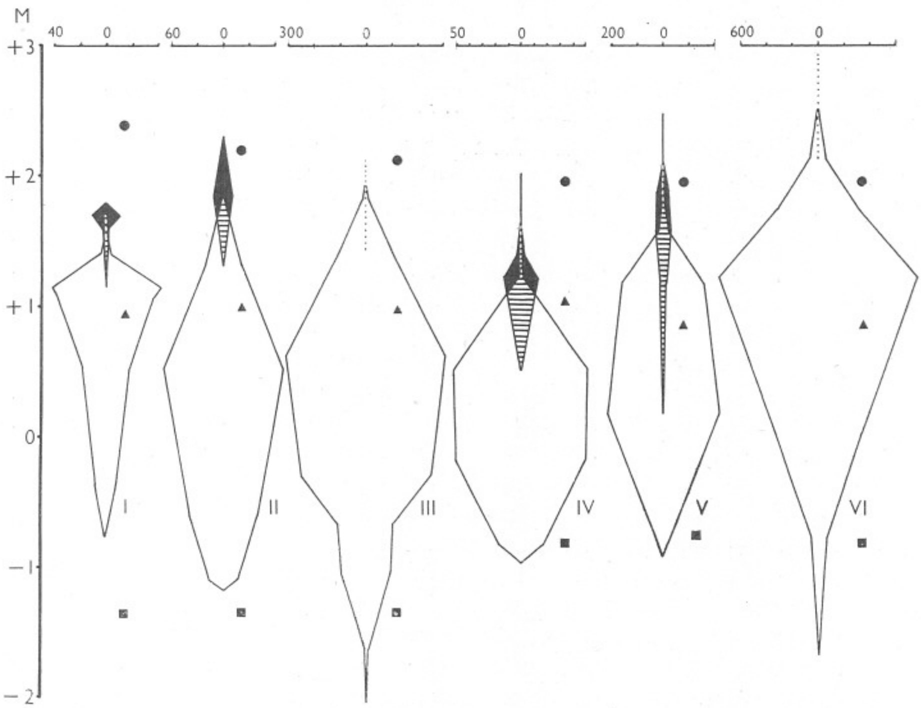

Fig. 1. Interrelation of *Chthamalus stellatus* (black) and *Balanus balanoides* (white) at a series of localities in Scotland. Quantities are measured in grammes (dry weight) of tissue per square metre. Levels (in metres) are referred to local mid-tide level. The approximate heights of other local levels are indicated as follows: mean low-water neap tides ■; mean high-water neap tides ▲; mean high-water spring tides ●. I, Òb Allt an Daraich, Skye; II, Port na Cullaidh, Elgol, Skye; III, Seana Chamas, Ross; IV, Bay of Stoer, Sutherland; V, Geodha Chobhair, Sutherland; VI, Skullomie, Sutherland.

operate against *Chthamalus*—as for instance the rubbing action of the fronds of the larger algae (see Kitching, 1935, p. 363), and competition for space with other sessile organisms such as *Corallina officinalis* (see Moore, 1935, p. 299, for competition of *Balanus balanoides* and *Spirorbis borealis*).

The extent of the competition between *Chthamalus* and *Balanus balanoides*, both for space and for food, remains unknown. The food of each species requires investigation. But in localities where both species flourish there must certainly be competition for space. Denudation of the rock takes place largely during winter as a result of storms, and since *B. balanoides* spat settle in early summer, whereas *Chthamalus* spat do not settle until autumn or winter, the *Balanus* will have time to become well established before the *Chthamalus* appear. In the absence of other disturbing factors this would favour a predominance of *Balanus*, and it probably does actually do so in regions where both species are common, and especially in the lower part of the shore. This effect may quite probably determine the lower limit of *Chthamalus* in these localities.

However, some important factor, other than competition with *Balanus balanoides*, must be operative. This is shown by the fact that in certain localities the lower limit of *Chthamalus* is above the upper limit of *Balanus balanoides*. For instance, as shown in Fig. 1, at Òb Allt an Daraich, in Skye, there was a zone a few centimetres wide of fairly abundant *Chthamalus*, below which there was an almost bare zone several centimetres wide with hardly any barnacles of either species; and below this again *Balanus balanoides* was abundant. Thus the two species intermingled only to a very slight extent. Fischer also (1928) has written (translation) that "at the Point of Granville, at the margin of their geographical distribution, the *Chthamali* are practically restricted to levels which are above the limit of *B. balanoides*...". In these localities it must be presumed that the lower limit of *Chthamalus* is determined by some harmful effect of excessive immersion in sea water (see below, p. 534).

In addition, the lower limit of *Chthamalus* varies with geographical situation. For instance, at the western extremity of the English Channel the vertical distribution embraces the whole littoral region, but as *Chthamalus* approaches the limit of its geographical distribution eastwards in the English Channel, so its lower limit rises (Fischer-Piette, 1936). For geographical reasons it is not possible to demonstrate this effect so clearly up the west coast of Britain as the northern limit of distribution of *Chthamalus* is approached; but the data illustrated in Fig. 1 are sufficient to show that a similar effect exists. In the west of Scotland (e.g. Skye) *Chthamalus* is probably approaching its limit of tolerance of low temperature (see p. 530); whereas in the middle region of the Channel it is near the limit of adequate penetration eastwards of Atlantic water (see p. 528). It is of course possible that either of these factors might exert a stronger influence nearer low water, thereby restricting the *Chthamalus* to the higher levels where such influence was less. This may well be true at the Point of Granville. But at Skye by far the lowest temperature will be experienced during the period when the barnacles are left exposed to the air (in winter), and not when they are covered with water. Therefore at Skye it might be expected that if temperature were the only factor concerned the *Chthamalus* would be restricted to the lower levels, where they would be exposed for the shortest periods to the cold air. It therefore became necessary to postulate that the lower limit of *Chthamalus* is determined by a harmful effect of excessive immersion, and that *Chthamalus* is more sensitive to this influence in localities which are unfavourable in some other respect also. Such modifications of sensitivity will be discussed later (p. 534). It should be realized that it is not possible to distinguish between a harmful effect of immersion and a beneficial effect of emersion. For convenience we have followed the former interpretation. This factor appears to exert a strong influence on *Balanus balanoides* also (Moore, 1935, p. 288).

Upper limit of vertical distribution

The upper limit of *B. balanoides*, when not elevated by splash nor (possibly) depressed by *Chthamalus*, is almost exactly at high water of mean neap tides (Fischer-Piette, 1929; Moore, 1935). That of *Chthamalus* is regularly higher, but information from localities undisturbed by splash is scanty. In Loch Sween the upper limit is near high water of spring tides (Kitching, 1935).

In most of the districts where both barnacles occur their zones overlap, and it is questionable whether or not the upper limit of *Balanus balanoides* may be depressed by the competition of *Chthamalus*. Actually there is no evidence of such an effect. From a comparison of the vertical distribution of the two species in regions where *Chthamalus* is relatively scarce (Fig. 1, p. 525 of this paper) and in regions where it is as abundant as *Balanus* (Moore, 1936, Fig. 4, p. 705), it appears that the effect of the occurrence of *Chthamalus* within the *Balanus* zone is to decrease the abundance of *Balanus*, but not to exclude *Balanus* completely. The nature of the competition between the two species is unknown. If it were merely competition for available space on which to settle, the *Balanus* would be the more likely to preponderate, as already suggested. It might, on the other hand, be a case of competition for the available food. Furthermore, at Plymouth *B. balanoides* is approaching a region which is apparently unfavourable to it. This is indicated by the fact that its progressive decrease in numbers westwards in the English Channel is accompanied, towards the extreme limit of its geographical distribution, by a failure of those individuals which survive to spawn. This has been found elsewhere (Moore, 1935, p. 290) to be an indication of unfavourable conditions. This might be expected to result in a decreased range of tolerance of *B. balanoides* towards certain other environmental factors. On the other hand, *Chthamalus* encounters a progressively more congenial environment westwards down the English Channel (see p. 526), and might therefore show an accompanying extension in range of tolerance for such factors. If then, owing to overcrowding, the two species are in conflict for a limited amount of food, the one with the greater tolerance for adverse conditions may be expected to survive, and to predominate over the less tolerant.

Relation to Atlantic Water

It has long been known that certain planktonic animals are characteristic of the enclosed waters of the North Sea, English Channel, and Irish Sea, whereas quite different ones characterize the open waters of the Atlantic and the western coasts of Ireland and Scotland washed by them. Russell (1935, 1936) has shown how some of these, and in particular *Sagitta elegans*, may be used as indicators of the movements of Atlantic water in and out of the mouth of the English Channel. An examination of the geographical distribution of *Chthamalus*, as shown in Fig. 2, makes it apparent that this species also is limited to those shores which are bathed by Atlantic water, being absent from the North Sea, upper Irish Sea, upper Bristol Channel, and eastern half of the English Channel. The only other instance, of which we are aware, of a non-planktonic organism for which a connexion has been suggested between geographical distribution and the presence of Atlantic water is *Echinus esculentus*. The occurrence of this species between tidemarks is, according to Reid (1935), limited to coasts bathed by water of Atlantic characters; although *E. esculentus* is more widely distributed at deeper levels. A comparison of the distributions of *Sagitta elegans*, intertidal *Echinus esculentus*, and *Chthamalus stellatus* reveals the following differences:

(1) In the English Channel *Chthamalus* extends plentifully up to Plymouth, and in small numbers up to Swanage; the eastern limit of *Sagitta elegans* fluctuates from the Scilly Isles eastwards; and intertidal *Echinus* only reach the Scilly Isles and the extreme tip of Cornwall.

(2) In the Irish Sea from its southern entrance *Chthamalus* penetrates farther northwards than does intertidal *Echinus*; *Sagitta elegans* occurs throughout the Irish Sea.

(3) In the Irish Sea from its northern entrance *S. elegans* and intertidal *Echinus* extend southwards to the Isle of Man, whereas *Chthamalus* does not come south of the Mull of Kintyre, as far as we know.

(4) In the North Sea, in its northern entrance, *Sagitta elegans* and intertidal *Echinus* penetrate a considerable distance southwards, whereas *Chthamalus* stops short at Dunnet Head (at the north-east corner of Scotland).

The explanation of these differences probably lies in the fact that the geographical ranges of *Sagitta elegans* and of *Echinus esculentus* extend northwards far beyond the British Isles; whereas *Chthamalus* reaches its northern limit in the north of Scotland, where it is probably limited by temperature. The unfavourable temperature conditions in the northern Irish Sea and in the north of Scotland probably render *Chthamalus* more sensitive to decrease in proportion of Atlantic water than it is in the warmer southern Irish Sea and English Channel; whereas *Sagitta elegans* and *Echinus*, not being on the edge of their geographical range, are not so affected. It must also be realized that *Sagitta elegans*, being planktonic, has a distribution that fluctuates considerably from time to time.

At present there is little or no clue as to what is the character which renders Atlantic water more favourable to *Chthamalus* than the water of an enclosed sea. It cannot be temperature, since this must be considerably higher on the Isle of Man, where *Chthamalus* is not found, than in the north of Scotland, where *Chthamalus* does occur. Similarly it cannot be salinity, since the

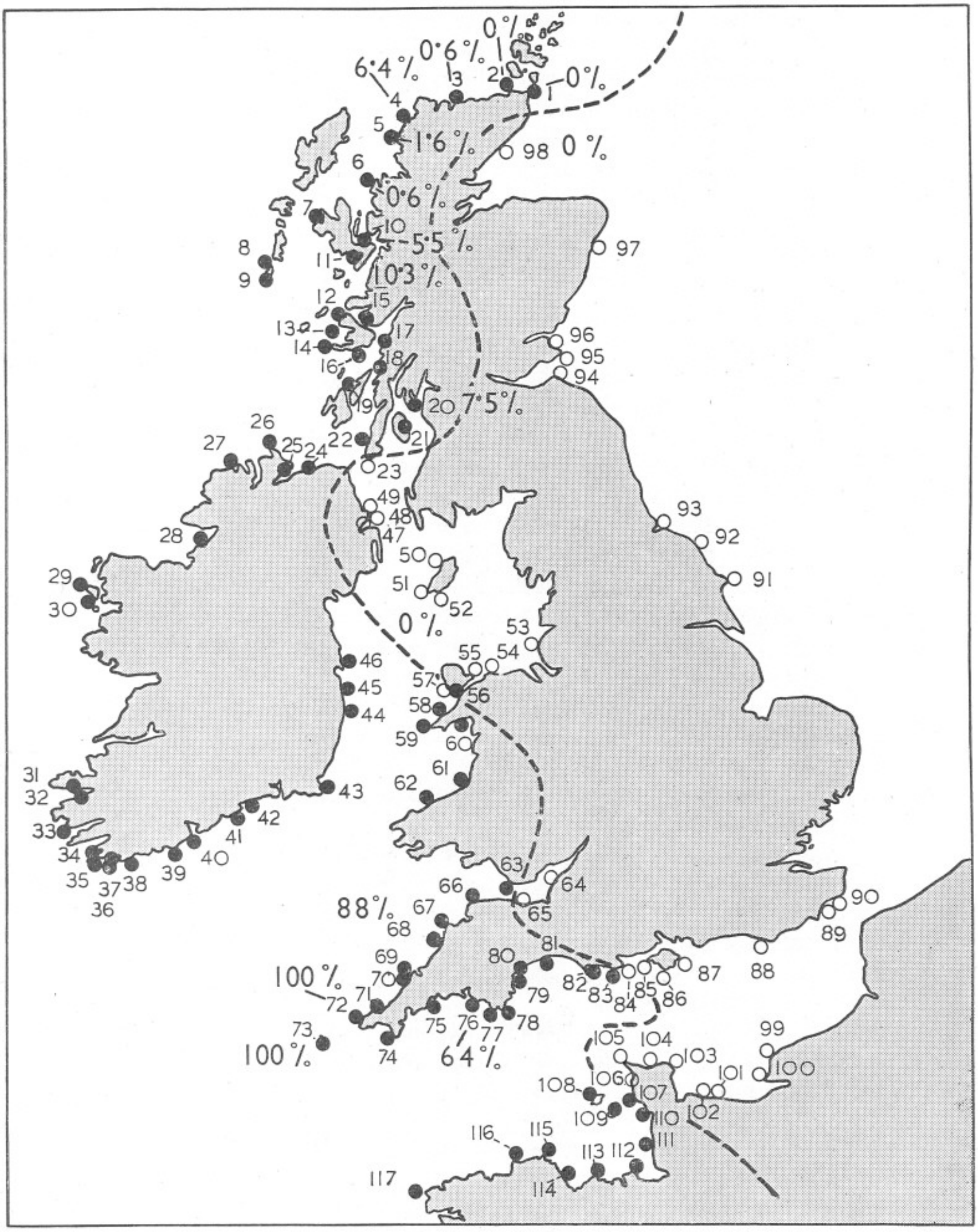

Fig. 2. The geographical distribution of *Chthamalus stellatus*. ○ indicates absent; ● indicates present. Numbers of stations (see Table I) are given in smaller type; the numbers in larger type represent the percentage by weight of *Chthamalus* in the total population of barnacles (*Chthamalus* and *Balanus balanoides*) between tide marks.

difference in salinity between the waters around Plymouth and those near Swanage is quite negligible in comparison with the range of salinity which *Chthamalus* tolerates in the estuary of the river Tamar at Plymouth. Perhaps it is the same unknown factor which Fischer-Piette (1936) has postulated to explain the preference of certain littoral species for regions which jut out into the neighbourhood of deep water, and of others for embayed regions.

Effects of Temperature, Salinity, Hydrogen Ion Concentration, and Currents; Penetration up Estuaries

Very little is known about the tolerance of *Chthamalus* for temperature. Moore (1935) has recorded a temperature of 36·3° C. within the mantle cavity of one *in situ* on the rocks during a low-tide period, and an even higher temperature could almost certainly be attained on a really hot day. No doubt a time factor would enter into any question as to the highest temperature consistent with survival. As regards the influence of low temperature, *Chthamalus* reaches its northern limit in the north of Scotland, where the February sea-surface temperatures, as given in Deutschen Seewarte Hamburg (1927), are about 6° C., although no doubt considerably lower temperatures occur on the shore itself. *Balanus balanoides*, on the other hand, extends northwards to the region where the shore is frozen in winter, and appears to be limited more by the mechanical action of the ice than by the low temperature.

The figures given for the salinity range tolerated by *Chthamalus* are of doubtful value for two reasons. A barnacle can close its aperture and so protect itself from a temporary lowering of the salinity of the surrounding water. And, in addition, minimal figures for salinity usually refer to the time of low water in the particular part of the estuary in question, whereas *Chthamalus* is usually restricted to a zone near the level of high water, and so is only covered by water of very much higher salinity. No figures are available for the minimal salinity which will allow either survival or feeding.

For the range of hydrogen ion concentration which *Chthamalus* can tolerate there are again no adequate figures. Fischer (1928) has recorded that *Chthamalus* can endure *p*H 9·0.

Wave action is favourable to *Chthamalus*, just as it is to *Balanus balanoides*, but water movement produced by a current can take the place of wave-produced movement. According to Fischer (1928) water movement produced in one way or the other is essential for its survival, and certainly we have found that *Chthamalus* does not survive nearly so well as *Balanus balanoides* in a tank supplied with running water and a tidal rise and fall but without wave action or a strong current. However, in Loch Sween, where conditions are for some unknown reason particularly favourable (Kitching, 1935), *Chthamalus* lives in extremely sheltered places where the current is slight. *Chthamalus* can also survive very muddy water, as for instance in the Tamar estuary.

The strong modifying influence which variation in one factor may have on the degree of tolerance of a given species for another factor is well illustrated by the relative penetration of *Chthamalus* and *Balanus balanoides* into different estuaries. In the lochs on the west coast of Scotland, where *Chthamalus* is near its northern limit, and may therefore be considered as living under generally less favourable conditions than *Balanus balanoides*, the latter penetrates usually to the extreme head of the lochs, if the shores are not too weed-grown, whereas *Chthamalus* usually stops short much nearer to the open sea. It may be either shelter from wave action or low salinity for which the tolerance of *Chthamalus* is here reduced. Farther south, in the Plymouth region, where *Chthamalus* and *Balanus balanoides* occur in more or less equal numbers, both species penetrate the estuaries of the Tamar and Avon to the same extent. Still farther south again in the neighbourhood of Roscoff, *B. balanoides*, which is here at the southern margin of its geographical range, is confined to wave-beaten rocks on the open shore, whereas *Chthamalus*, which is nearer to the centre of its range, extends far up the estuaries into the region occupied by the brackish water alga *Fucus ceranoides*.

Nature of Substratum

The distribution of *Chthamalus* along the coast of the "Isle" of Purbeck (Dorset) was studied in considerable detail, since here *Chthamalus* reaches the eastern limit of its distribution in the English Channel. However, this investigation was complicated by changes in the lithology. The chief rock formations contributing to the shore of the Isle of Purbeck are the Kimmeridge clay, Portland stone, Purbeck stone, Wealden sands, lower greensand, and chalk (Strahan, 1898). Of these only the harder rocks form substrata suitable for barnacles. The Portland stone (a hard limestone), Purbeck stone (also limestone), and chalk reach the shore at various positions along the coast, and *Chthamalus* was found to show a marked preference for Portland stone (Table II). On chalk it was only recorded on the sheltered sides of boulders or on flints. *Balanus balanoides* also was usually absent from chalk, especially when this was covered with green algal slime, but was plentiful on the clean chalk of the Old Harry Rocks. In other localities the abundance (or otherwise) of *B. balanoides* corresponded fairly closely with that of *Chthamalus*. The most likely alternative explanations of the undesirability of chalk are either (more probably) that it affords insecure holding (either for the larvae or for the adults) because of its smooth or even slimy surface, or that being porous it allows the barnacles to be desiccated from below in dry weather.

At two stations on the Purbeck coast both *Chthamalus* and *Balanus balanoides* were present in sufficient numbers for a detailed examination to be made of their vertical distribution. On the eastern promontory of Lulworth Cove the levels of maximal population density of the two species are separated by a vertical distance of about $1\frac{1}{2}$ m., and in the region of overlap of the two zones both species are very sparse. This seemed to indicate that the lower limit of *Chthamalus* was here in no way influenced by the competition of *Balanus balanoides*, but was on the other hand determined by "excessive immersion", just as is already believed to apply in northern Scotland. However, such a conclusion, though possibly correct, does not necessarily follow in this instance. The rock surface at Lulworth is much rougher near the level of high water of spring tides than it is lower down, and *Chthamalus* here shows a marked preference for rough patches of rock. It is therefore possible that towards lower levels sites suitable for *Chthamalus* become progressively fewer.

TABLE II

Locality*	Rock	Nature of surface	*Chthamalus*	*Balanus balanoides*
Swyre Head†	Upper chalk	Smooth, rather slimy chalk	On flints only, sparse	Absent
Durdle Door (west side)	Purbeck stone	Generally smooth	In cracks only	In cracks only
Lulworth Cove (west side)	Portland stone	Variable	Chiefly in crevices	Chiefly in crevices
Lulworth Cove (east side)	Portland stone	Variable	Plentiful in hollows, scarce on open rock	Plentiful
Arish Mell Gap (west side)	Upper chalk	Chalk boulders	Sparse; usually only on landward side of boulders	Sparse; usually only on landward side of boulders
Arish Mell Gap (east side)	Upper chalk	Nearly vertical; smooth, green and slimy	Only one specimen found	Absent
Tilly Whim	Portland stone	Variable, chert bands	Plentiful in hollows and on chert bands	Plentiful
Old Harry Rocks	Upper chalk	Smooth	Absent	Plentiful

* Localities are given in geographical order, from west to east.

† This headland is about three-quarters of a mile west of Durdle Door, and must not be confused with another "Swyre Head" farther east.

The influence of lithology and of texture of rock surface was more strongly marked on the cliffs below the Tilly Whim caves, near Swanage. Here the bedding planes are horizontal and there is therefore a vertical succession of various bands of limestone and chert, each weathered at its surface to a characteristic texture. As will be seen from Fig. 3 and Table III, the vertical distribution of *Chthamalus* does not conform to the usual arrangement of a belt with the maximal population density near the middle, and regions of less density above and below. There are here three levels of high population density, namely, bands A, E, and G, of which E and G are especially thickly populated. E and G are hard cherty bands, with coarse-textured surface weathered in an angular way; and the surface of A is also rather coarse. D, which also has a considerable population of *Chthamalus*, has coarse cherty nodules in it. On the other hand, the bands with relatively smooth surfaces, B, C, and F, have small populations of *Chthamalus*. It is noticeable also that

Chthamalus is specially abundant in certain small upward-facing pockets in the surface of band A, although the reason for this remains doubtful.

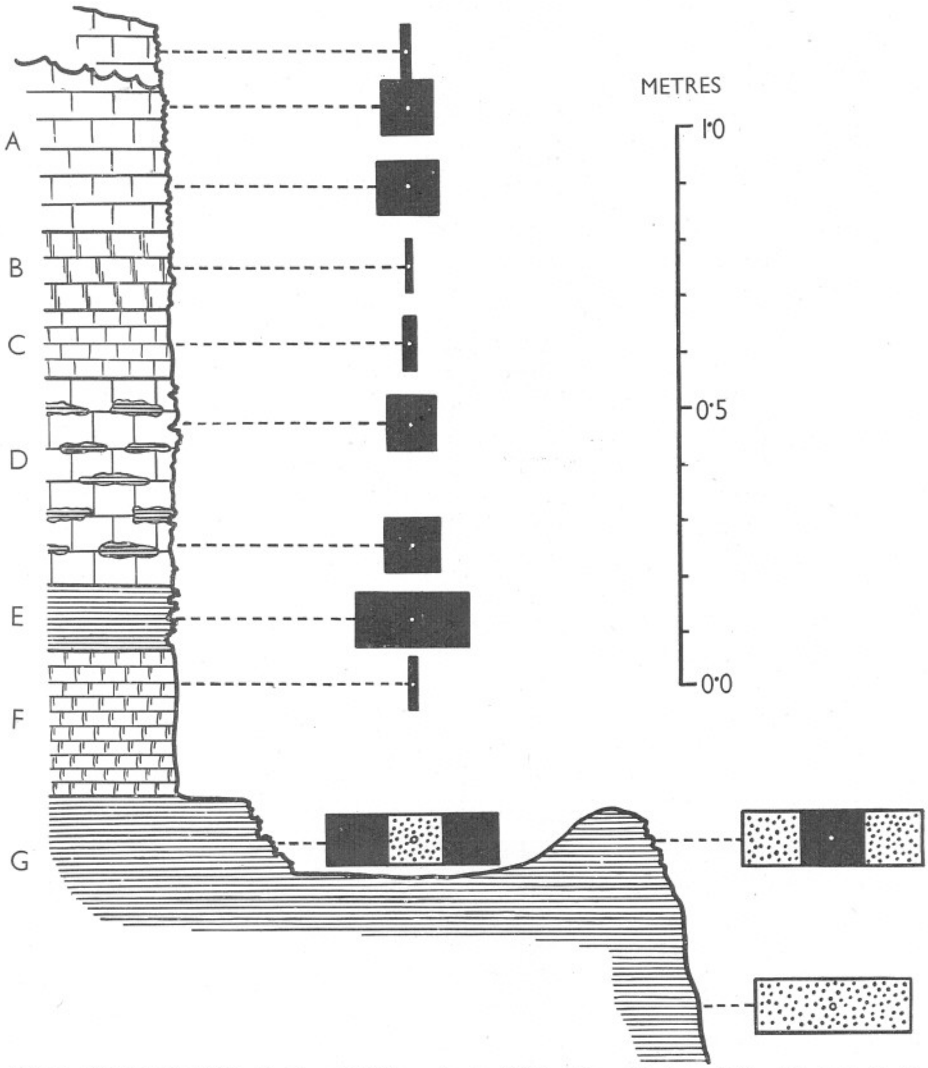

Fig. 3. The vertical distribution of *Chthamalus* (solid black) and *Balanus balanoides* (stippled) in relation to lithology at Tilly Whim, near Swanage, Dorset. For explanation of lettering see Table III. Brick pattern indicates limestone and horizontal shading indicates chert. The texture of the rock surface is indicated diagrammatically.

It appears from these observations that *Chthamalus* prefers a hard rough limestone to a soft smooth one, but it can exist on the latter in positions sheltered from violent wave action. Hatton (1938), in an experiment on

Balanus balanoides, found that the larvae failed to settle on polished marble except in depressions or scratches in the surface. He suggested that they were dragged away by water currents. On the other hand, it has also been shown (Kitching, 1935) that an excessively coriaceous surface is unfavourable to *Chthamalus*. It is also clear that on limestone shores, where the texture of

TABLE III

			Mean no. of barnacles per m.^{2}	
Band	Nature of rock	Nature of surface	*Chthamalus*	*Balanus balanoides*
A (top)	Limestone	Coriaceous	125	0
A (upper half)	Limestone	Coriaceous	620	0
A (lower half)	Limestone	Coriaceous	750	0
B	Limestone	Less coriaceous	80	0
C	Limestone	Smooth, greenish	180	0
D (upper part)	Limestone and chert	Uneven	600	0
D (lower part)	Limestone and chert	Uneven	670	0
E	Chert	Angular and creviced	1370	0
F	Limestone	Rather smooth, greenish	110	0
G	Chert	Hard, angular	2075	650
G (same level at outer edge of shelf)	Chert	Hard, smoother	730	2170
G (lower down, on outer side of shelf)	Chert	Hard, smoother	0	1875

N.B. The above figures can only be regarded as very rough. Each mean has been compiled from between three and ten counts. Each count was made on a separate 10 × 10 cm. square of rock surface, selected as typical of the band in question.

the rock surface is liable to show progressive changes from high water of spring tides downwards, it is necessary to interpret with great caution observations of the vertical distribution of littoral organisms.

Modifications of the Range of Tolerance towards Environmental Factors

In a number of instances, in attempting to explain the distribution of *Chthamalus*, we have suggested that its ability to endure conditions which are unfavourable in respect of one environmental factor may be modified by the action of another factor. For instance, its resistance to excessive immersion is thought to be reduced by deficiency of Atlantic water in the English Channel and probably by low temperature in the north and west of Scotland (p. 526). In addition, its tolerance of sheltered water and its power of penetration up estuaries are similarly reduced in both these regions. On the other hand, in the northern part of the Sound of Jura (west coast of Scotland), and in the lochs opening into it, *Chthamalus* is markedly more tolerant of environmental factors than it is on the neighbouring parts of the coast. In this quite restricted favourable area *Chthamalus* penetrates far into extremely sheltered arms of the sea lochs, and is very much more abundant than in wave-exposed, and therefore presumably favourable, situations on the western (Atlantic) coast of Jura. This curiously local vigour of *Chthamalus* is difficult to explain, but is possibly connected with the abnormal tidal conditions in this area, which are such that the *Chthamalus* zone remains uncovered but subject to splashing for prolonged periods. Whatever may be the explanation, *Chthamalus* appears in this area to be unusually tolerant of various environmental factors. Some beneficial influence appears to ameliorate locally an environment which in some other respect (probably temperature) is none too satisfactory.

It might in certain cases be argued that there is no proof that one factor may modify the tolerance of *Chthamalus* towards another factor. For instance, as already suggested, unsuitable water might prove especially adverse in the lower part of the shore, and so raise the lower limit of *Chthamalus*. It is, however, difficult to frame plausibly any comprehensive explanation of the distribution of *Chthamalus* in terms of the direct action of environmental factors upon an organism with unvarying limits of tolerance. Why, for instance, should *Chthamalus* be able to withstand in Loch Sween or in the Tamar conditions towards which, on the north-west coast of Scotland or in the English Channel, it cannot make any approach?

Although the idea of modified tolerance seems obvious enough, we have not been able to find many comparable examples. The tolerance of *Procerodes* (=*Gunda*) *ulvae* for low salinity is dependent on the presence of sufficient calcium in the external medium (Pantin, 1931), but this is probably a direct effect of the calcium ion on the permeability of cell membranes. Although it is not possible to decide definitely until the interplay of all the various factors involved has been analysed, it seems that in *Chthamalus* the modification of tolerance takes effect by a change in the general vigour of the organism, rather than by the direct action of one factor on some particular part of the organism which is especially susceptible to the influence of another factor.

Perhaps a more satisfactory parallel example is provided by the effect of competition with one another on the temperature range of fresh-water planarians. Beauchamp & Ullyott (1932), working in parts of eastern and southern Europe, investigated the distribution of *Planaria montenegrina* and *P. gonocephala* in swiftly flowing streams in which the temperature of the water increased progressively from the source downwards. In streams in which both species occurred, *P. montenegrina* occupied an upper section extending from the source down to where the temperature reached 13–14° C., and *P. gonocephala* ranged from this latter level downwards. There was scarcely any overlapping of the two species. But in certain streams, from which *P. montenegrina* was absent, *P. gonocephala* extended up to sources as cold as those normally occupied exclusively by *P. montenegrina* (e.g. 8·5° C.).

And in certain streams, from which *P. gonocephala* was absent, *P. montenegrina* extended down to parts of the stream which would, in the presence of the other species, have been too hot (16–17° C.). Thus competition seems to influence the range of temperature tolerated by these planarians.

In addition, Broekhuysen (1936) has recorded a decrease in tolerance of low salinity in *Carcinus maenas* (the shore crab) in winter, as compared with summer when the temperature is higher.

In general, therefore, it seems permissible to postulate that departure from the optimal condition for one environmental factor may reduce the tolerance range of a species for a second factor. It seems possible that this effect will be found to play an important part in the distribution of organisms in an environment such as the shore, where conditions are so exceptionally varied.

Growth Rate

Hatton (1938), in a supplement to previous work of Hatton & Fischer-Piette (1932), has given figures relating to the growth of newly settled *Chthamalus* at different levels, during a period of 18 months. In a wave-exposed locality the lengths (mm.) attained were:

	1930–1 spat		1931–2 spat	
	After 9 months	After 18 months	After 9 months	After 18 months
Slightly above high water of neap tides	2·6	5	2	4·1
Slightly below high water of neap tides	3·6	4·1	2·5	3·6
Mid-tide level	4·1	4·2	2·7	3·4

Thus in the first year growth was greatest at the lowest level, but in the second year at the highest. However, in a more sheltered locality growth was greatest at the highest level in both years. Seasonal variation in growth rate was slight.

An attempt was made to estimate the growth rate of *Chthamalus* at Drake's Island, Plymouth, by means of periodic measurements of a number of barnacles belonging to several year groups at three different levels on the rocks, the individual barnacles being recognized from a photograph. Unfortunately, the extreme irregularity of their outline, and the smallness of the growth observed, introduced too great an error to permit any deductions on seasonal variation in growth rate to be made, so that only the total growth for the period is used here. Hatton (1938), however, found little variation in growth rate throughout the year. The three levels selected represent the upper, middle and lower regions occupied at Plymouth by *Chthamalus*, and it is unfortunate that there is so little difference in level between them. It would be better if the experiment could be repeated somewhere where *Chthamalus* occupies a wider zone on the shore. The results obtained during 10 months' growth are shown in Fig. 4. All sizes of barnacle show definitely greater growth rates at lower levels. The newly settled 1936 spat, when measured in December 1936, averaged $\left(\frac{\text{length} + \text{breadth}}{2}\right)$ 1·61, 2·22 and

2·19 mm. respectively at the upper, middle and lower station, and in October 1937 these spat had grown to 3·07, 3·99 and 4·18 mm. respectively. On the same date the 1937 spat averaged 0·65, 0·79 and 1·15 mm. From the measurements made on Drake's Island the following averages were derived for the size $\left(\frac{\text{length} + \text{breadth}}{2}\right)$ of *Chthamalus* of various ages at the three levels

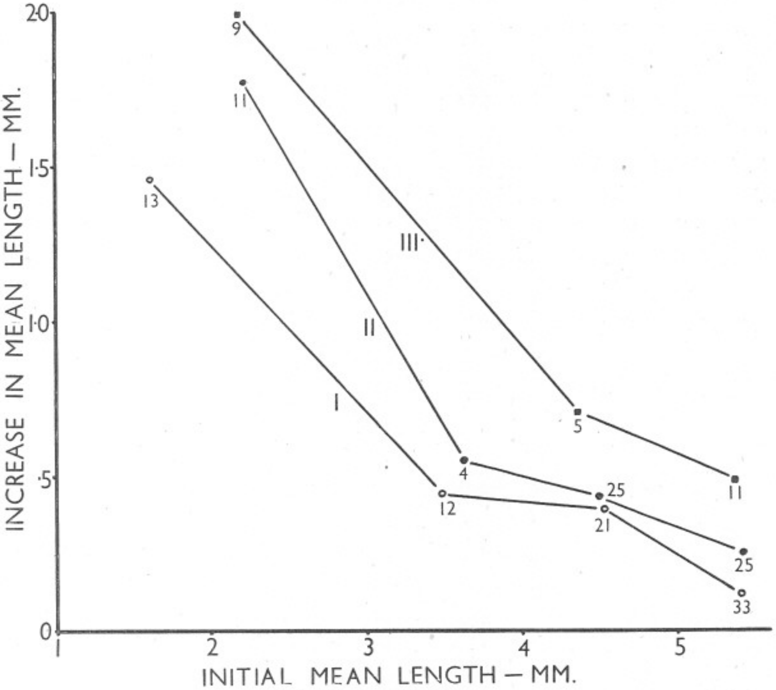

Fig. 4. Increase in mean length $\left(\frac{\text{length} + \text{breadth}}{2}\right)$ of *Chthamalus stellatus* at three levels at Drake's Island, Plymouth, between December 11, 1936 and October 20, 1937. The figures alongside the curve indicate numbers of specimens. Levels: I, +1·36 m. (O.D.); II, +0·81 m. (O.D.); III, +0·41 m. (O.D.).

in question, but it must be emphasized that these values are no more than very rough approximations:

Level*	Number of months since settlement of spat			
	12	24	36	48
+1·36 m.	2·0	3·7	4·2	4·6
+0·81 m.	3·8	4·5	5·0	5·4
+0·41 m.	3·9	5·0	5·6	6·0

* Levels above ordnance datum.

Whereas at Plymouth the rate of growth remained greatest at the lowest level, at St Malo there appears to have been some unfavourable influence at the lower levels which operated progressively more severely as the *Chthamalus* grew older, and which was also rendered more effective by lack of wave action. Further observations are desirable from localities near the centre and at the edge of the geographical range of *Chthamalus*.

Mortality Rate

Figures for the mortality rate of barnacles are somewhat scarce. In the sublittoral region, although in some places the barnacles may persist for long periods, in general it is probable that they appear as early colonists of areas denuded by winter storms and other means, but that they are soon smothered by later arrivals such as ascidians, sponges, and algae (Kitching, 1937). The mortality rate of *Balanus balanoides* found by Moore (1934) for a small number of individuals of over 4 months old was 35 % per annum in the lowest levels and 3 % in the uppermost. Hatton (1938) has also found a higher mortality rate for *B. balanoides* at the lower levels. The figures for *Chthamalus* on Drake's Island were as follows:

Level	No. of individuals	Mortality rate % per annum
+1·36 m. O.D.	71	3·3
+0·81 m.	70	16·6
+0·41 m.	30	46·5

Hatton (1938) found a mortality rate near St Malo of 24–25 % per 20 months around the level of high water of neap tides, and of 96 % at about mid-tide level, in a wave-beaten situation. In a sheltered situation the rate was higher.

It is noteworthy that most of the deaths at Plymouth occurred during a period of severe winter gales when the shore showed signs of considerable disturbance, and numbers of *Patella* were found with their shells fractured, apparently by blows from boulders. Probably therefore most of the *Chthamalus* were killed by stones pounded against the rocks by waves.

Enemies

The enemies of *Chthamalus* are much the same as those of *Balanus balanoides*, with the difference that where *Chthamalus* occupies a higher zone on the shore it is less liable to be attacked by *Purpura lapillus*. *Purpura* is undoubtedly their chief enemy. In addition no doubt many are killed or fractured by wave-borne stones and then eaten by small carnivores such as crabs and certain amphipods. Some are displaced by *Patella* in its wanderings (Hatton, 1938), and at the lower levels some are smothered by the overgrowth of algae and *Mytilus*. A certain number are probably killed and eaten by crabs and by shore fish such as wrasse. Herring gulls have been found to eat barnacles on occasions, but not in large quantities. Finally, an enemy which may play at the lower levels almost as serious a part as does *Purpura* is the polychaete, *Eulalia viridis*. As we are not aware of any previous record of the attacks made by *Eulalia* on barnacles, a note is given below of observations made by one of us (H. B. M.) at Drake's Island.

On a number of occasions when the shore was visited as the tide was receding, *E. viridis* was observed feeding in considerable numbers on barnacles on those rocks which were still wet, and on which the sun was not shining. After from half an hour to an hour of emersion the *Eulalia* had usually all disappeared. In June 1937, in an area of about 6 sq. m., about twenty *Eulalia* and a single specimen of a species of nemertine were seen feeding on *Balanus balanoides*. The movements of one *Eulalia* were watched in detail. First it moved for some distance across the barnacles. Then it stopped and explored the orifice of one barnacle for a period of a minute or more, during which it several times moved its head away a centimetre or so from the barnacle. It next applied its mouth to the opercular plates of the barnacle, the proboscis not being everted, and after a few seconds one of the plates burst outwards with an audible click. The *Eulalia* then arched its front end off the ground and everted its proboscis downwards into the aperture of the barnacle. For about 5 min. peristaltic movements were visible in the proboscis, and once or twice this was withdrawn for an instant from the barnacle. At the end of this time the worm left the barnacle, and moved off in search of another; and on examination the shell of the barnacle was found to have been completely emptied.

Acknowledgements

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Summary

Chthamalus stellatus is a littoral barnacle very similar in habitat and general ecological relations to another littoral barnacle, *Balanus balanoides*. In those localities where both species flourish they compete considerably for space, and also possibly for food. The fact that *B. balanoides* settles sooner after the winter storms than does *Chthamalus* probably favours the former.

Chthamalus is characteristically a southern species and *Balanus balanoides* a northern one, but the north and south ranges of the two species overlap in the British Isles and in France. The determining factor is presumably temperature.

Chthamalus is an Atlantic species, and *Balanus balanoides* is more characteristically a North Sea species. The essential factor in Atlantic water remains unknown, although in respect of a need for Atlantic water *Chthamalus* resembles *Sagitta elegans* and intertidal *Echinus esculentus*.

Except in especially favourable districts (see below), *Chthamalus* is usually

restricted to a zone in the upper part of the shore, whereas *Balanus balanoides* occupies a zone mainly below the *Chthamalus* zone. In certain places where the two zones do not overlap it is clear that the lower limit of *Chthamalus* is determined, not by the competition of *Balanus balanoides*, but by some adverse effect of excessive immersion.

Towards its northern limit of geographical distribution and towards regions where Atlantic water is deficient, *Chthamalus* extends less far down on the shore and less far into sheltered waters and estuaries. It seems that its tolerance of excessive immersion and of certain conditions characteristic of bays and estuaries becomes reduced in an environment unfavourable in respect of Atlantic water or temperature.

On Drake's Island, Plymouth, the growth rate and rate of mortality of *Chthamalus* were found to be greater at the lower levels.

The chief enemy of *Chthamalus*, as of *Balanus balanoides*, is *Purpura* (= *Nucella*) *lapillus*. The polychaete *Eulalia viridis* was observed feeding on *Balanus balanoides*. Many barnacles are probably killed by stones pounded against them by the waves.

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