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(Text-figs. 1-3)

CONTENTS

DACE

							PAGE	
Introduction							129	
The faunas of the s	eaw	eeds:						
Pelvetia canalicul	ata						136	
Fucus spiralis							136	
Lichina pygmaea							138	
Fucus vesiculosus							140	
Ascophyllum nodo	sum	and J	Polysi	phonia	lan	osa	142	
Fucus serratus							151	
Gigartina stellata					•		155	
Laminaria digitat	a ho	oldfast	ts				157	
Summary and com	pari	son of	these	e fauna	is		168	
Comparison with p	opu	lation	s of s	oil, etc		• •	173	
Distribution of the	ani	mals o	on the	shore			174	
List of species							178	
Acknowledgements							181	
Summary .							182	
References .							182	

INTRODUCTION

While I was Student Probationer at the Plymouth Laboratory I started an examination of the faunas associated with seaweeds on Church Reef in Wembury Bay. I set out to find there the limits of distribution of as many intertidal species as possible, to estimate the numbers of each species present in each weed, and to compare, both qualitatively and quantitatively, the faunas of the various weeds with each other. I have omitted the phylum Protozoa.

First of all it was necessary to find out the limits of the zones of seaweed in relation to tidal levels, and this part of the work has been described in a previous paper (Colman, 1933). While the seaweeds were being surveyed, samples of them were collected whose animal contents formed the material for the present paper. It is therefore necessary to recapitulate briefly the methods and results of that survey.

Wembury Bay lies between the Great Mewstone and Gara Head just to the eastward of Plymouth Sound, and is mostly less than 5 fathoms (9 m.)

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deep (see Map, Fig. 1). It is partly sheltered by the Great Mewstone from the full weight of south-westerly gales, but is exposed to considerable seas from the southward. Church Reef projects about a quarter of a mile towards the middle of the bay, and is almost entirely covered at high-water of spring tides. On its landward parts it supports dense growths of algae and lichens.

The zonation of the seaweeds was examined on a system of four linear traverses. Three of them radiated out from a high point near the middle of



Fig. 1. Map showing the position of Church Reef in the Plymouth District.

the reef which I have called Central Rock or C.R. Each traverse was marked out by triangular holes cut in the rock at intervals of about 45 ft. (14 m.). Some of these marks are still visible after nine years. Traverse A, 222.5 ft. (67.9 m.), lay towards the Coastguard look-out on Gara Head; Traverse B, 367.5 ft. (III.6 m.), towards the Great Mewstone; Traverse C, 382 ft. (II6.0 m.), towards Wembury Church. In addition, a fourth line, Traverse D, was laid out from the landward end of Traverse C for 198 ft. (60.3 m.) in an easterly direction. A and B reached low-water mark on the east and west sides respectively of the reef, C was almost all between high- and low-water neaps, and D went above the limits of marine algal vegetation. Table I gives the details of the four traverses. Their approximate positions on the reef are

130

shown in the Map, Fig. 2, which is taken from the Devonshire sheet CXXX 6 of the 1 in 2500 Ordnance Survey. Each traverse was levelled to the nearest hundredth of a foot by Mr Michael Spender, using as starting and finishing point a bench mark, 20.56 ft. (6.27 m.) above Ordnance Datum, on the southwest corner of the house adjoining Wembury Hill, and 2.70 ft. (0.82 m.) from the ground.

Traverse True bearing	I	A 59°	2	B 45°		C 4°	D 94°		
	Feet	Metres	Feet	Metres	Feet	Metres	Feet	Metres	
C.R. to Mark I	50	15.2	43.5	13.3	65	19.8			
CVII to DI							60	18.3	
I to II	52	15.8	44	13.4	41	12.5	61	18.6	
II to III	39.5	12.0	41	12.5	42	12.8	57	17.3	
III to IV	35	10.6	41	12.5	44	13.4	20	6.1	
IV to V	46	14.0	74	22.5	67	20.4			
V to VI			35	10.6	64	19.5			
VI to VII			30	9.1	59	17.9			
VII onwards			59	17.9					
Total*	222.5	67.9	367.5	111.6	382	116.0	198	60.3	

TABLE I. DIMENSIONS AND TRUE BEARINGS OF TRAVERSES

Table II shows the tidal data for Devonport, which are applicable also to Wembury Bay. In this survey all heights are given relative to Ordnance Datum. This is a fixed level throughout Great Britain, whereas Chart Datum, which is about mean low-water springs, varies from place to place according to the range of the tides.

The tidal levels are not directly applicable in the field, on account of the "splash" or "wash" zone formed by breaking waves. This zone raises the effective level of the sea by an amount difficult to compute exactly, but which I estimate to be on the average about 2 ft. (0.6 m.) on Church Reef. In the previous paper (Colman, 1933, p. 453) I used the term "splash-zone",

TABLE II. TIDAL LEVELS AT DEVONPORT, 1930, IN RELATION TO ORDNANCE DATUM

	Predicte	d levels	of 2 ft. o	r wash zone r o∙6 m.
	Feet	Metres	Feet	Metres
Extreme high-water springs	+ 8.68	+2.65	+ 10.68	+3.25
Mean high-water springs	+ 7.28	+2.22	+ 9.28	+2.82
Mean high-water neaps	+ 3.83	+1.12	+ 5.83	+1.75
Extreme (lowest) high-water				
neaps	+ 2.18	+0.66	+ 4.18	+1.56
Ordnance Datum	0.0	0.0		
Mean sea-level	- 0.27	-0.08	+ 1.73	+0.52
Extreme (highest) low-water				
neaps	- 2.82	-0.86	- 0.82	-0.56
Mean low-water neaps	- 3.82	-1.10	- I·82	-0.26
Mean low-water springs	- 8.24	-2.21	- 6.24	-1.91
Chart Datum	- 8.42	-2.62		
Extreme low-water springs	- 10.42	-3.52	- 8.42	-2.65
* S	ee note on pag	ge 183.		

9-2





Fig. 2. Positions of the traverses and marks on Church Reef.

"splash-zone" and modified the terminology. He divides the region affected by wave action into three zones:

(a) The wash zone, immersed by each wave and effectively almost as wet as though completely submerged; this is the same as my "splash zone".

(b) The splash zone, splashed by individual drops but not by whole waves. I do not think that this zone is of much significance at Wembury, because owing to the shallowness of the bay the waves break before washing onto the reef in the region I surveyed, and do not throw up much heavy spray. I realize, however, that on coasts subjected to heavy wave action breaking directly on the rocks, as on much of the South African shore, this zone will have very real significance. I will therefore refer henceforward only to a wash zone on Church Reef.

(c) The spray zone, reached by spray in the form of fine mist in heavy weather. This zone again will be important in regions subjected to really heavy seas, but I do not take it into account in Wembury Bay. On-shore gales in the Plymouth district are usually accompanied by heavy rain which will mitigate to a large extent the effects of salt spray, while dry gales are usually off-shore, from the north-west.

When the distribution of animals and plants is given below in terms of tidal levels, it will be assumed that these levels have been raised 2 ft. (0.6 m.) by the wash zone.

Samples of seaweed were taken more or less at random along each traverse, the exact position and height of each sample being determined. From Traverse A there were taken nine samples of four species of weed; from Traverse B, eighteen samples of five weeds; from Traverse C, ten samples of four weeds; from Traverse D, thirteen samples of three weeds. There were thus fifty samples in all. They were divided among eight different seaweeds, which can now be listed, giving for each the number of samples and the limits of distribution on Church Reef, the heights being given above or below Ordnance Datum (see Table II). Each sample was given a number consisting of a letter referring to the plant, and a numeral. In this paper the samples will always be referred to on this system.

Pelvetia canaliculata (five samples, AI to A5); from +7.49 ft. (2.3 m.) down to +4.91 ft. (1.5 m.), or from half way between mean high-water springs and neaps down to just above extreme (lowest) high-water neaps.

Fucus spiralis (six samples, BI to B6); from +5.79 ft. (1.9 m.) down to +3.19 ft. (1.0 m.), or from mean high-water neaps down to a foot below extreme (lowest) high-water neaps.

Lichina pygmaea (four samples, CI to C4); from above +6 ft. (2 m.) down to +0.04 ft. (0.0 m.), or from above mean high-water neaps down to just above extreme (highest) low-water neaps.

Fucus vesiculosus (three samples, D1 to D3); all just above mean low-water neaps); limits of distribution not determined.

Ascophyllum nodosum and Polysiphonia lanosa (twelve samples, EI to EI2); from +3.40 ft. (1.0 m.) down to -4.11 ft. (-1.3 m.), or from just below extreme (lowest) high-water neaps down to half-way between mean low-water neaps and springs. These two algae are treated as a unit, since wherever Ascophyllum occurs on Church Reef, Polysiphonia is growing as an epiphyte upon it. Fucus serratus (ten samples, FI to FIO); from +1.40 ft. (0.4 m.) down to -8.6 ft. (-2.6 m.), or from mean sea-level down to extreme low-water springs. Gigartina stellata (four samples, GI to G4); from -5.0 ft. (-1.5 m.), or from above mean low-water springs, down to below all tide-marks.

Laminaria digitata holdfasts (six samples, HI to H6); from -6.23 ft. -1.9 m.), or from mean low-water springs, down to below all tide-marks.

Table III shows the date of collection, position on the traverses, height on the shore and weight, of each sample, and the Map, Fig. 3, shows their distribution along the traverses. The samples were measured by damp weight, and no allowance has been made for differential water loss by evaporation at the various levels on the shore, though it must be considerable as between, say, *Pelvetia canaliculata* and *Fucus serratus*. The weight of the sample in each case

TABLE III. PARTICULARS OF THE FIFTY SAMPLES OF EIGHT SPECIES OF WEED

** * *

	Sample	Weight		Position on	relative
Seaweed	no.	in g.	Date	traverse in m.	in m.
Pelvetia canaliculata	A 1 A 2 A 3 A 4 A 5	197 52 51 53 97	30. vi. 30 10. vii. 30 11. vii. 30 6. i. 31 20. iii. 31	D I 11.2 D II D III 4.6 D IV D II 2.1 D III D I 18.3 D II D I 7.3 D II	+1.52 +1.95 +1.76 +2.01 +1.49
Fucus spiralis	B 1 B 2 B 3 B 4 B 5 B 6	408 94 80 93 56 77	24. vi. 30 10. vii. 30 11. vii. 30 6. i. 31 6. i. 31 20. iii. 31	D I 0.9 D II D II 1.8 D III D I 5.2 D II D I 0.3 D II D II 0.6 D III D I 7.0 D II	+1.18 +1.67 +1.37 +1.15 +1.17 +1.49
Lichina pygmaea	CI C2 C3 C4	11 12 14 24	5. ix. 30 5. ix. 30 7. i. 31 20. iii. 31	CR 11.5 AI CR 0.9 AI CR 1.8 BI CR 1.5 BI	+0.06 +1.34 +1.51 +1.51
Fucus vesiculosus	D I D 2 D 3	87 78 87	15. vii. 30 15. vii. 30 7. i. 31	CV 13.7 CVI CV 11.5 CVI CV 13.1 CVI	-0.40 -0.52 -0.46
Ascophyllum nodosum and Polysiphonia lanosa	E I E E 2 E E 2 E E 5 E E 5 E E 5 E E 10 E E 112	350 670 529 151 119 103 202 84 96 84 117 68	13. v. 30 14. v. 30 2. vii. 30 15. vii. 30 23. vii. 30 23. vii. 30 24. vii. 30 25. vii. 30 28. viii. 30 5. i. 31 6. i. 31 20. jii. 31	B II 1*8 B III C IV 2*4 C V C VII 4*6 D I C VI 13*7 C VII C V 14*6 C VI C 1 4*6 C VI C 1 5*5 C II B II 9*4 B III B I 9*4 B III C VI 8*2 D I C VI 8*2 D I	$\begin{array}{r} -0.52 \\ +0.40 \\ +0.27 \\ +0.67 \\ -0.09 \\ -0.30 \\ +0.37 \\ -1.00 \\ -0.43 \\ -1.00 \\ +0.73 \\ +0.06 \end{array}$
Fucus serratus	F 1 2 3 4 5 6 7 8 9 10	364 335 395 91 131 82 85 99 93 77	2. vi. 30 11. vi. 30 23. vii. 30 26. vii. 30 28. viii. 30 28. viii. 30 5. i. 31 5. i. 31 3. iv. 31	B III 8'2 B IV AI 12'2 A II C I 12'2 A II C I 12 C II B V 4'3 B VI B V 4'3 B VI B V 7'9 B VI B I 12'8 B II B III 11'8 B IV B VII 0'9	- I·49 - I·31 - I·86 - 0·40 - I·95 - I·37 - I·89 - 0·58 - I·83 - I·76
Gigartina stellata	G 1 G 2 G 3 G 4	70 60 62 47	26. vii. 30 28. viii. 30 7. i. 31 3. iv. 31	A IV 0.9 A V B VI 7.9 B VII B VII 6.7 B VII 0.6	- 1.98 - 1.64 - 1.89 - 1.70
Laminaria digitata holdfasts	H 1 H 2 H 3 H 4 H 5 H 6	17 63 92 25 52 104	27. viii. 30 27. viii. 30 27. viii. 30 27. viii. 30 27. viii. 30 7. i. 31 3. iv. 31	A V A V 1.2 B VII + B VII + B VII 9.1 Near A V	-1.98 -2.59 -2.65 -1.86 -2.77 -2.7

134

includes that of the animals living in it. The weights of the samples ranged from 11 to 670 g., which perhaps merits some explanation. The early samples were large, but were found to take so long to examine thoroughly that a smaller



size was adopted, the collecting unit being in most cases a I lb. honey-jar. In *Lichina pygmaea*, the fauna proved to be so abundant that the contents of a 3 by I in. tube were sufficient for comparison with the other weeds. Each sample of *Laminaria digitata* consisted of one holdfast.

THE FAUNAS OF THE SEAWEEDS

The fauna of each weed will now be considered in detail, working roughly from high-water downwards.

Pelvetia canaliculata (Table IV)

This seaweed lives higher up the shore than any other, and supports a very scanty fauna. *Hyale milssoni* was the only animal that occurred in all five samples, once in fair abundance (48 per 100 g. in A 1). There was one *Ligia oceanica* in A 1 and several in A 2 and A 3, but none in either of the other two samples; *Ligia* was not found among any other algae in this survey. *Pelvetia* lives well outside the ranges of *Littorina littorea* and *L. obtusata*, but *L. saxa-tilis* was not uncommon. *L. neritoides* was not identified but may form part

TABLE IV. PELVETIA CANALICULATA. ANIMALS INHABITING FIVE SAMPLES, IN NUMBERS PER 100 G. OF DAMP WEED

Sample no. Weight in g. Date Position in m.		A 1 197 30. vi. 30 D I 11.2 D II	A 2 52 10. vii. 30 D III 4.6 D IV	A 3 51 11. vii. 30 D II 2.1 D III	A 4 53 6. i. 31 D I 18·3 D II	A 5 97 20. iii. 31 D I 7.3 D II
Height in m.	• •	+1.25	+1.62	+1.26	+2.01	+1.49
Nematoda			17			
Oligochaeta		I				
Isopoda Ligia oceanica		I	38	37		
Amphipoda Hyale nilssoni		48	6	6	2	15
Insecta Libura maritima					2	
Diptera (larvae)			2			
Gastropoda						
Littorina saxatilis			17	6	2	
Littorinidae (juv.)	5	14			
	Total	55	94	49	6	I5

of the young Littorinidae in A I and A 2. There were no copepods or polychaetes. Curiously enough, the lowest sample, A 5 at +1.5 m., contained the smallest number of species, 15 *Hyale nilssoni* making up the whole catch, while the highest sample, A 4 at +2.0 m., gave the smallest total catch, including only two each of *H. nilssoni*, *Lipura maritima* and *Littorina saxatilis*. Sample A 2, though from a level only 0.06 m. lower than that of A 4, contained the largest and most varied fauna found among *Pelvetia*. There is no correlation with height on the shore between these samples, but the very small catches in January and March may indicate a seasonal dearth of animals. The number of insects was remarkably low when compared with those in habitats farther down the shore.

Fucus spiralis (Table V)

Fucus spiralis occurs on the rocks immediately below Pelvetia canaliculata, and occupies a zone around high-water neaps with a vertical range of rather more than 0.6 m. The six samples, B I to B 6, cover most of this range. All

except B I contain faunas similar to each other and to those of *Pelvetia*. Hyale *nilssoni* is again the most abundant animal, varying from 7 to 85 per 100 g. No correlation with tidal levels can be seen in this case; it is true that the lowest sample but one, B 5, contains the fewest *Hyale* and the highest sample, B 2, the most, but B I and B 4 from almost exactly the same level as B 5 each contain 70 *Hyale*. The latter sample and B 4 were collected, too, on the same day, which seems to rule out any seasonal difference as regards this species.

TABLE V. FUCUS SPIRALIS. ANIMALS INHABITING SIX SAMPLES, IN NUMBERS PER 100 G. OF DAMP WEED

Sample no		B r	B 2	B 2	B 4	B 5	B 6
Weight in g		108	01	80	03	56	77
Date		24 11 20	TO VII 20	TT vii 20	6 i. 31	6. i. 31	20. iii. 31
Date Position in m	•.•	D L 0:0 D II	D II * 9 D III	DI CODII I	LOS DIL	DIL 0.6 DIII	DI 7.0 DII
Height in m	•••	DIOGDII	D II 1.6 D III	1.32 0 11 1	+ 1.15	+1.17	+1.40
Height in m.	• •	+1.19	+1.02	+1.3/	+115	1 /	
Nematoda		6	I	I		4	/
Turbellaria or Nemertinea		2					
Polychaeta							
Fabricia sabella			I			4	
Sabellidae (juv.)			I				
Oligochaeta		I				18	
Ostracoda		2	I				
Copepoda Harpacticoida							
Harpacticus chelifer		3					
H. gracilis		6	I				
H. flexus		12					• •
Zaus spinatus		15					
Idva furcata		102					
Parathalestris harbacticoi	des	3					
Westwoodia nobilis		2					
Dactylopusia brenicornis		т					
Laophonte littoralis			r				
Laophonte sp.		· · ·		I			2
Harpacticoida (indet.)		2					
Isopoda		5					
Idotea granulosa		т					
Naesa hidentata		Ť			2		
Amphipoda		<u>^</u>					
Hyale nilesoni		70	85	25	70	7	18
Decanoda		10	05	-5	1-		
Carcinus maenas		т					
Insecta		^					
Libura maritima							I
Aptera (indet)		•••					
Diptera (larvae indet)		*				2	
A carina			4		6	2	2
Gastropoda		3	3	-			
Littoring obtweata		*			т	9	I
Linorina oblusata		1					
Lamma en		1	2				
Littorinidae (ium)		3	3		21		6
Littorinidae (Juv.)		24	9	2	~1	6	27
	Total	266	114	30	100	40	37

Acarines were always present, though scarce, and these samples also contained occasional nematodes, oligochaetes and young Littorinidae. Still rarer were copepods (except in B I), ostracods, *Lipura maritima*, and the larvae of diptera.

These remarks apply equally well to sample B I except for one group, the copepods, which in this sample alone were quite numerous and were represented by at least ten species. Of 149 per 100 g., 102 were *Idya furcata*, 15 *Zaus spinatus*, 12 *Harpacticus flexus* and 6 *H. gracilis*. A total range in height of only 0.03 m. covered the three samples B I, B 4 and B 5, and B I was only 0.6 m. away from B 4; yet the copepods occurred only in B I. It is difficult to account for this on a seasonal basis, for B 3 was collected only

a fortnight later than B I and from a level only 0.2 m. higher on the shore, but contained the smallest numbers both of individuals and species of any of the samples of *Fucus spiralis*. It is true that B I was much larger than the other samples, but with the exception of the copepods its contents were very similar to those of the others, indicating that the latter were large enough to give valid results. Had copepods been present in any number in the other samples they could not have been missed.

Lichina pygmaea (Table VI)

The population inhabiting the lichen *Lichina pygmaea* is perhaps the most remarkable on the shore. This lichen grows as small tufts only about 2 cm. in height on rocks between high-water springs and mean sea-level or a little lower. These tufts may grow closely enough together to form a more or less continuous covering of the rock over a few square feet at a time, but the

TABLE VI. LICHINA PYGMAEA. ANIMALS INHABITING FOUR SAMPLES, IN NUMBERS PER 100 G. OF DAMP WEED

Sample no.		Сг	C 2	C 3	C4
Weight in g.		II	12	14	24
Date		5. ix. 30	5. ix .30	7. i. 31	20. iii. 3I
Position in m.		C.R. II'S A I	C.R. 0.0 A I	C.R. 1.8 B I	C.R. T.S.B.I
Height in m.		+0.06	+1.34	+1.21	+1.21
Nematoda Oligochaeta		9			
Lumbricillus pumilio		27	8	7	
Chripedia Chthamalus stellatus			202	202	47.7
D -louis L -louis		/3	292	293	417
Balanus balanoides		55	••	••	• •
Isopoda			269 4	* ⁹ ***	
Cumpecopea nirsuta		3772	2005	2890	2204
Amphipoda Hauda milacomi				96	0
Insecta		40		80	0
Libura maritima		OT			
Petrobius maritimus		18			
Geranomyia unicolor (larvae)		46	175	64	104
Other Diptera (larvae)		40	*/5	04	104
A corino		109		170	29
Pelegranda		1401		1/9	07
Mytilus edulis (inv.)		OT		τ.4	21
Lasaea rubra		0418	1550	12140	TTETE
Gastropoda		9410	4550	12140	115/5
Littoring littoreg (inv.)		245	182	120	50
I obtugata (inv.)		-45	10	165	421
I constilie (nuv et ad)		22	40	105	421
L. suxutins (Juv. et ad.)	_		100	00	333
	Total	15536	8033	16050	15246

lichen never affords a dense mass of cover such as is provided by the fucoid algae. *L. pygmaea* seems to prefer the more exposed parts of the reef where it receives nearly the full force of the waves, but nevertheless the fauna it supports is by far the most abundant on the shore, at any rate in individuals, not being exceeded even by that of the *Laminaria* holdfasts.

The samples of *Lichina* collected were much smaller than those of the other weeds, being such as would fill a 3 by I in. glass tube, whereas the other plants were collected into I lb. honey-jars. *Lichina* is a small plant, so in order to fill a honey-jar with it it would be necessary to denude a considerable area of rock. Since *Lichina* grows on rather steep places it would be difficult

138

both to do this and to collect the whole sample from the same height on the shore. The population among *Lichina* is, however, so dense that the small samples collected were quite large enough for comparison with those of other weeds.

Four samples in all were examined, C I to C 4, and they contained 1709, 964, 2247 and 3659 animals in actual count, the samples weighing only II, 12, 14 and 24 g. respectively. The analysis of these samples is shown in Table VI, in numbers per 100 g. of damp lichen. These figures, when compared with those of other weeds on the shore, show how astonishingly numerous are the animals living among Lichina pygmaea. By far the most abundant is the small bivalve mollusc Lasaea rubra, with 9418, 4550, 12,140 and 11,575 in the four samples. This species is noted in the Plymouth Marine Fauna (1931) as "abundant between tide-marks on all rocky shores, in crevices, etc....rocks below the Hoe, very common among barnacles and the roots of Fucus, etc." I have not made comparative counts of Lasaea rubra in these different habitats, but they never appear to be so numerous as among Lichina; I have found none among the holdfasts of fucoid algae at Wembury, and the species occurred in no other samples in this survey. The density of its population can evidently vary somewhat, being in C 2 less than half what it is in any of the other samples.

The next most numerous animal is the isopod *Campecopea hirsuta*, whose numbers varied from 2204 to 3772 per 100 g. and were thus slightly more regular than those of *Lasaea*. Like *Lasaea rubra*, *Campecopea hirsuta* occurred in no other samples than those of *Lichina pygmaea*. The two species appear to share the same habitats among the lichen and barnacles.

Acarines were very numerous in one sample, C I, but were either absent or only moderately common in the others. C I is about 1.5 m. lower than the other three samples, which seem therefore to be at about the upper limit of distribution of the mites *Rhombognathus pascens* and *R. seahami*, which make up the bulk of the acarine population. This is borne out by the rarity of mites in *Fucus spiralis* from similar levels.

A considerable part of the fauna of this part of the shore consisted of the larvae of diptera. Only one species, *Geranomyia unicolor*, was at all surely identifiable from *Lichina*, but it formed either the whole or a large part of the insect population. It is a fairly large and conspicuous animal about 12 mm. long, and must make up an important part of the animal matter present.

The levels from which these four samples were taken were not chosen very well, being 0.06, 1.34, 1.51 and 1.51 m. respectively above Ordnance Datum. That is to say, while the first sample was from below mean sea-level near the bottom of *Lichina's* range, the other three were all from a little below mean high-water neaps and about 0.6 m. from the top of *Lichina's* range, but none came from intermediate positions. Nevertheless some changes in the faunas due to differences in level are indicated fairly clearly, as has been shown in the mites. Two barnacles are present, *Chthamalus stellatus* and *Balanus*

balanoides. The former occurred in all four samples, but was much less abundant in the lowest sample, C I, than in the upper three; although *Chthamalus* can be found on the shore 2 m. below Ordnance Datum, it is most abundant on the higher parts of its range. *B. balanoides* occurred only in the lowest sample; its upper limit on Church Reef varies between +0.76 and +1.31 m., and the other three samples of *Lichina* were all higher than this.

Some of the molluscs also showed the effects of tidal level. Young *Mytilus* edulis were present in fair numbers in the lowest sample, absent from C 2, and scanty in C3 and C4. Littorina saxatilis occurred in the three high samples, but its lowest recorded limit on Church Reef is +0.43 m. and it was absent from C I. L. obtusata and L. littorea, whose ranges on the shore are almost identical, were both present in fair numbers in all four samples, but in very different proportions. In CI and C2 L. littorea outnumbered L. obtusata by $4\frac{1}{2}$ to 1; in C 3 their numbers were nearly equal, while in C 4 L. obtusata outnumbered L. littorea by $8\frac{1}{2}$ to I. These differences cannot be due to altitude, for in C I and C 2, with levels I.3 m. apart, the two species were present in almost identical proportions, and these were collected on the same day. On the other hand samples C 2, C 3 and C 4 were collected from almost the same level but on widely different dates in September, January and March respectively, and showed great changes in the distribution of L. littorea and L. obtusata. These changes must therefore be seasonal in character.

According to Linke (1933), L. littorea at Heligoland lays eggs in the spring and early summer, from January at the earliest till June at the latest; larvae may be present in the plankton until November, but are most abundant during the summer. It is possible then, that the small L. littorea in C I and C 2 in September had settled during the previous months, and that the decrease in their numbers in January (C 3) and March (C 4) can be accounted for by a natural mortality rate. Linke says also that L. obtusata lays spawn most frequently during the summer and that the young forms hatch out during the same season. It is therefore difficult to explain the marked rise in the numbers of this species from 55 and 40 in C I and C 2 to 165 in C 3 and 421 in C 4.

Fucus vesiculosus (Table VII)

This seaweed is abundant on some of the rocks in Wembury Bay, but on the traverses surveyed it occurred only as a small patch on Traverse C a little above mean low-water neaps. Three samples, D I, D 2 and D 3 were taken; their greatest distance apart was only $2 \cdot 2$ m., and $0 \cdot 12$ m. was the greatest difference in level between them, D I and D 2 were collected on the same day, July 15, 1930, and contained faunas which were in many ways very like each other, though the population was on the whole less dense in D I than in D 2. Thus D I contained 6 ostracods, 115 copepods, 20 acarines and 75 young littorinids as compared with 41, 538, 37 and 87 respectively in D 2,

and the total populations per 100 g. were 252 and 750; otherwise the catches were remarkably similar. Although the bulk of each fauna consisted of copepods, it was among this group the the greatest differences lay. In D 1, out of 115 copepods, 63 were *Idya furcata*, 17 *Machairopus minutus* and 14 *Harpacticus gracilis*. In D 2 there were almost identical numbers of *Idya*

TABLE VII. FUCUS VESICULOSUS. ANIMALS INHABITING THREE SAMPLES, IN NUMBERS PER 100 G. OF DAMP WEED

Sample no		DI	D 2		D ₃
Weight in g.		87	78		87
Date		15. vii. 30	15. vii. 30		7. i. 31
Position in m.	(C V 13.7 C VI	CV II.5 CVI	CV	13.1 C VI
Height in m.		-0.40	-0.2		-0.46
Turballaria and Mamartinas		6	- 5-		. 40
Normatada		6	10		
Oligesheats		0	4		
Sinungulaidae		I			
Sipunculoidea			-		
Phaseolosoma minutum		,	0		
Cananada Calanaida		0	41		I
Copepoda Calanoida					
Pseudocalanus elongatus		I			
Copepoda Harpacticoida					
Ectinosoma melaniceps			6		
Harpacticus chelifer		4			
H. gracilis		14	13		
H. uniremis		2	••		
Idya furcata		63	64		2
Thalestris purpurea		2	83		
Parathalestris clausi			187		3
P. harpacticoides			109		
Rhinchothalestris rufocincta		2	6		
Microthalestris forficula			13		
Westwoodia nobilis			6		I
Machairopus minutus		17			
Amphiascus sp.			6		
Laophonte proxima			13		
Laophonte sp.		I			
Harpacticoida (indet.)		9	32		3
Isopoda					
Naesa bidentata		7	4		
Idotea granulosa			I		
Cryptoniscid (indet.)		I			
Amphipoda					
Pseudoprotella phasma			I		
Amphipoda (indet.)			3		
Acarina					
Rhombognathus pascens and	L				
Rhombognathus seahami		17	29		338
Acarina (indet.)		3	8		12
Insecta					
Diptera (larvae)			5		2
Gastropoda			-		
Gibbula umbilicalis			I		
Lacuna sp.		6	. 4		
Littorina obtusata		9	9		12
Littorinidae (juv.)		75	87		
	Total	252	750		274
	1 Otal	**] **	/50		3/4

furcata (64) and H. gracilis (13), but no M. minutus. In addition, however, D 2 contained 187 Parathalestris clausi, 109 P. harpacticoides and 83 Thalestris purpurea, these species being absent from D I except for a mere couple of T. purpurea. This is a good example of the patchiness of the distribution of so many of the smaller inhabitants of the seaweeds. The sample D 3 came from a position between those of D I and D 2, but was collected some six months later, January 7, 1931. Its total number of animals, 374, was more than the 252 of D I and less than the 750 of D 2, but was made up almost entirely of 350 acarines, 338 of which were Rhombognathus pascens and R. seahami.

There were no young littorinids and only nine copepods. The latter figure may be due to the time of year, for copepods were scarce during the winter in both *Fucus serratus* and in *Ascophyllum*.

Ascophyllum nodosum and Polysiphonia lanosa (Tables VIII-X)

As mentioned in my previous paper (Colman, 1933) these two algae are treated as a unit, since they always seem to occur together on Church Reef, the *Polysiphonia* living as an epiphyte on the *Ascophyllum*. *P. lanosa* grows as dense tufts of dichotomously branching twigs, whose ends are curved and interlock intimately. It provides a favourite harbouring place for many small animals, in particular ostracods, copepods and mites, the last two of which usually die *in situ* with the legs clasped right round the *Polysiphonia* stems. This makes them difficult to see and to dislodge, a fact which was not at first realized.

Twelve samples of Ascophyllum were collected, E I to E I2, and the first three were much larger than the others, weighing 350, 670 and 529 g. respectively. The first two were the first samples of any weed examined in this survey, and far fewer small animals are recorded from them than from any of the other samples of Ascophyllum; they have only been included in order to illustrate the points now under discussion. These samples were merely divided into small portions and washed vigorously in bowls; animals such as oligochaetes, isopods, amphipods and gastropods, which on dving do not clasp the weed and in any case are fairly large and conspicuous, appeared in similar numbers to those in other samples and were probably collected satisfactorily, but the ostracods, copepods, acarines and perhaps the nematodes were mostly left behind among the weed and so were missed. When this was realized, the next sample, E 3, was examined completely, and every twig of Polysiphonia was teased out from every other with needles under a dissecting microscope and the animals carefully picked off. This entailed the handling one by one of 3926 animals, with subsequent sorting and counting, not to mention the identification of many of them, and it took so long that the smaller size of weed sample used in the rest of the survey was decided on. The samples in general are admittedly too small to be quite satisfactory, but they are as large as it is practicable for one person to examine thoroughly, and in all the samples except E I and E 2 I counted all the animals.

Ignoring for the moment those two samples, four groups stand out as the most abundant among *Ascophyllum*, namely ostracods, copepods, acarines and gastropods. The ostracods were often extraordinarily numerous, with 1480 per 100 g. in E 6. Their numbers seem to vary widely at the same season on different parts of the reef. The six samples E 3 to E 8 inclusive were all collected during July and August, but the numbers varied from 90 to 1480; the poorer of these catches all came from the landward end of Traverse C, while the others were from nearer the middle of the reef (see Map, Fig. 3).

There is apparently no correlation between abundance of ostracods and height on the shore, at any rate within the range of *Ascophyllum nodosum*.

The catches of ostracods were rather perplexing as regards seasonal abundance. On August 28 E 8 contained 805, while the number dropped to 24 and 11 in E 9 and E 10 which were both collected on January 5, E 10 being from exactly the same place as E 8. It would be tempting to conclude from these figures that there is a winter minimum for intertidal ostracods, but sample E 11, collected next day, contained 201, although it came from the landward end of Traverse C where the numbers were smaller than elsewhere during the summer. These results might be due to seasonal migration, but it is idle to speculate on this until the species inhabiting *Ascophyllum* have been worked out. I found myself unable to identify ostracods with any confidence, and unfortunately my collection of them was destroyed. Recently (April 1939) I collected some from Church Reef which Mr A. G. Lowndes was kind enough to examine; he found that they were all *Xestoleberis aurantia* (Baird). They were not abundant, however, and during the summer there is certainly more than one species present.

The copepods (Tables IX and X) were identified fairly completely with the exception of young stages, and the results show, as in *Fucus vesiculosus*, that the *total numbers* of copepods have only a limited significance. Twentythree species were identified from *Ascophyllum*, but only one species, *Westwoodia nobilis*, occurred with any regularity and was, indeed, absent from only one sample, E 5. In the samples in which it was found its numbers varied from 2 in E 9 (January) to 203 in E 6 (July). The next largest catch of *W*. *nobilis* was 104 in E 12 collected in March, after three poor catches in January. This seems to indicate a winter minimum for the species, but the summer figures are too irregular to show any definite seasonal maximum. While E 6 with 203, and E 7 with 93, were both collected in the fourth week in July, E 5 collected on July 15 contained no *W. nobilis* at all, and the numbers were small in the other two July samples. Another species of the same genus, *Westwoodia pygmaea*, was present in quite large numbers (136) in E 12, but was not represented in any other sample.

The other species of Harpacticoida appeared only sporadically, though several of them were occasionally numerous. The samples E 3, E 4 and E 5, all collected in the first half of July, were the richest in species, and several families here make practically their only appearance in these catches of *Ascophyllum. Harpacticus gracilis* was quite abundant with 129, 165 and 33 in these three samples, and there were 16 *H. uniremis* in E 5. The only other species of the family Harpacticidae was represented by a solitary *H. chelifer* in E 10 in January. Of the Idyidae, there were 373 *Idya furcata* in E 5, which was the largest number of one species of copepod in any sample of *Ascophyllum*, and 61 in E 4; no adult Idyids appeared after mid-July. Apart from the two species of *Westwoodia* already mentioned, various Thalestridae were found from time to time of which three were occasionally abundant; there

TABLE VIII. ASCOPHYLLUM NODOSUM AND POLYSIPHONIA LANOSA. ANIMALS INHABITING TWELVE SAMPLES, IN NUMBERS PER 100 G. OF DAMP WEED

Sample no.	E 1	E 2	E 3	E 4	E 5	E 6	E 7	E 8	Fo	E to	ETT	F 12
Weight in g.	. 350	670	529	151	119	103	202	84	06	84	117	68
Date .	13. v. 30 B II	14. v. 30 C IV	2. vii. 30 C VII	15. vii. 30 C VI	15. vii. 30 C V	23. vii. 30	25. vii. 30	28. viii. 30 B II	5. i. 31	5. i. 31 B II	6. i. 31	20. iii. 31
Position in m.	I.8 BIII	2.4 C.V	4.6 D I	13.7 C VII	14.6 C VI	CI	5.5	9'4 9'1	1.8	9.4	8.2	0.3
Height in m.	-0.52	+0.40	+0.27	+0.67	-0.00	-0.30	+0.37	- I:00	B 11	B III	D1	CIII
Coelenterata #					,	- 50	1031	1.00	-0 43	-100	+0.73	+0.00
Clava squamata (polyps)		+	+									
Laomedea flexuosa						+					- 33	
Dynamena pumila	common		+ ·				+				••	
Sertulariidae (indet.)					• • •	+			Ŧ	Ŧ		÷
Stauromedusae (juv.)												
Turbellaria and Nemertinea	I	3	10	47	20	82	=6			06		
Nematoda	17	12	61	126	59	62	20	94	28	80	187	121
Polychaeta	/	- 5	01	120	00	49	12	01	44	46	211	153
Nereidae (indet.)												
*Sabellidae			5					••		•••	•••	2
Spirorhis borealis			3	40	••	••			I	0	744*	60*
Oligochaeta				15				• •		••	••	••
Lymbricillus scoticus)			(20	20	10							
I pumilio	II	82	145	20	4			3	14	17	3	2
L spn (iuv.)			(45	20	4	17	I	7	IO	6	19	40
Ostracoda				222			0		• •		53	66
Copenada (see Table IX)	4		90	232	351	1480	815	805	24	II	201	225
Tanaidacea	2	2	2/9	570	731	358	613	168	49	56	62	372
Tanais cavolini											1.20	
Isopoda							1			•••	2	• •
Naesa bidentata	2	I	т	1000	3	26	2	26				- 0
Idotea granulosa	10	IO	Т	6	3	1	2	20	4	2		18
Amphipoda						*	40	13	54	75	97	10
Astacilla longicornis		I										
Apherusa jurinei									••		•••	• •
Melita sp.							1	• •			2	
Gammarus marinus										•••	I	
Hyale nilesoni	28	12		78							I	••
Amphithöe rubricata	20	- 3	. /	10		53	20	03	84	86	73	96
Amphipoda (jug_indet)		1			4	•• -			2			3
(uvi, macti)					5				• •			

Decanoda												
Carcinus maenas (megalona)					т							
Xantho incisus (inv.)												
Pychogonida		•••									10.1	
Aumothea echinata											т	12533
Purpagonid (indet)						•••					-	
A series	• •					1						
Rearing Discourse and												
Rhomoognathus pascens and				2=0		60			105	257	2.19	678
Rnombognathus seanami	•••	•••	30	278	42	02	173	148	195	251	240	69
Acarina (indet.)	9	9	19	30	73	31	13	40	9	24	227	00
Insecta											-	
Lipura maritima				40		••	• •		••	•••	7.	
Collembola (indet.)	•••				• •							I
Thalassomyia frauenfeldi and												0
Clunio marinus (larvae)	• •		73	73	140	134	15				171	28
Ephydridae (pupa)		••								• •		2
Diptera (larvae, indet.)	I								2	6		• •
Diptera (adults, indet.)												3
Coleoptera (indet.)												2
Insecta (pupae, indet.)				••								3
Pelecypoda												
Mytilus edulis (juv.)	I	I										
Pelecypoda (indet.)	I				4	17	8	43	15	36	13	40
Gastropoda												
Lacuna sp.			5	2	2							
Littorina obtusata	3	2	4	2	I						2	5
L. obtusata (spawn)		I		I								I
+Littorinidae (juv.)	19	32	67	72	55	487	92	252	75	160	355	260
Bryozoa						• •						
Flustrella hispida										I	I	
Total	109	176	742 +	1597	1519	2798 +	1891 +	1729	610+	869+	2714	2259+

* Mainly Fabricia sabella.

† Mainly Littorina obtusata

10

JOURN, MAR, BIOL, ASSOC, vol. XXIV, 1939

TABLE IX. ASCOPHYLLUM NODOSUM AND POLYSIPHONIA LANOSA. COPEPODA IN SAMPLES E 3 TO E 12.IN NUMBERS PER 100 G. OF DAMP WEED

Sample no.		E 3	E 4	E 5	E 6	E 7	E 8	E 9	E IO	EII	E 12
Weight in g.		529	151	119	103	202	84	96	84	117	68
Date	••	2. vii. 30 C VII	15. vii. 30 C VI	15. vii. 30 C V	23. vii. 30	25. vii. 30 C I	28. viii. 30 B II	5. i. 31 B I	5. i. 31 B II	6. i. 31 C VII	20. iii. 31 C II
Position in m.	••	4.6 D I	CVII	14.6 C VI	CI	5.5 C II	9 ^{.4} B III	I.8 BII	9 ^{.4} B III	8·2 D I	C III
Height in m.		+ 0.27	+0.67	-0.09	-0.30	+0.32	- I.OO	-0.43	- I.OO	+0.23	+0.06
Harpacticidae											
Harpacticus chelijer									1	••	
H. gracilis		129	105	33		••			••		
H. uniremis				10		••	• •		••		
Idvidae		I					••				
Idva furcata		20	61	373							
I. gracilis		I		515							
Idvidae (indet.)				8							
Thalestridae											
Thalestris longimana			1						4		21
T. purpurea			40	30							
T, sp. (indet.)		4	4-	5-	37						
Parathalestris clausi			13	3	57			II			9
P. harpacticoides		7				280					
Microthalestris forficula		4									
Dactvlopusia tisboides			146								
D. mulgaris		6	-40		117		17				
D. brevicornis					/		- /	I			
Westwoodia nobilis		1.4	46		203	03	48	2	24	30	104
W. pygmaea			40				4-			5-	136
Diosaccidae											- 5 -
Amphiascus mirutus		т	46	0.00		2104	112121	10000		1000	
Canthocamptidae			40								
Nitocra typica		0.02	13							·	
Mesochra pygmaea		22	*3								
Ameira tenuicornis				156							
Laophontidae		1.1		1)0							
Laophonte corruta							102231	3123	122	1000	т
I hrenirostris			20								
I. littoralis			20								
I spp (indet)		55	20	06							27
(letodidae (indet))		33		-90	1						21
Harpacticoida (iuv. indet)		14		16		240	102	25	27	22	74
rarpacticolda (juv., muct.)		14		10		240	103	33	-/	54	/4
	I otal	279	570	731	358	613	108	49	56	62	372

were 280 Parathalestris harpacticoides in E 7, 146 Dactylopusia tisboides in E 4, and 117 D. vulgaris in E 6. Several species of other families occurred in fair numbers once or twice, such as 46 Amphiascus minutus in E 4, 156 Ameira tenuicornis in E 5 and 96 Laophonte spp. in E 5. This genus Laophonte is perhaps the most easily recognized of all the harpacticoid genera, but it is also one of the hardest in which to determine the species; L. brevirostris and L. littoralis were both identified for me by Dr R. Gurney.

TABLE X. ASCOPHYLLUM NODOSUM AND POLYSIPHONIA LANOSA. FAMILIES OF COPEPODA HARPACTICOIDA IN SAMPLES E 3 TO E 12, IN NUMBERS PER 100 G. OF DAMP WEED

Sample no. Weight in g. Date Position in m. Height in m.		E 3 529 2. vii. 30 C VII 4.6 D I +0.27	E 4 151 15. vii. 30 C VI 13.7 C VII +0.67	E 5 119 15. vii. 30 C V 14.6 C VI -0.09	E 6 103 23. vii. 30 C I -0.30	E 7 202 25. vii. 30 C I 5.5 C II +0.37
Harpacticidae Idyidae Thalestridae Diosaccidae Laophontidae Cletodidae (Juv., indet.) Total	2	130 21 35 1 22 55 1 14 279	226 245 46 13 40 570	49 381 33 156 96 16 731	 357 	373 240 613
Sample no. Weight in g. Date Position in m. Height in m.	 	E 8 84 28. viii. 30 B II 9·4 B III – 1·00	E 9 96 5. i. 31 B I 1.8 B II -0.43	E 10 84 5. i. 31 B II 9.4 B III - 1.00	E 11 117 6. i. 31 C VII 8.2 D I +0.73	E 12 68 20. iii. 31 C II 0·3 C III +0·06
Harpacticidae Idyidae Thalestridae Diosaccidae Canthocamptidae Laophontidae Cletodidae (Juv., indet.)	e Total	65 103	 	I 28 27 56	 30 32 62	270 28 74

These copepods have been discussed at some length in order to bring out the patchiness of their distribution. Only one species out of 23 or more occurred regularly, though seven were present in one sample or another in numbers exceeding 100 each. Infrequency of occurrence is here at any rate no true measure of rarity. Many young forms were found in samples E 7 to E 12. They may have been young stages whose adults were not represented, or those of the species present in these samples; they were mostly less than 0.5 mm. in length, which made their dissection difficult and their determination a matter of great uncertainty.

Table X shows the occurrence of the seven families of copepods found in *Ascophyllum*. It emphasizes the importance of the Thalestridae, and shows that adults of other families were not present in any number after the middle of July.

The other two groups generally present in large numbers were acarines and the Littorinidae. The numbers of acarines, leaving out of consideration

10-2

samples E 1 and E 2, varied from 55 in E 3 to 746 in E 12. No good correlation with either seasons or heights on the shore is apparent, though on the whole they appear to be most plentiful in the winter and early spring. The most abundant catch, 746 in E 12, was in March, the next most abundant, 475 in E 11, was in January, and the third, 308 in E 4, in July; the other July catches, however, were among the poorest. Then again E 12 was at +0.06 m., E 11 a good deal higher at +0.73 m., and E 4 almost as high at +0.67 m., while E 10 down at -1.00 m. was almost as rich as E 4. Most of these mites were *Rhombognathus pascens* and *R. seahami*; other species were present, including *Halacarus basteri* and *Hydrogamasus littoralis*, and were on some occasions quite numerous, as in E 5 and E 11. These mites were identified for me by Mr J. N. Halbert.

The Littorinidae include several individuals of a species of *Lacuna* which were too young to be determined, several *Littorina obtusata*, and large numbers of young stages which appear to be mostly *L. obtusata*. The adults of this latter species, though apparently so numerous in the field, are in reality not nearly so abundant as many of the smaller animals, and it seems to be a matter of chance whether or not a sample of 100 g. or so will contain any *L. obtusata* large enough to be recognizable. The young Littorinidae, however, were always present in fair or large numbers, from 67 in E 3 to 487 in E 6. Here again no correlation can be shown with either season, height or position on the reef. It is surprising that the spawn of *L. obtusata*, which often seems so common, appeared only three times, on May 14, July 15 and March 20.

The several other groups can now be considered, taking them in their zoological order. Three species of hydroid were identified, *Clava squamata*, *Laomedea flexuosa* and *Dynamena pumila*. They were not counted, except for a rather straggling colony of *Clava* in E 11 in which there were 33 polyps. *Dynamena pumila* is the only hydroid which was common, but it is restricted to the *Ascophyllum* holdfasts and the proximal portions of the plant. This part was not studied as closely as the distal portions with their epiphytic tufts of *Polysiphonia*, and this omission probably causes a considerable gap in the collection of the fauna inhabiting *Ascophyllum*. There was one young stauromedusan in sample E 7, which is noteworthy on account of the height of this sample on the shore, 0.37 m. above Ordnance Datum, or about mean sea-level.

Turbellaria and Nemertinea (lumped together throughout this paper) occurred in moderate numbers, fluctuating fairly widely without correlation with either season, height or position. The same applies to the nematodes. This last group has not been worked out sample by sample, but a batch from *Ascophyllum* was determined for me by Dr Baylis and contained the following species: *Anticoma limalis* (numerous), *Oncholaimus brachycercus* (numerous), *Enoplus communis, Symplocostoma longicolle*, and *Thoracostoma figuratum*.

Polychaetes were on the whole few or absent. Two small nereids appear in E 12, and 13 *Spirorbis borealis* in E 4. Small sabellids occurred more fre-

quently, and on one occasion were really numerous, 744 in E 11; these were mainly, if not entirely, *Fabricia sabella*, a worm about 3 mm. long, but the tube containing them was unfortunately destroyed before they could be examined completely. This was unlucky because this sample was the highest of all the *Ascophyllum* samples, at 0.73 m., and *F. sabella* did not appear again in large numbers until the laminarian zone was reached some 3 m. lower down the shore.

Two species of oligochaete were usually present and sometimes quite numerous. These were *Lumbricillus scoticus* and *L. pumilio*, identified for me by the late Dr J. Stephenson (1932). *L. pumilio* is so far the only new species identified from these collections. *L. scoticus* is about 5 mm. long and *L. pumilio* about 3 mm. Both are orange in colour in contrast with the dark-red *Polysiphonia* among which they live, and they are easy to see in the field as they are often on the move, writhing round each other and the twigs of the alga. It is surprising that they have not been previously recorded from Plymouth. They were most numerous in May and early July (E 2, E 3 and E 4) and in January and March (E 11 and E 12). In the last two samples most of them were so small that the species could not be separated; this perhaps indicates that the young worms appear in mid-winter, reach adult size in late spring, and then gradually become fewer during the summer, the survivors giving rise to next year's brood.

The specimens of *Tanais cavolini* from E 7 and E 11 were the only tanaids collected from other than the laminarian zone, but this species did not occur elsewhere than in these two samples of *Ascophyllum*.

Of the isopods, Astacilla longicornis occurred once, in E 2 at +0.4 m. This is a sublittoral species and is found at 40 fathoms off the Eddystone. Perhaps this individual was washed loose from its normal habitat by wave action, carried up the reef in the surf and entangled in the weed as the tide fell. This would explain the presence of individuals of a number of species which are not normally found between tide-marks. The isopods Naesa bidentata and Idotea granulosa, both widely distributed intertidal species, occurred in nearly all the samples. I. granulosa was quite abundant in January, but otherwise was not numerous; these January forms were mostly young.

The amphipods include five species, of which only *Hyale nilssoni* was either numerous or of regular occurrence; it was most abundant in January and March, but not markedly so. A noteworthy feature of these samples is the great rarity of the genus *Gammarus*, which is indeed represented only by a single *G. marinus* in E 11. This emphasizes the difference between the fauna inhabiting seaweeds and that living below stones at the same level, for in the latter habitat *G. marinus* and *G. locusta* are everywhere abundant. *Amphithöe rubricata* is an amphipod which makes a nest, and two of these were found in broken nodes of *Ascophyllum*, in samples E 5 (July 15) and E 9 (January 5). These nests measure only about 12 by 6 mm., but may contain quite a rich fauna. The one in E 5 included 11 turbellarians or nemertines, 25 nematodes,

100 copepods (made up of 11 Idya furcata, 16 Thalestris purpurea, 3 Parathalestris clausi, 46 Ameira tenuicornis and 24 Laophonte spp.), and 4 acarines, giving a total of 140. The nest in E 9 was less remarkable and contained only 26 copepods, of which 7 were Parathalestris clausi. A female of Amphithöe rubricata in E 2, May 14, ejected 32 young on being killed.

The crabs *Carcinus maenas* and *Xantho incisus*, like *Gammarus marinus* and *G. locusta*, are common under stones when the tide is out, but evidently avoid the seaweed; they are represented only by a *Carcinas maenas* megalopa in E_5 and a young *Xantho incisus* in E_4 , both collected on July 15.

It was surprising that of the two pycnogons captured one should be an *Ammothea echinata* found in E 11, for this is not usually an intertidal species and E 11 is the highest *Ascophyllum* sample. It may be another stray washed up by the surf and trapped in the weed.

Insects, and in particular the larvae of diptera, form an important ingredient of the fauna around mean sea-level. The collembolan Lipura maritima was found only in two samples, but it is notoriously patchy in its distribution; it is probably much more abundant on *Ascophyllum* than these figures would suggest. Chironomid larvae, belonging probably (according to Dr Edwards) to the two species Clunio marinus and Thalassomyia frauenfeldi, were sometimes common, particularly in the samples from high up on the shore. The lowest level at which these species occurred was 0.3 m. below Ordnance Datum, and they were found in all samples collected above this level except for E 2 at +0.4 m. (This sample was examined somewhat cursorily as regards the smaller forms, as already mentioned, but I would not have missed any animals as large as these chironomid larvae, for they are not only bigger than Lumbricillus scoticus but also let go on being killed and are less liable than some other species to get tangled up in the weed.) They were most abundant in E 11, the highest sample, in January, with 171; next came E 5 on July 15 with 140 at -0.09 m., but there were still 134 in E 6 on July 23 at -0.3 m., the lowest sample in which they occurred; the March sample, E 12, contained 28. The fact that these larvae were found in January, March and July seems to mean either that there are several broods in the year or that these two species have an unusually prolonged larval life. Besides the two species mentioned above, other dipteran larvae were occasionally found, one in E I at -0.52 m., two in E 9 at -0.43 m. and six in E 10 at -1.0 m., three of the four lowest samples of Ascophyllum. The catch in E 12 at +0.06 m. included ephydrid and other insect pupae, adult diptera and coleoptera, and a collembolan which was certainly not Lipura maritima.

The samples E 10 and E 11, January 5 and 6, each contained one colony of the bryozoan *Flustrella hispida*, at -1.0 and +0.73 m. respectively. No other bryozoan was taken higher than -1.64 m., so that the occurrence of *F. hispida* as high as +0.73 m., or a little below high-water neaps, is remarkable.

Fucus serratus (Table XI)

Fucus serratus is widely distributed on Church Reef, but it does not cover so great an area as *Ascophyllum nodosum*. The range of the latter, from 0.9 m. above to 1.2 m. below Ordnance Datum, includes many wide, level stretches of the reef on which it can grow abundantly; *Fucus serratus* extends from 0.4 m. above to 2.75 m. below Ordnance Datum, a vertical range of more than 3 m., but much of this coincides with the sloping edges of the reef. On Church Reef *F. serratus* is on the whole more exposed to wave action than is *A. nodosum*. Ten samples, F I to F IO, were collected, ranging in height from -0.40 m. down to -1.95 m. Samples F 4 and F 8 (-0.40 m. and -0.58 m.) were higher than the two lowest samples of *Ascophyllum*; F I, F 2 and F 6 (-1.49, -1.31 and -1.37 m.) were from about the middle of the range of *F. serratus*, while F 3, F 5, F 7, F 9 and F IO (from -1.76 to -1.95 m.) were from similar levels to those of the four samples of *Gigartina stellata* and just above the laminarian zone.

On the whole, *Fucus serratus* has a poorer fauna than either its higher neighbour *Ascophyllum* or its lower neighbour *Gigartina*, which is, I think, largely due to the differences in growth form of these algae. The fauna of *Ascophyllum* is mainly contained in the tufts of *Polysiphonia*, while the fronds of *Gigartina stellata* are covered with warty protuberances to which many small animals can cling; *Fucus serratus*, on the other hand, is usually rather smooth and affords poor holding ground for copepods, mites and so on. Occasionally, however, it carries epiphytic growths of a brown, filamentous alga, *Elachistea fucicola*, which grows in small arthropods. The sample F 3 had a fair growth of *Elachistea* and contained 1189 animals per 100 g.; F 5 had a slight growth and contained 465, while the other eight samples were free of the epiphyte and the numbers of their faunas ranged from 311 down to only 61. The increase in the populations of F 3 and F 5 was made up largely of copepods.

Coelenterates were remarkably scarce on *Fucus serratus*, one colony of *Dynamena pumila* on each of F I and F 2 being the sum total. This affords a striking contrast with *Gigartina stellata* from the same levels, on which hydroids are numerous.

Turbellarians and nemertines hardly appear at all though there were many of them on Ascophyllum; and nematodes, though usually present, were numerous in only one sample, F 3, which was infested with Elachistea. Most of the nematodes in this sample (identified by Dr Baylis) were young Pontonema (Paroncholäimus) ?ditlevseni, with a few Enoplus communis and Symplocostoma longicolle. Polychaetes, oligochaetes and sipunculids appeared occasionally, but usually only one at a time.

Ostracods were surprisingly rare when compared with those in Ascophyllum at similar levels. For example, Ascophyllum, sample E 6, from a height of

TABLE XI. FUCUS SERRATUS. ANIMALS INHABITING TEN SAMPLES, IN NUMBERS PER 100 G. OF DAMP WEED

Sample no.		FI	F 2	F 3	F 4	F 5	F 6	F 7	F 8	Fo	E to
Weight in g.		364	335	395	91	131	82	85	99	93	77
Date	••	2. VI. 30	11. vi. 30	13. vi. 30	23. vii. 30	26. vii. 30	28. viii. 30	28. viii. 30	5. i. 31	5. i. 31	3. iv. 31
Position in m.		8·2 B IV	I2·2 A II	9'4 1V		0'7	4'3 P.VI	В V 7.9 В VI	B I 12.8	B III II·8	B VII
Height in m.		-1.49	-1.31	-1.86	-0.40	-1.02	- I.37	- T-80	B 11	B IV	-1.76
Coelenterata							- 57	,	0 90	1 03	1 /0
Dynamena pumila (col	lonies)	I	I								
Turbellaria and Nemer	tinea			I							
Nematoda		IO		163	3	13	2		10		
Polychaeta					5				10	10	1
Nereidae (indet.)				I							
Fabricia sabella				I				т.			
Oligochaeta (indet.)		I	I					-	4		
Sipunculoidea											
Phascolosoma minutum	1		I	2							
Ostracoda		I		8	7	8					
Copepoda Harpacticoida	1				· ·				2		1
Harpacticus chelifer		53	32	404	2	27	8	т			
Zaus spinatus		19	IO	247		5		3			
Porcellidium fimbriatus	m			IO							
Idya furcata		50	114	13	7		I	3			
Aspidiscus fasciatus				7							
A. littoralis		I		·'		230		150			
Parathalestris clausi		60	7	47		52	4	3			21
P. harpacticoides		15	2	17		32	-	5			
Dactylopusia tisboides				14							
D. vulgaris		7	2								
Canthocamptidae (ind	let.)		2								
Laophonte sp. (indet.)				3	2	3					
Harpacticoida (indet.)	6	7	3	13		2			2	42	26
Isopoda									5	45	20
Naesa bidentata		5	9	I	12	I	I		6	4	
Idotea baltica									I	4	
I. neglecta									I		
I. granulosa		2	I	6		2	5	I	20		3

Amphipoda										
Apherusa jurinei	2	I		3				2		
Hyale nilssoni								12	2	
Amphithöe rubricata	I	I								
Pleonexes gammaroides			2							
Biancolina cuniculus	I									
Pseudoprotella phasma					I					
Amphipoda (juv., indet.)	3		3		4			6	I	
Decapoda	5		5		4					
Carcinus maenas (megalopa)			I							
Acarina										
Rhombognathus pascens and										
Rhombognathus seahami	37	34	114	42	46	21	31	198	194	18
Acarina (indet.)					4	12		2	I	
Insecta										
Diptera (larvae, indet.)	I		II		5	I		2		
Pelecypoda (juv., indet.)			3		2			3		
Gastropoda										
Patina pellucida	I	I	12	1	2	4	15			I
Gibbula cineraria				2						
G. umbilicalis		<i>.</i> .		I				I		
Lacuna sp.				I						
Littorina obtusata	I	3	Ĩ	-7	I	I		6		
L. obtusata (spawn)	I	I	I	I						
L. littorea				I						
Littorinidae (juv.)	23	8	80	22		I	3	26	2	
Gastropoda (juv., indet.)	I		3							
Bryozoa										
Membranipora pilosa					5		22			9
Flustrella hispida					II		13			I
Tota	al 304	234	1189	113	465	61	256	311	257	87

-0.30 m. contained 1480 ostracods, whereas *Fucus serratus* sample F 4 from -0.40 m. contained only 7. These two samples had a difference in height of only 0.1 m., were from places on the reef only 1.2 m. apart, and were collected on the same day, July 23 1930.

There were twelve species of copepod in the samples of F. serratus, and the total number of this group varied from 3 to 775. On the whole they were rarest in January and April, most abundant in June, and erratic in August, but there were not enough samples to make clear any marked seasonal variations. Only four species found in F. serratus were not found also in Ascophyllum, namely Porcellidium fimbriatum, Aspidiscus fasciatus, A. littoralis and an unidentified canthocamptid. In spite of this, however, the two populations were not alike in general make-up, since the species common to the two are present in very different proportions. In addition there are several species, occasionally common in Ascophyllum, which are absent from Fucus serratus, such as Harpacticus gracilis, Thalestris purpurea, Westwoodia nobilis, W. pygmaea, Amphiascus minutus and Ameira tenuicornis. In Fucus serratus six species appeared in fair or large numbers. Harpacticus chelifer was present in all the June, July and August samples and was commonest in June. In F 3 at -1.86 m. it was really numerous (404), making up more than half the copepods present; it was the second most abundant in F I (53) and in F 2 (32). (Only a single specimen of this species was found in Ascophyllum.) Zaus spinatus occurred in five samples but was common only once, with 247 in F 3. Idva furcata, found on six occasions, led the rest with 114 in F 2, came third with 50 in F I, but was not numerous in its other samples. Aspidiscus littoralis, a relatively large harpacticoid, was abundant in F 5 (239) and in F 7 (159); these are both low samples (-1.95 and -1.89 m.) and it was not found above -1.5 m.; in F 7 it formed all but 10 of the copepod population. This species was also the only one identified from the January and April samples, at which time there were present a number of immature forms, as in Ascophyllum. Parathalestris harpacticoides and P. clausi were not uncommon and generally occurred together.

The isopods *Naesa bidentata* and *Idotea granulosa* were widely but not abundantly distributed; they occurred sparingly in nearly all the samples, as in *Ascophyllum*.

Amphipods were rather scarce, but were none the less represented by six species. *Hyale nilssoni*, so plentiful in *Ascophyllum* and other weeds higher up on the shore, was found in only two samples of *Fucus serratus*; there were 12 in F 8 from -0.58 m., well within the range occupied by *Ascophyllum*, and 2 in F 9 from -1.83 m. at the top of the laminarian zone, which must be very near the lower limit for *Hyale nilssoni* (see also the reference to this species in the section on *Gigartina stellata*).

The acarines occurred more steadily than any other group, and in five of the seven summer samples their numbers varied only from 31 to 42. The other two of the seven, F 3 and F 5, have already been mentioned as supporting

growths of *Elachistea fucicola*; F 3 carried a fairly heavy epiphytic growth and 114 mites, while on F 5 there was a slight growth and only 50 mites. The acarines were much more numerous in the two January samples (200 and 195), but there were only 18 of them in F 10 in April. Nearly all the acarines belonged to *Rhombognathus pascens* and *R. seahami*, but Mr J. N. Halbert also found *Halacarus basteri* in a batch from F 3.

A few larvae of diptera were to be found in five samples. There were 5 even in F 5 which was the lowest sample of *Fucus serratus*, from -1.95 m. or about mean low-water springs; two occurred in mid-winter, in the January sample F 8. No insects or their larvae were found among *Gigartina* from similar levels.

Among the molluscs, young specimens of *Patina pellucida* appeared in samples as high as -1.31 m., though the adults are not found above the laminarian zone 0.6 m. further down. *Littorina obtusata* was the only other gastropod which occurred at all regularly, and its spawn was found in the four samples between June 2 and July 23, but not in any others. The number of young littorinids varied from none to 80.

Three of the lowest samples, F 5 at -1.95 m., F 7 at -1.89 m. and F 10 at -1.76 m., supported several colonies of the bryozoa *Membranipora pilosa* and *Flustrella hispida*. These were never so abundant as on the neighbouring *Gigartina stellata*, and *Alcyonidium hirsutum*, which is fairly common on the latter weed, was not found at all on *Fucus serratus*.

Gigartina stellata (Table XII)

This red alga is abundant from above mean low-water springs down to below tide-marks. The highest position recorded was 1.5 m. below Ordnance Datum, and the four samples G I to G 4 came from -1.98, -1.64, -1.89and -1.70 m., with a range in level of only 0.34 m. in all. In spite of the fact that they came from similar heights, however, the fauna of each sample differed in several important respects from the others, though they also show some features in common. G I and G 2 were collected at the height of summer in July and August, G 3 in January and G 4 at the beginning of April, yet none of the differences between these faunas can be set down as seasonal.

Certain animals were present in all four catches with fair regularity, such as *Idotea granulosa*, young *Mytilus edulis* and *Patina pellucida*, and the bryozoa *Membranipora pilosa*, *Alcyonidium hirsutum* and *Flustrella hispida*. Of these animals only *Idotea granulosa* and *Mytilus edulis* are found farther up the shore, the others all belonging to the sublittoral fauna, some members of which can live as far up as low-water neaps but as a rule no higher.

Polychaetes, copepods and amphipods were, as a rule, represented by a few individuals of several species which are more common in other zones; the species of copepod are usually more numerous farther up the shore, especially among *Ascophyllum*, while the polychaetes belong to the laminarian

zone. A point of interest is the overlap in G 4 of the closely related amphipods $Hyale \ nilssoni$ and $H. \ pontica$. The former is ubiquitous and often abundant from the *Pelvetia* zone down to around low-water neaps, while the latter species is normally sublittoral and is only occasionally to be met with between tide-marks.

Apart from the animals so far considered from *Gigartina*, from 50 to 90% of each catch was made up of one or two groups present in quite exceptional

TABLE XII. GIGARTINA STELLATA. ANIMALS INHABITING FOUR SAMPLES, IN NUMBERS PER 100 G. OF DAMP WEED

Sample no.		GI	G 2	G 3	G4
Weight in g.		70	60	62	47
Date Desition in m		26. vii. 30	28. viii. 30	7. i. 31	3. iv. 31
Height in m	••	AIV 0.9 AV	B VI 7.9 B VII	B VII 6.7	B VII o∙6
Contactor in III.		-1.98	-1.04	-1.88	-1.20
Coelenterata					
Danguage duricula	h	7	:.	••	•••
Turbellaria and Nemertin	nes)	17	601	127	III
Nematoda	ca	9		2	
Polychaeta		4	47	2	13
Odontosyllis ctenostoma				2	
Eusyllis lamelligera				3	
Nereidae (indet.)					1
Polydora ciliata			2		
Amphiglena mediterranea			2	2	II
Fabricia sabella		14		2	II
Oridia armandi				3	9
Spirorbis borealis		19	47	164	
Sipupgulaidae					2
Phaseologoma minutum		12			
Ostracoda		43		••	
Copepoda Harpacticoida				2	
Harpacticus chelifer		86	2		
Zaus spinatus			2	2	
Psamathe longicauda		1985	-	32	0
Aspidiscus littoralis		585	2	6	32
Idyidae (nauplii)		3930			
Parathalestris clausi					13
P. harpacticoides				3	
Dactylopusia tisboides			••		II
Ciminadia					4
Verruea stramia					
Ralanus halanoides				3	••
Isopoda			••		2
Naesa bidentata		4	2		2
Idotea granulosa		56	37	16	2
Cryptoniscidae (indet.)			37	10	2
Amphipoda					2
Apherusa jurinei		5		5	.:
Hyale nilssoni			38		2
H. pontica				2	2
Pleonexes gammaroides		•••	8		
Amphipodo (indet)		248	2	6	II
Acarina				5	
Rhomhognathus bascens	nd				
Rhombognathus seaham	i	117	1272	122	
Acarina (indet.)		T.4	12/3	422	1209
Pelecypoda		*4		2	
Mytilus edulis (juv.)		21	115	12	10
Gastropoda				13	19
Patina pellucida		17	18	3	13
Lacuna sp.		7		3	- 3
Littorinidae (juv.)		35	155		19
Gastropoda (juv., indet.)			5	2	II
bryozoa					
Alexanipora pilosa		. 40	25	37	115
Flustrella hisbida		35	52	42	6
1 motretta mopula	-	43	21	86	132
	Total	734I	2457	997	1785

numbers. In G I, out of a total of 734I no fewer than 6586 consisted of the two copepods *Psamathe longicauda* and *Aspidiscus littoralis* and their nauplii. These species are closely related; both are broad, powerful forms, flat ventrally and stream-lined dorsally and apparently well adapted to withstand wave action. The nauplii are interesting for they are not free-swimming; they crawl over the surface of the weed, and those of *Psamathe longicauda* can cling on very tightly by means of a ventral sucker (Gurney, 1933). Other note-worthy animals in G I were 43 of the sipunculid *Phascolosoma minutum*, 86 of the copepod *Harpacticus chelifer* and 248 of the amphipod *Jassa falcata*. None of these was present in any quantity in the other samples of *Gigartina*.

In G 2, half the catch consisted of the mites *Rhombognathus pascens* and *R. seahami* (1273), and half the remainder was made up of branches of the hydroid *Dynamena pumila* (601). *Hyale nilssoni*, *Mytilus edulis* and young littorinidae were present in fair numbers, but the most noticeable feature otherwise was the dearth of copepods, which were more than 1000 times as few as in G 1.

In G 3 the total numbers were much less than in the other catches, but here again half the total consisted of the acarines *Rhombognathus pascens* and *R. seahami* (424). *Dynamena pumila* (127 branches) was fairly abundant, and there were many more of the polychaete *Spirorbis borealis* (164) than usual, but otherwise the fauna though varied was not numerous.

Much the same is true of G 4, where the same two species of mite form over two-thirds of the total. Here again there is considerable variety of species, but few of them are present in any number. It was only in this sample that *Hyale nilssoni* and *H. pontica* were found together.

The most distinctive feature of the *Gigartina* fauna as a whole is the large number of the acarines *Rhombognathus pascens* and *R. seahami*. These two species make up almost the entire acarine population in most of the weeds above the laminarian zone; only in *Ascophyllum* are other species at all common, and even then only occasionally.

Laminaria digitata holdfasts* (Tables XIII-XVIII)

Laminaria digitata is predominantly a sublittoral alga, and does not live higher (except in tide-pools) than low-water springs; most of the animals living among its holdfasts are also distributed mainly below tide-marks. This fauna, as is well known, is extremely numerous and contains a great variety of species, particularly of polychaetes, of which there were found over forty different kinds in this survey. The form of the rhizoids making up the holdfast, which intertwine closely round each other, does not leave much space

^{*} I have not studied at all thoroughly the animals living on the fronds of *Laminaria digitata*. They do not appear to be numerous or of many species. On 5. iv. 39 I examined one frond and stalk of average size, and on it I could find only the following: 71 copepods, made up of 3 *Aspidiscus littoralis*, 38 *Zaus spinatus*, 28 *Parathalestris clausi*, and 2 not determined; in addition there were a number of acarines, but nothing else.

between them, and such room as there is appears to be filled with fine and coarse sand, small stones, broken bits of shell and so on. Nevertheless, it is among this detritus that most of the extensive fauna is to be found, though some animals live on the surface of the holdfast such as barnacles, hydroids and bryozoa, while a few polychaetes and gastropods bore into the tissues of the Laminaria. In addition there is a hard veneer, I or 2 mm. thick, between the Laminaria holdfast and the rock. This veneer is a calcareous, encrusting alga, kindly identified for me by Dr Margery Knight as Lithophyllum incrustans (Philippi). It appears to extend under all the holdfasts, but does not always cover the surface of the rock between them; I have therefore considered it to be, from an ecological point of view, part of the Laminaria. It is riddled with wormholes, probably made by *Polvdora*, but which may contain many other forms such as nematodes, the small sabellid Fabricia sabella and so on. I have not attempted to analyse in detail the different parts of a Laminaria holdfast, but it is evident that each one contains a number of more or less separate habitats, each with its own association of animals; such habitats are the general surface, the deep interstices between the rhizoids, the tissues of the Laminaria itself, and finally the encrusting alga beneath the whole.

Some instructions for collectors state that the fauna of a Laminaria holdfast can be examined by placing the holdfast in a jar of sea water and leaving it overnight, after which the contained animals will have emerged and will be found on the walls of the jar. I have tried this method, but found it grossly misleading and of no value. Some of the syllids come out, it is true, but all the syllids together make up only about one-tenth of the total polychaete population. Most of the animals remain in their burrows and die there, and will be partially decomposed and unfit for identification by the time they can be examined; it is astonishing how quickly amphipods, in particular, rot and fall to pieces. There is, in fact, no short cut to the estimation of the fauna of a Laminaria holdfast. The whole must be preserved, broken up, and picked to pieces with needles under a dissecting microscope, leaving no piece with a greater diameter than about 3 mm.; then the detritus must be gone through grain by grain and the animals removed. In the case of the large holdfast H 6 this dissection, with the sorting, counting and identification of species, took more than two months.

Six individual holdfasts were examined, samples H I to H 6. The two smallest, H I and H 4, which weighed 17 and 25 g., came from the top of the laminarian zone or about low-water springs; the others were all collected from as low as possible during very good tides, which on occasions fall 0.5 m. or more below the official level of low-water of ordinary springs. H 6 was as large a holdfast as could be found and weighed 104 g. The total number of animals per 100 g. varied from 1653 in H I to 5662 in H 4. It was curious to find the densest population in the highest holdfast of all, considering that most of the animals were sublittoral forms.

Table XIII shows the laminarian population. Certain groups which contain a good many species each are not analysed fully here, but are dealt with in separate tables below; these groups are Polychaeta, Copepoda, Tanaidacea, Isopoda, Amphipoda, Bryozoa and Tunicata.

TABLE XIII. LAMINARIA DIGITATA HOLDFASTS. ANIMALS INHIBITING SIX SAMPLES, IN NUMBERS PER 100 G. OF DAMP WEED

Sample no.		Нт	H 2	H 3	H4	H 5	H 6
Weight in g		17	62	02	25	52	104
Date		27 viii 20	27 111 20	27. viii. 30	27. viii. 30	7.1.31	2. iv. 31
Position in m		A V	A V 1.2	B VII +	B VII +	B VII OT	Near A V
Height in m.		- 1:08	-2.50	-2.65	- 1.86	-2.77	-2.7
D 10	•••	1 90	2 39	203	1 00	- //	- /
Porifera							
Leucoselenia sp.			3			•••	
Halichondria panicea			+		20	+	
Haliclona macandrewii							4
Porifera (indet.)		+		I			
Coelenterata							
*Sertularella polyzonias							+
*Kirchenpaueria pinnata		+	+	7	4	+	+
*Dynamena pumila		+	+	+	76	+	2
Actiniaria (juv., indet.)			3	I	4		
Turbellaria and Nemertinea		12	3	167	32	13	14
Nematoda		82	189	410	640	38	128
Polychaeta (see Tables XVI	I						
and XVIII)		1259	1924	2275	3992	1280	1606 .
Oligochaeta (indet.)			5	15	48		2
Sipunculoidea				-			
Phascolosoma minutum				3	4		2
Ostracoda (indet.)			8		12	25	
Copepoda (see Table XIV)		53	78	27	36	65	65
Cirripedia		55					
Verruca stroemia		20	20	19	172	2	5
Balanus crenatus				Ĩ			
Tanaidacea (see Table XV)		18	19	8	28	4	5
Isopoda (see Table XV)			5	3	16	2	12
Amphipoda (see Table XV)		129	76	129	148	175	95
Decapoda		/	, -			-,5	
Pilumnus hirtellus				I	16	2	2
Brachvura (juv., indet.)			3				
Pvcnogonida			5				
Ammothea echinata		18	3	I			
Acarina (indet.)			II	10	8	8	7
Pelecypoda							,
Mytilus edulis (juy.)		12	14	85	148	123	т
Anomia ephippium (juv.)		17		2	4		13
Musculus marmoratus (inv)	- /		T	-		- 5
Hiatella arctica (iuv.)				Ť			т
Pelecypoda (juy., indet.)		6	16		64	40	Â
Gastropoda			10			40	4
Patina pellucida		6	2	15	10	8	т
Gastropoda (iuv., indet.)		6	8	- 5	4	0	12
Gastropod egg			Ŭ	-4 T	4	,	-3
+Bryozoa (see Table XVI)		+	22	05	122	+	25
+Tunicata (see Table XVI)		6	52	20	132	6	33
I a unicata (see Ausie 2011)			14			-0-6 -	
-1	otal	1653 +	2458 +	3302 +	5662	1800 +	2017+
* Count	ed by	v branches.	+	Counted b	v colonies.		

Sponges occur on *Laminaria* but were not found elsewhere in this survey; there were three species, of which the commonest was *Halichondria panicea*. They were not so abundant or conspicuous here as under shaded, overhanging rocks at higher levels on the shore. Perhaps there is too much fine sand to suit them.

Coelenterates, also, were not very well represented, though two species, *Kirchenpaueria pinnata* and *Dynamena pumila*, were always present. They appeared to be more or less smothered in detritus and worm tubes. Occasional small anemones were found, but none large enough for identification. Flatworms or nemertines were generally present in small numbers, and were quite numerous (167) in sample H 3, but these forms were very small. It was rather surprising to find no nemertines large enough to be recognizable.

Polychaetes were extremely abundant, making up from two-thirds to fourfifths of the total, their numbers varying from 1259 to 3992. They will be discussed by themselves after the less abundant animals.

Oligochaetes were not common and have not been identified. They did not include either *Lumbricillus scoticus* or *L. pumilio*. The small sipunculid *Phascolosoma minutum* occurred sparingly in three samples, as did the few ostracods present.

TABLE XIV. LAMINARIA DIGITATA HOLDFASTS. COPEPODA HARPACTI-COIDA IN SIX SAMPLES, IN NUMBERS PER 100 G. OF DAMP WEED

Sample no. Weight in g. Date Position in m. Height in m.	 	H 1 17 27. viii. 30 A V - 1.98	H 2 63 27. viii. 30 A V 1·2 -2·59	H 3 92 27. viii. 30 B VII + -2.65	H 4 25 27. viii. 30 B VII + - 1.86	H 5 52 7. i. 31 B VII 9.1 -2.77	H 6 104 3. iv. 31 Near A V -2.7
Ectinosoma sp.							2
Zaus spinatus							6
Alteutha depressa						2	I
Alteutha sp.				I			
Idya furcata							5
I. minor							13
I. ensifera				I			6
Psamathe longicauda		6					
Aspidiscus fasciatus							2
A. littoralis		6				13	
Idyidae (indet.)						12	5
Parathalestris harpacticoides Rhinchothalestris				4	12	1,3	I
rufocincta			5			6	
Dactylopusia tisboides							2
D. brevicornis							I
Thalestridae (indet.)		6					
Amphiascus sp.		• •		2			2
Laophonte cornuta		18	49	19	36	13	13
Laophonte spp. (inder	t.)	17	24			6	4
Harpacticoida (indet.)						2
, To	otal	53	78	27	48	65	65

There were at least fifteen species of copepod (see Table XIV), but the total numbers of the group were small, varying from 27 to 78. Alteutha depressa, Idya minor and I. ensifera were found only in Laminaria but were not common, while the other species all occurred in one or more other weeds. Laophonte cornuta is the only species which occurred in all six samples and was also the most numerous; only one individual of it was taken in another alga, in Ascophyllum sample E 12 where it was probably a wave-washed stray. It is remarkable that this copepod, so constantly present among Laminaria holdfasts, should not have been found on either Gigartina or Fucus serratus collected from the same level as the highest Laminaria. Parathalestris harpacticoides occurred in four samples, but the other species in only one or two samples each.

The barnacle Verruca stroemia seems to inhabit all Laminaria digitata holdfasts, but in these samples the density of its population varied widely

160

from 5 to 172 per 100 g. (None were recorded from H 5, but since I did not specifically note at the time that they were absent, it is more likely that they were omitted by mistake.) *Verruca stroemia* does not live on the rock itself higher than about -2.5 m.; when associated with *Laminaria* it extends its range some 0.7 m. higher. One other barnacle was recorded, a single small individual of *Balanus crenatus* in H 3 from -2.65 m. *B. crenatus* is a common sublittoral species which is hardly ever found between tide-marks, and indeed this sample was from below low-water of ordinary springs (-2.51 m.).

TABLE XV. LAMINARIA DIGITATA HOLDFASTS. TANAIDACEA, ISOPODA, AND Amphipoda in Six Samples, in numbers per 100 g. of Damp Weed

Sample no		LI .	LI a	II a	TT .	TT -	TTC
Sample no.		n i	FI Z	П 3	H 4	. H 5	по
Weight in g.		17	03	92	25	52	104
Date Desition in m		27. VIII. 30	27. VIII. 30	27. VIII. 30	27. VIII. 30	P.VII 0.7	3. IV. 31
Position in m.		AV	A V 1.2	D VII +	D VII +	B VII 9.1	Near A V
rieight in m.		-1.98	-2.29	-2.05	-1.90	-2.77	-2.7
Tanaidacea	12				100		
Apseudes latreill	ei			I	8		
Heterotanais oer	stedi	•••		4	16		I
Paratanais batei		18	19	2	4	4	4
Tanaidacea (ind	et.)			I			
	Total	18	19	8	28	4	5
Isopoda							
Anthura gracilis				т			
Gnathia maxilla	ris						2
G. dentata					16		~
Gnathia sp. (juy	., indet.)		3				
Idotea granulosa	,		5				т.
Janira maculosa				T			5
Janiridae (indet.)		2	-		2	5
Munna kröveri	/		-	т.		~	
initia hitojent	Tetal			-			4
	Total	• •	5	3	10	2	12
Amphipoda							
Leucothöe incisa							2
Stenothöe monoci	uloides			I			2
Apherusa jurinei				13		20	7
Elasmopus rapax			3	23	8	8	2
Tritaeta gibbosa	2						2
Microdeutopus de	amnoni-						
ensis			•••	2	20	• •	9
Microdeutopus ch	ielifer			6			
Lembos websteri		• •		• •	12		2
Eurystheus macul	latus			17		2	6
Amphithöe rubric	cata			I			
Jassa falcata						6	4
J. dentex		• •		3	32		
Microjassa cumbi	rensis	19		•••			
Podocerus variego	atus			26			7
Caprella acanthij	tera	• •		2			
C. linearis			2		••.		
Amphipoda (juv.	., indet.)	110	71	35	76	139	52
	Total	129	76	129	148	175	95

The Tanaidacea (see Table XV) produced three species, *Apseudes latreillei* in two samples, *Heterotanais oerstedi* in three, and *Paratanais batei* in all six; even the last, however, was never numerous, 19 in H 2 being the largest catch of it. These were the only tanaids collected, except for one or two *Tanais cavolini* in *Ascophyllum*.

Although six species of isopod were identified (see Table XV), there were never more than 16 individuals present per 100 g. The single specimen of *Idotea granulosa* in H 6 is worth noting; this sample was one of the lowest,

JOURN. MAR. BIOL. ASSOC. vol. XXIV, 1939

-2.7 m., but this species also occurs as high up on the shore as +1.2 m., just below mean high-water neaps, which is an unusually extensive range for an intertidal animal.

The amphipods (see Table XV) were more numerous, and form quite an important part of the laminarian fauna. Their numbers varied from 76 to 175, and there were always a considerable number of young forms present which were not identified. The proportion of these young individuals varied from 35 out of 129 in H 3 to 71 out of 76 in H 2. Sixteen species were identified from *Laminaria*; seven of these occurred in only one sample each, five species occurred twice, three species three times, and one species, *Elasmopus rapax*, five times. None was found in all six samples. Thirteen of these species were found only on *Laminaria* holdfasts, while three occurred elsewhere, namely *Apherusa jurinei* (on *Fucus serratus and Ascophyllum*), and *Jassa falcata* (on *Gigartina*).

Other arthropods were not numerous. There are usually one or two of the crab *Pilumnus hirtellus* in a *Laminaria* holdfast; in these samples it was absent from only H I and H 2. *Pilumnus hirtellus* often seems to take shelter in the pits excavated by the limpet *Patina pellucida*. There were a few of the pycnogon *Ammothea echinata* in the first three samples. Acarines were usually to be found, but in small numbers only, from 7 to II mites being present in all the samples (except H I where there were none); none of them belonged to the genus *Rhombognathus*. The poverty of acarines and copepods on *Laminaria* holdfasts is remarkable, and in strong contrast with the situation on neighbouring weeds such as *Gigartina*. No insects were found on *Laminaria*.

Pelecypods were fairly numerous, but most or all of them were young. *Mytilus edulis* and *Anomia ephippium* appeared in all six samples, the former being as a rule the commoner. There were occasional specimens of *Hiatella arctica*, and in H 3 a solitary young *Musculus marmoratus*; this last species usually lives in the test of tunicates. It is difficult to know how to treat a group like this, where the animals are fixed and where there are apparently no adults. It seems that the young stages on *Laminaria* are more tolerant both of sedimentation and of overcrowding by other species than are the adults; this is rather surprising if one considers the density of population of a mussel bed. It can hardly be exposure that prevents these young *Mytilus* from growing up, for they are uncovered only on exceptionally low tides, and even then will be kept wet by the waves unless the low-tide coincides with a glass calm.

Patina pellucida, ubiquitous on Laminaria stems and holdfasts, was the only gastropod identified, though a few young individuals of other species were always present.

There is a considerable growth of bryozoa (see Table XVI) on the holdfasts; they are mostly encrusting, though there are usually several tuft-like colonies present also. The encrusting bryozoa are difficult to count. They are very

thin and fragile and are usually covered with worm-tubes and sand; even when they are clean it is not easy to see where one colony ends and another begins. In the samples H I, H 2 and H 5 they were not examined in detail. Holdfasts H 3, H 4 and H 6, however, were worked up in the British Museum (Nat. Hist.) where the help of experts could be obtained. Each of these samples was carefully cleaned, and a small piece broken off each bryozoan before the holdfast was cut up. These fragments were then very kindly identified by Dr Hastings. Nine species in all were present (see Table XVI). Schizoporella hyalina and Cellepora costazii occurred in all three samples, and the former was on the whole the most abundant species, though outnumbered (58 to 30) in H 3 by Membranipora lineata. Six species were found on H 3, six on H 4 and four on H 6, but each sample contained one or two species not found on either of the others. It would be necessary to examine more Laminaria holdfasts to obtain an accurate estimate of the bryozoan population.

TABLE XVI. LAMINARIA DIGITATA HOLDFASTS. BRYOZOA AND TUNICATA IN THREE SAMPLES, IN NUMBERS PER 100 G. OF DAMP WEED

Sample no.			H 3	H 4	H 6
Weight in g.			92	25	104
Date			27. viii. 30	27. viii. 30	3. iv. 31
Position in m.			B VII +	B VII +	Near A V
Height in m.			-2.65	- I·86	-2.7
Brvozoa					
Membranipo	ra lineata		58	4	
Microporella	a ciliata			4	4
Umbonula v	errucosa			16	
Mucronella	coccinea				2
Schizoporell	a hyalina		30	48	27
S. unicornis			I		
Cellepora co	stazii		3	36	2
C. pumicosa			I	24	
Tubulipora j	plumosa		2		
	Т	otal	94	132	35
Tunicata					
Botrylloides	leachi		8		
Sidnyum tun	rbinatum		2		
Aplidium po	ıllidum		4		
Diplosoma la	isterianum		5		
Didemnidae	e (indet.)		I		
	Т	otal	20		

Of the three samples just considered, only H 3 supported any tunicates (see Table XVI). These numbered 20 per 100 g. and were also identified by Dr Hastings. They were divided among four species as follows: 8 *Botrylloides leachi*, 5 *Diplosoma listerianum*, 4 *Aplidium pallidum* and 2 *Sidnyum turbinatum*, with the addition of a very young didemnid. Of these species *Botrylloides leachi* and *Sidnyum turbinatum* are elsewhere found between tide-marks and in shallow water, while *Diplosoma listerianum* and *Aplidium pallidum* are common sublittoral forms.

Laminaria digitata holdfasts: Polychaeta.

The polychaetes in *Laminaria* holdfasts (see Tables XVII and XVIII) were extremely numerous, running from 1259 to 3992 per 100 g. In each of the six samples the total number was counted accurately, but only in samples

11=2

H 3, H 4 and H 6 were the species determined at all completely. These three holdfasts were worked up at the British Museum (Nat. Hist.) where I could avail myself of the advice and criticism of Mr C. C. A. Monro. Samples H 1, H 2 and H 5 were examined when I was out of reach of specialists, and in them I have recorded only those species about whose identity I was in no doubt.

There are at least 43 species of polychaete in these catches from *Laminaria* holdfasts, divided among thirteen families. Few species occurred in all samples, but there were at least 26 in each of H 3 and H 6, 17 in H 2 and H 5, 16 in H 4, and 6 in H 1.

TABLE XVII. LAMINARIA DIGITATA HOLDFASTS. FAMILIES OF POLYCHAETA IN THREE SAMPLES, IN NUMBERS PER 100 G. OF DAMP WEED

Sample no. Weight in g. Date Position in m. Height in m.	::	H 3 92 27. viii. 30 B VII + -2.65	H 4 25 27. viii. 30 B VII + - 1.86	H 6 104 3. iv. 31 near A V -2.7
Aphroditidae Phyllodocidae Syllidae Nereidae		1 3 236 45	4 412 40	3 3 241 140*
Spionidae Cirratulidae Capitellidae Maldanidae		760 3 6 48	24 260	59 4 7
Sabellariidae Terebellidae Sabellidae Serpulidae Indet.		1083 89	3084 32 24	935 53
	Total	2275	3992	1606

* Including 85 larval Nereidae from one tube.

Before the individual species are considered, it is worth while examining briefly the distribution of families in H 3, H 4 and H 6, as set forth in Table XVII. In each of these samples the sabellids are the most numerous, and form from almost a half to more than three-quarters of the total, or on an average about two-thirds. A long way after the sabellids come the syllids, the spionids and the maldanids. Except in H 3 the syllids were the second most numerous family, but were always outnumbered by the sabellids by from four to seven times. The 760 spionids in H 3 made up one-third of the total number of polychaetes in that sample, but there were only 24 and 59 of them in the other two. On a preliminary examination of a holdfast, the serpulids appear to be more numerous relatively than they are in fact, owing to their conspicuous white shells. The remaining families are not, as such, sufficiently numerous to call for comment.

With the exception of the syllids and one or two very small species such as *Micromaldane ornithochaeta*, *Fabricia sabella* and *Spirorbis borealis*, most of the species of polychaete in *Laminaria* holdfasts are smaller than normal, usually about one-half of the sizes given by Fauvel (1923, 1927).

164

TABLE XVIII. LAMINARIA DIGITATA HOLDFASTS. POLYCHAETA IN SIX SAMPLES, IN NUMBERS PER 100 G. OF DAMP WEED

Sample no			HT	Ha	Ha	H	Не	HG
Weight in g			17	62	02	25	52	104
Date .			27. viii. 30	27. viii. 30	27. viii. 30	27. viii. 30	7. 1. 31	3. iv. 31
Position in m.			AV	AVI'2	B VII +	B VII +	B VII 9.1	Near A V
Height in m.			-1.98	-2.29	-2.65	-1.86	-2.77	-2.7
Aphroditidae								
Lagisca extenuat	a							I
Pholöe minuta				3	I		6	2
Phyllodocidae								
Eulalia bilineata				I				
Eulalia sp. (inde	et.)						4	
Eteone picta	and and a					4		
Phyliodocidae (1	ndet.)		••		3		••	3
Sullis gracilis			26	7.4	4	16	6	5
S. (Typosyllis) p	rolifera		30	**	4	10		
S. (Typosyllis) v	ariegata					12		
S. (Typosyllis) a	rmillaris					12		
S. (Ehlersia) ferr	rugina							I
Trypanosyllis zei	bra		6	5			8	IO
Odontosyllis cten	ostoma				2	4	2	• •
Pionosyllis sp. (1	ndet.)				I	••	•• .	
Sobacrocullic oni	aana		•• •		1		4	
Sphaerosyllis ool	geru			3		222	8	
Exogone gemmife	ra		30	1/	07	334	6	7
E. brevides								í
E. verrugera				I				
Autolytus sp. (in	det.)				3		2	
Syllidae (indet.)					129	36		205
Nereidae								
Perinereis cultrif	era			5			••	
Platynereis aume	rui		••		• • • •		12	
Funicidae)			12	45	40	40	140
Lumbriconereis s	n. (indet.)			2				
Spionidae	pr (macer)			5				
Polydora ciliata					45	4		I
P. caeca					28			
P. hoplura				• • •	I			
P. giardi					399	20		53
Polydora spp. (11	ndet.)		• •	12	287		4	4
Cirratulidae)							I
Heterocirrus alat	215							т
Dodecaceria conc	harum							3
Capitellidae				2	5			5
Capitellides giard	li				4	108		
Capitellidae (juv	., indet.)				2			7
Maldanidae								
Micromaldane or	mithochaeta	τ			47	260		160
Sabellariidae	., maet.)				1			
Sahellaria spinul	asa				1.00	4	1 2202	
Terebellidae	0.500					4		
Polycirrus calient	drum				I			I
Sabellidae								
Potamilla renifor	mis							6
P. torelli								5
Dasycnone bomby)x		•••		I			I
Fabricia sabella	lerranea		106	57	24	2228	34	750
Oridia armandi			100	02	60	48	44	163
Jasmineira elegar	15					40		I
Sabellidae (indet	.)							2
Serpulidae					1. 1. 1. C.C.			
Hydroides norveg	ricus			I				
Pomatoceros triqu	ueter		18	II	7	•••	6	•••
Polychaeta (indat)			48	82	82	32	34	53
r orychaeta (indet.)	-	1	1015	1021		24	1012	
	Tot	al	1259	1924	2275	3992	1280	1606

* Including 85 larval Nereidae from one tube.

APHRODITIDAE. (From now on, see Table XVIII.) Lagisca extenuata occurred once and *Pholöe minuta* in four samples, but only in small numbers.

PHYLLODOCIDAE. *Eulalia bilineata* and *Eteone picta* each occurred in one sample, and there were occasionally other members of this family.

SYLLIDAE. At least 16 species of this family were found (including species of *Pionosyllis* and *Autolytus* which were not determined further than the genus), but only two of them occurred in all six samples, namely *Syllis gracilis* and *Sphaerosyllis erinaceus*. The former species is relatively large and, for a syllid, easy to identify; probably all those present were found and counted, so that although it occurred in all the holdfasts it cannot be considered abundant, for its numbers ranged only from 5 to 36. *S. erinaceus*, on the other hand, is minute, and determinable only if well preserved. These holdfasts were pickled whole, and evidently in some the formalin took some time to penetrate and thus gave some of the smaller and more delicate animals time to decompose sufficiently to become unfit for identification. There were probably a good many *S. erinaceus* among the unidentified syllids in H 3, H 4 and H 6, and among the unidentified polychaetes in the other three samples. *Trypanosyllis zebra* is a readily recognizable species which occurred sparingly in four samples.

NEREIDAE. This family includes many of the larger polychaetes, but those found on *Laminaria* holdfasts did not exceed about 2 or 3 cm. in length and were usually even smaller. The identification of nereids depends largely on the arrangement of the paragnaths in the pharynx, so that unless the pharynx is extruded the fore-part has to be dissected. This was not practicable on such small worms as these. A few *Perinereis cultrifera* in H 2 and some *Platynereis dumerili* in H 5 died with the pharynx protruded and were identified, but the majority were not determinable. At first I thought that all these small nereids were young ones which would later on migrate to other habitats, but the presence of at any rate some adults is shown by a tough and leathery tube in H 6. This tube, which was about 2 cm. long and closed at both ends, was entirely filled by 85 very young nereids each about 2 mm. in length and bright yellow in colour. It must have been used by a mature worm to lay eggs in, if not also to inhabit. Mr Monro was unable to say to what species either tube or young worms belonged.

EUNICIDAE. This family was represented only by three *Lumbiconereis* sp. in H 2.

SPIONIDAE. All but one of these consisted of species of the genus *Polydora*, nearly all of which were *P. giardi*, which is somewhat surprisingly not included in the *Plymouth Marine Fauna* (1931). *P. giardi* was abundant in H 3; some 400 per 100 g. were identified, and probably the bulk of the 287 unidentified *Polydora* belonged to this species. The same sample also contained 45 *P. ciliata*, 29 *P. caeca*, and a solitary *P. hoplura*. These *Polydora* riddle with their tubes the calcareous alga, *Lithophyllum incrustans* (Philippi), which cements the *Laminaria* to the rock. In samples H 4 and H 6 there were

very few *Polydora* present, but the *Lithophyllum* was in each case extensively tunnelled with burrows which I attribute to this genus. In these samples the tunnels were occupied by sabellids, syllids and other worms.

CIRRATULIDAE. There was a single specimen of *Heterocirrus alatus* in H 6, and a few of the boring worm *Dodecaceria concharum* in H 2, H 3 and H 6 (but none in H 4).

CAPITELLIDAE. The minute species *Capitellides giardi* was quite common (108) in H 4, and there were 4 specimens of it in H 3. The occasional young capitellids in H 3 and H 6 were not of this species. *C. giardi* is not given in the *Plymouth Marine Fauna* (1931).

MALDANIDAE. This family included one common species, *Micromaldane* ornithochaeta, and one young individual in H 3 of another species. *M.* ornithochaeta is evidently one of the commonest polychaetes in *Laminaria* holdfasts, for there were 47 in H 3, 260 in H 4, and 160 in H 6. It is not an easy animal to find as it is colourless and very small, measuring only about 1.5 mm. by 0.1 mm., and is hardly visible to the naked eye.

SABELLARIIDAE. Sabellaria spinulosa occurred once, in H 4.

TEREBELLIDAE. There was a single specimen of *Polycirrus caliendrum* in each of the two samples H 3 and H 6.

SABELLIDAE. There were seven species of this family, including the commonest polychaete on the shore, *Fabricia sabella*, a small and active worm about 3 mm. long. Oridia armandi, about the same size and difficult to distinguish from *Fabricia sabella*, was always present but in smaller numbers. *Amphiglena mediterranea*, which measures about 1 cm., was very common (708) in H 4, but less numerous in the other samples, for 57 in H 2 was the next largest catch. The abundance of *Fabricia sabella* is quite extraordinary; it is found mainly in the fine detritus near the surface of the holdfast, but also occurs in interstices in the deeper parts. Although it is so small, it is sufficiently numerous to make up a considerable part of the total animal material present. The other sabellids only occurred in ones and twos in H 6, with the addition of a single Dasychone bombyx in H 3. The specimens of D. bombyx, Potamilla reniformis and P. torelli were all less than half the sizes given by Fauvel (1927).

SERPULIDAE. Spirorbis borealis was always present and in fair numbers, varying from 32 to 82; as has been mentioned, special search was made for other species of Spirorbis, but without success. Pomatoceros triqueter is not common or even always present on Laminaria holdfasts, though abundant on stones nearby; it was missing from H 4 and H 6, but occurred in small numbers on the other four samples. There was also, on H 2, a single Hydroides norvegicus, a species which might be expected to occur more frequently in such a habitat.

SUMMARY AND COMPARISON OF THESE FAUNAS

The faunas of these various seaweeds can now be compared as a whole. The species inhabiting the different plants have been dealt with in the foregoing sections.

In Table XIX the distribution of the various groups is shown in all fifty samples, and it can be used as a summary of Tables IV-XVIII in the previous sections. Table XX shows the average number of each group per 100 g. of each weed, and summarizes Table XIX.

Pelvetia canaliculata is the highest marine alga on the shore at Wembury, and supports the most meagre fauna which averages only 43.8. The dominant animals are the isopod *Ligia oceanica*, the amphipod *Hyale nilssoni*, and young Littorinidae most of which are probably *Littorina saxatilis*. Notable absentees are polychaetes, ostracods, copepods and acarines.

The fauna of *Fucus spiralis* is more varied and somewhat more abundant, averaging 98.8. *Ligia oceanica*, which lives mainly above high-water mark, no longer makes its appearance, but acarines and copepods are now found in most samples in small numbers; in one sample, B I, the copepods were numerous. *Hyale nilssoni* is the dominant species, and on an average makes up almost half of the population.

The faunas of the fucoid algae all have certain features in common and grade into one another to some extent, but the population of *Lichina pygmaea* is unlike any other on the shore. The lichen does not contain a particularly large number of species, but is nevertheless from 10 to 100 times richer in individuals than are algae from similar levels, and its animal population averages no less than 13,716 per 100 g. More than nine-tenths of these animals consist of two species, the pelecypod *Lasaea rubra* and the isopod *Campecopea hirsuta*, neither of which was found elsewhere; the larvae of the fly *Geranomyia unicolor* were also confined to *Lichina*. Nematodes, ostracods and copepods were either very scarce or altogether absent, in strong contrast with the neighbouring fucoids.

The three samples of *Fucus vesiculosus* came from levels corresponding with about the middle of the *Ascophyllum nodosum* zone, and many species are common to the two algae. In two of the *F. vesiculosus* samples the numbers of copepods and young Littorinidae were similar to those in *Ascophyllum*, and in the third sample there were many acarines. Otherwise, however, the fauna in *F. vesiculosus* was much the more scanty, with an average of $458^{\circ}5$.

In Ascophyllum nodosum both species and individuals are numerous, due in large part to the popularity of the tufts of Polysiphonia lanosa as a habitat; the average population numbers 1417.7. Ostracods, copepods, acarines and young Littorinidae are all abundant, and several other groups appear in numbers greater than 20 per 100 g. instead of in twos and threes as in the

TABLE XIX. VARIOUS GROUPS OF ANIMALS IN EIGHT SPECIES OF WEED, IN NUMBERS PER 100 G. OF DAMP WEED

Seaweed	Sample no.	Weight in g.	Date	Height relative to O.D. in m	Porifera	Coelenterata Turbellaria ano	Nematoda	Polychaeta	Oligochaeta	Sipunculoidea	Ostracoda	Copepoda	Cirripedia	Tanaidacea	Isopoda	Amphipoda	Decapoda	Pycnogonida	Acarina	Insecta	Pelecypoda	Gastropoda	Bryozoa	Tunicata	Total
Pelvetia	AI	197	30. vi. 30	+1.52					I						128	48				•••		5			55
Fucus spiralis	A 3 A 4 A 5 B 1 B 2 B 3	51 53 97 408 94 80	10. vii. 30 11. vii. 30 6. i. 31 20. iii. 31 24. vi. 30 10. vii. 30 11. vii. 30 11. vii. 30	+1.95 +1.76 +2.01 +1.49 +1.18 +1.67 +1.37	··· ···		··· ··· ···	 	 		 _2 I	 150 2 1	··· ··· ···	··· ···	37 	6 2 15 71 86 25	 	··· ··· ···		 2 1 4	 	2 2 27 14 2 27		 	49 6 15 266 114 30
Lichina pygmaea	B 5 B 6 C 2 C 3 C 4	93 56 77 11 12 14 24	6. i. 31 6. i. 31 20. iii. 31 5. ix. 30 5. ix. 30 7. i. 31 20. iii. 31	+1.15 +1.17 +1.49 +0.06 +1.34 +1.51	:: :: ::		4 7 9	 	18 27 8 7	··· ··· ···	 	2 	 137 292 293	· · · · · · · · · · · · · · · · · · ·	3770 2683 2886 2205	7 18 45 86	··· ···	··· ···	2 2 1480 178 87	2 1 264 175 71	9505 4550 12150	9 7 300 325 379 808		··· ··· ···	46 37 15536 8033 16050 15246
Fucus vesiculosus	DI D2 D3	87 78 87	15. vii. 30 15. vii. 30 7. i. 31	-0.40 -0.22 -0.46		10	6 4		 	6	6 41	115 538			8	··· 4			20 37 350			90 100 11			252 750 374
Ascophyllum	EI	350	13. v. 30	-0.52		+ 1	17		II		4	2			12	28			9	I	I	23			109+
Polysithonia	E 2	670 520	14. v. 30	+0.40	•••	I 3	13	••• •	83	•••	2	270	•••	••	10	14	•••	•••	9		I	35	•••	•••	170 + 742 + 100
lanosa	E4	151	15. vii. 30	+0.67		47	126	53	46	11	232	570			6	18	ī	11	308	113		77			1597
	ES	119	15. vii. 30	-0.09		35	60		8		351	731			3	9	I		115	140	4	58			1519
	E 6	103	23. vii. 30	-0.30		+ 82	49		17		1480	358			27	53		I	93	134	17	487			2798 +
	E 7	202	25. vii. 30	+0.32		1 + 56	72		I	•••	815	613		I	4	27			186	15	8	92			1891 +
	ES	84	28. VIII. 30	-1.00	• •	94	61	•••	IO	••	805	108	• •	• •	39	03	••	••	194	•••	43	252	••	••	1729
	E 9	90	5. 1. 31	-0.43	•••	+ 28	44	1	24	•••	24	49	• •	•••	50	86	•••	•••	204	6	15	75	•••	•••	860 +
	EIT	117	6 1 31	+0.73	•••	22 187	211	744	23		201	62		2	07	77		Ť	475	178	13	357	Ť		2714
	E 12	68	20. 111. 31	+0.06		+ 121	153	62	109		225	372			26	99			746	38	40	268			2259 +
Fucus serratus	FI	364	2. vi. 30	-1.49		I	IO		I		I	212			7	7			37	I		27			304
	F 2	335	11. vi. 30	-1.31		I			I	I		172			IO	2			34			13			234
	F3	395	13. vi. 30	-1.80	••	· · I	163	I	• •	2	8	775		••	7	5	I	••	114	II	3	97	••	••	1188
	F 4	91	23. VII. 30	-0.40	••		3		•••	•••	2	260	•••	• •	12	3	•••	•••	42	•••		35	16	•••	113
	FG	82	28. viii. 30	-1.32		•• ••	13					13			6	5			33	Ĩ		6	10		61
	F 7	85	28. viii. 30	-1.89		I		I				169			I				31			18	35		256
	F 8	99	5. i. 31	-0.28			3				5	3			28	20			200	2	3	33			311
	F9	93	5. i. 31	-1.83			IO					43			4	3			195			2			257
a	F 10	. 77	3. iv. 31	-1.26	• •		I	••		••	I	53	• •		3	••	••	••	18			I	10	••	87
Gigartina	GI	70	26. VII. 30	-1.08		24 9	4	33	• •	43	••	0580	•••	• •	60	254	•••	•••	129	•••	21	00	118	•••	7341
stellata	Ga	62	20. VIII. 30	-1.04	••	127	47	50	•••	••		5	•••	•••	40	40	•••	•••	12/4		115	1/6	164	••	2457
	GA	47	2 17 21	-1.09	•••	12/ 2	12	28	• •	•••	2	44	3	• •	10	10	•••	•••	1208		13	43	252	•••	1785
Laminaria	HI	17	27. viii. 30	-1.08	+	+ 12	82	1250				53	20	18		129		18			35	12	+	6	1653 +
digitata	H ₂	63	27. viii. 30	-2.59	3 +	3 3	189	1924	5		8	78	29	19	5	76	3	3	II		43	IO	32	14	2458 +
holdfasts	H 3	92	27. viii. 30	2.65	I	8 167	410	2275	15	3		27	20	8	3	129	I	I	10		89	20	95	20	3302
	H ₄	25	27. viii. 30	-1.80	20	84 32	640	3992	36	4	12	48	172	28	16	148	16	••	8		220	44	132	•••	5662
	HS	52	7.1.31	-2.77	+	+ 13	38	1280	•••	• •	25	65	+	4	2	175	2	••	- 8	• •	171	17	+	6	1806+
	LI 0	104	3, 17, 31	-2.7	4	2 + I/	128	1000	2	2		05	5	5	12	05	2		7		10	14	35		$2017 \pm$

other fucoids. Of all the groups listed in Tables XIX and XX, only Porifera, Sipunculoidea, Cirripedia and Tunicata are unrepresented in *Ascophyllum*. Many of its species are true intertidal forms which are not found except between high- and low-water marks.

The population of *Fucus serratus* resembles that of *F. vesiculosus* in many ways. The average total numbers are 324.6 and 458.5 respectively, in each of them copepods and acarines form the bulk of the fauna, and ostracods are very rare when compared with *Ascophyllum*. Although individuals are in many cases scarce in *Fucus serratus*, the number of species represented by them is large.

		Pelvetia canaliculata	Fucus spiralis	Lichina pygmaea	Fucus vesiculosus	Ascophyllum nodosum and Polysiphonia lanosa	Fucus serratus	Gigartina stellata	Laminaria digitata holdfasts
Porifera									8.3
Coelenterata Turbellaria	and					3.0	0.5	216.0	31.0
Nemertinea			0.3		5.3	63.6	0.2	2.8	40.2
Nematoda		3.4	3.2		3.3	76.1	21.2	16.2	247.8
Polychaeta			0.8			72.6	0.6	73.8	2056.0
Oligochaeta		0.5	3.2	II.O	0.3	39.2	0.5		9.7
Sipunculoidea	1.1.1.1.1.1				2.0		0.3	10.8	1.2
Ostracoda			0.5		16.0	353'3	3.0	0.2	7.5
Copepoda			25.8		221.0	272.2	178.1	1676.2	54.0
Cirripedia				287.0				1.5	51.0
Tanaidacea						0.5			13.7
Isopoda		15.2	0.5	2886.0	4.3	30.0	8.1	32.2	6.3
Amphipoda		15.4	46.3	35.0	1.3	48·1	4.3	83.8	125.3
Decapoda			0.5			0.5	0.I		4.0
Pycnogonida						0.5			3.7
Acarina			3.2	436.0	135.7	222.4	75.6	758.8	7.3
Insecta		0.8	1.3	161.0	2.3	58.3	2.0		
Pelecypoda				9447.0		14.8	0.8	42.0	96.2
Gastropoda		8.8	13.2	453.0	67.0	163.3	23.5	72.2	19.5
Bryozoa						0.5	6.1	158.2	73.5
Tunicata									7.8
	Total	43.8	98.8	13,716.0	458.5	1417.7	324.6	3145.0	2864.3

TABLE XX. AVERAGE POPULATIONS OF EIGHT SEAWEEDS, IN NUMBERS PER 100 G.

In Gigartina stellata the acarines are more abundant than they are anywhere else, and average 758.8 out of a total population of 3145. In one sample the copepods reached the very large number of 6586 per 100 g., but were rare in the other three samples. Thanks to the one rich catch, however, their average in the four samples of Gigartina is some six times as high as in Ascophyllum. Otherwise Gigartina is distinguished from the other weeds mainly by the larger numbers of hydroids and encrusting bryozoa, by the presence of small numbers of several species which belong more properly to the sublittoral region, and by the complete absence of oligochaetes and insect larvae.

In Laminaria digitata holdfasts there is a very great increase in the number of species present. Polychaetes are the dominant group, and on an average make up more than two-thirds of the population (2056 out of 2864.3); by far the most abundant worm is *Fabricia sabella*. Sponges and tunicates were found only on Laminaria, while insects were the only group missing. Nematodes, tanaids and amphipods all occurred in larger numbers than on any

other weeds, but copepods and acarines were notably scarce. Speaking generally, it can be stated that on the levels around mean sea-level and mean low-water neaps the most abundant groups are ostracods, copepods, acarines and young littorinids, and that in the holdfasts of *Laminaria* their place is taken by polychaetes.

So far, in this paper, the densities of the various populations have been expressed only in relation to a given mass of weed, 100 g. In comparing the numbers of animals in different weeds I have to some extent implied that 100 g. of one weed represents the same amount of environment as 100 g. of another. This implication, while not accurate, is by no means grossly misleading. It is true that, on the whole, samples collected near low-water mark will contain relatively more water than those from higher up the shore which have been exposed to the drying power of the air for some hours; nevertheless it is remarkable how quickly a weed such as *Gigartina stellata*, growing in separate tufts, loses any superficial water and becomes quite dry outside, and also how wet all but the most superficial layers of a densely growing plant like *Ascophyllum nodosum* remain on even the hottest day. On the whole, I do not think that it is seriously wrong to compare the populations of the weeds by numbers per 100 g.

Another matter is the estimation of the fauna of each weed over a given area of rock; this can be done from the figures given for 100 g. if the weight of each weed per sq. m. is known. I have measured this very roughly by the use of a simple piece of apparatus consisting of a band of galvanized iron 10 cm. wide and 115 cm. long. Allowing for an overlap of 3 cm. for rivetting the ends together, this can be bent to form a circle with a circumference of 112 cm., which encloses an area of 0.1 sq. m. The circular shape is maintained by means of two wooden pieces set at right angles and each 35.7 cm. in length. In use, the gear was placed firmly on the seaweed and a knife was run round the outside as deep as the underlying rock; then the weed inside the sampler was all cut away from the rock and weighed. This weighing was done in a bucket with a spring-balance, a method which, though crude, should give comparable results from weed to weed. I weighed from 4 to 7 samples of o'I sq. m. of each weed except for Lichina pygmaea, of which I weighed 4 samples each covering only 0.01 sq. m. The weights of the weeds in kg. per sq. m. are shown in Table XXI; these figures are admittedly rough.

TABLE XXI

Seaweed	Wt. per sq. m. in kg.
Pelvetia canaliculata Fucus spiralis Lichina trugmaea	5·5 5·7
Fucus vesiculosus Ascophyllum nodosum and Poly-	10.0
siphonia lanosa Fucus serratus	14·3 8·2
Laminaria digitata (holdfasts only)	2.7 2.5

Since in the foregoing sections the numbers of animals were given per 100 g. or 0.1 kg., the numbers per sq. m. can be obtained by multiplying those in each weed by 10 times the weight in kg. per sq. m. The result is shown in Table XXII, and this can now be compared with Table XX, where the numbers are given per 100 g.

	Pelvetia canaliculata	Fucus spiralis	Lichina pygmaea	Fucus vesiculosus	Ascophyllum nodosum and Polysiphonia lanosa	Fucus serratus	Gigartina stellata	Laminaria digitata holdfasts
Porifera								208
Coelenterata Turbellaria and					429	16	5833	775
Nemertinea		17		530	9095	41	76	1005
Nematoda	187	182		330	10880	1738	445	6195
Polychaeta		46			10380	49	1993	51400
Oligochaeta	II	182	220	30	5606	16		242
Sipunculoidea				200		25	292	38
Ostracoda		28		1600	50530	246	13	188
Copepoda		1471		22100	38920	14600	45240	1350
Cirripedia			5740				32	1275
Tanaidacea					29			342
Isopoda	836	28	57720	430	4290	664	870	158
Amphipoda	847	2639	700	130	6877	353	2262	3132
Decapoda		II			29	8		100
Pycnogonida					29			92
Acarina		182	8720	13570	31810	6189	20490	182
Insecta	. 44	74	3220	230	8337	164		
Pelecypoda			188940		2115	66	1134	2405
Gastropoda	484	770	9060	6700	23350	1927	1949	488
Bryozoa					29	500	4273	1838
Tunicata								195
Total	2409	5630	274,320	45,850	202,735	26,621	84,902	71,608

TABLE XXII. AVERAGE POPULATIONS OF EIGHT SEAWEEDS, IN NUMBERS PER SQ. M. OF ROCK SURFACE

The largest population is still that of *Lichina pygmaea*, with over a quarter of a million per sq. m., but it is now closely followed by *Ascophyllum* with over 200,000, owing to the much greater bulk of this alga. The other weeds come in the same order as before. This table brings out again the numerical importance over wide ranges of the shore of copepods, acarines and young gastropods, and emphasizes the exceptional abundance of ostracods among *Ascophyllum*. The figures for the holdfasts of *Laminaria* are minimal; at the levels exposed by the tide at the time that these measurements were made there were only 78 holdfasts per sq. m., but there are probably two or three times as many immediately below low-water of ordinary springs, and these would have been exposed had the tide reached the predicted level.

No fewer than eight large groups of animals reach their maximum in *Ascophyllum*, namely Turbellaria and Nemertinea (9095), Nematoda (10,880), Oligochaeta (5606), Ostracoda (50,530), Amphipoda (6877), Acarina (31,810), Insecta (8337) and Gastropoda (23,350). Cirripedia (5740), Isopoda (i.e. *Campecopea hirsuta* (57,720)) and Pelecypoda (i.e. *Lasaea rubra* (188,940)) are most abundant among *Lichina pygmaea*; Coelenterata (5833), Sipunculoidea (292), Copepoda (45,240) and Bryozoa (4273 colonies) among *Gigartina stellata*; and Porifera (208), Polychaeta (51,400), Tanaidacea (342), Decapoda (100), Pycnogonida (92) and Tunicata (195 colonies) on *Laminaria digitata*

holdfasts. These figures once again emphasize the general importance of *Ascophyllum nodosum* and *Polysiphonia lanosa* as a habitat for intertidal invertebrates on Church Reef.

COMPARISON WITH POPULATIONS OF SOIL, ETC.

These intertidal numbers are large, and I have collected a few other examples of big populations of small animals for comparison. The population of the soil is frequently cited as an example of exceptional abundance (e.g. Elton, 1927, p. 107) and in Table XXIII there are shown the populations of eight types of soil and of the tussocks of a grass. In the original reports they were mostly given in numbers per acre, but when necessary I have reduced them to numbers per sq. m. so that these figures are directly comparable with those in Table XXII.

TABLE XXIII. THE POPULATIONS OF NINE TYPES OF SOIL, ETC., IN NUMBERS PER SQ. M., FOR COMPARISON WITH TABLE XXII

	Comoron tota			Morris, 1922				Baweja, 1939	
	Ungrazed	Grazed	Morris, 1920	Man- ured	Not manured	Ford, 1935	Ford, 1937	Normal soil	Sterilized
Turbellaria						7			
Nematoda						(592		200	14
Enchytraeidae	• •			891	196	liii		350	55
Lumbricidae				240	II3	656			
Isopoda						692		90	48
Myriapoda						538		2515	545
Diplopoda				338	147	55-		-5-5	545
Chilopoda				550	53				
Arachnida					55			1685	1176
Acarina				T 2 T	52	2421	2085	100)	**/0
Araneidae				*3*	33	100	3903		
Opiliones						100			
Gastropoda						-43			
Other species						101		42	4
Insects							205	••	
Desture									
Collorabele				• •	••	• ;		I	
Collembola	••		140	590	171	59640	6766	7427	14100
Thysanura	• •			27	II	86		45	29
Orthoptera				3	3			7	I
Hemiptera			4	3	2	25		258	678
Psocoptera								25	8
Thysanoptera			II	5	6	. 25	543	18	31
Lepidoptera			4	7	12			IO	48
Coleoptera	1010		184	196	93	789		607	615
Hymenoptera			2	732	176	57		181	28
Diptera			542	350	135	61		2317	0173
Indet.				55-	-55	51		-3-7	9-13
Total Insects	207	280	00-	1000	6	60001			
Total other In-	207	300	005	1908	110	60734	. ••	10900	24711
vertebrata				1821	612	6013		5000	1842
Grand Total		• •	•••	3729	1223	66,747	11,499	15,900	25,553

The survey of Cameron (1917) went to a depth of 1 ft. (0.3 m.) in an ungrazed meadow and in alluvial pasture at Holmes Chapel, Cheshire. Morris (1920) worked to the same depth in permanent pasture in the same locality. Morris (1922) examined manured and unmanured soils down to 9 in. (0.23 m.) at Rothamsted. Ford (1935) surveyed the soil and surface populations in a meadow at Botley, near Oxford; the surface population was much the smaller,

and in Table XXIII I have added it to the soil fauna. Ford (1937) investigated the tussocks of a grass, *Brometum*, at Headington, also near Oxford. Finally, Baweja (1939) compared at Rothamsted the population of untreated soil under grass with that of soil which had been previously sterilized.

It will be at once apparent that the populations of soil are, on the whole, very much smaller than those of intertidal algae, with the exception of one group, the Collembola, which are really abundant in some soils (e.g. Ford, 1935). The larvae of Diptera are usually an important component of the soil fauna, but even so they rarely approach the numbers present in *Ascophyllum* (over 8000). Only in previously sterilized soil (Baweja, 1939) was this figure exceeded, for in this soil there were 9173 fly larvae per sq. m. Ford (1938) compares the population of grass tussocks (Ford, 1937) with that of human communities. He concludes that, allowing for the difference in size between the animals concerned, "the population of the Brometum, at its greatest density, is rather less crowded than are the inhabitants of Belgium".

Two other examples of the enormous numbers of animals to be met with between tide-marks may be mentioned. On rocks exposed to wave-action barnacles may become extremely numerous, and may occupy all the available space. Moore (1935, p. 305) mentions several examples where the population of *Balanus balanoides* exceeds 100,000 per sq. m.; small, first-year barnacles may even reach 200,000 if no space is already occupied by older and larger individuals. Secondly, Mr P. R. Crimp (personal communication) is finding nematodes to the number of upwards of a million per sq. m. in intertidal muds in the Tamar estuary.

DISTRIBUTION OF THE ANIMALS ON THE SHORE

This account will conclude with a list of species found during the survey, which are new to the *Plymouth Fauna*, with their habitats, but first it is necessary to mention the distribution of the main groups of animals, since in some of them the species have been worked out in part only or not at all. The basis of the following section is Tables XX and XXII.

PORIFERA. Sponges were found only on the holdfasts of *Laminaria*, and it was not easy to count them because they grow round each other and the branches of the holdfast; this makes it difficult to see where one sponge ends and the other begins, when two or more neighbouring sponges belong to the same species. At least three species were present, and the average number of sponges, 8.3 per 100 g., can probably be taken as below the true figure.

COELENTERATA. Five species of hydroid were found, but none above +0.73 m., the highest sample of *Ascophyllum*. They were never really common on *Ascophyllum*, they were scarce on *Fucus serratus* (though they were more plentiful on the stalks of these algae than on the fronds which were the parts examined), and absent from all the other fucoid algae. There was a fair quantity of *Dynamena pumila* on *Gigartina*, and hydroids were not uncommon

174

on Laminaria. In this last habitat they appear to be more or less smothered by fine sand and worm-tubes. The sessile stauromedusa Haliclystus auricula was found on Gigartina, and one young stauromedusa on Ascophyllum. There were occasional very small anemones on Laminaria.

TURBELLARIA AND NEMERTINEA. These two phyla have perforce been grouped together, though at times they were not rare. They consisted in the main of very small worms about 2 mm. long, which shrivelled up on being killed. This made them impossible to recognize without cutting sections of each. There were a few in occasional samples of *Fucus spiralis*, *F. vesiculosus*, *F. serratus* and *Gigartina stellata*, an average of 63.6 in *Ascophyllum nodosum*, and of 40.2 in *Laminaria*. They never formed a dominant part of the fauna.

NEMATODA. Nematodes are widely distributed on the shore and were found in all the weeds except *Lichina*. Dr Baylis has identified six species and two other genera. Nematodes were present in all samples of *Ascophyllum*, *Gigartina* and *Laminaria*, and were common in the last-named with an average of 247.8. Very few of them were longer than I cm.

POLYCHAETA. With the exception of one sample of *Ascophyllum*, E 11, which contained 744, polychaetes were not abundant until the *Laminaria* holdfasts were reached, where they were extremely numerous. They were not very rare in *Gigartina*, but otherwise they were found only in occasional samples, and were absent altogether from *Pelvetia*, *Lichina* and *Fucus vesiculosus*. There were at least 43 species of this group.

OLIGOCHAETA. This group occurred only sporadically in most weeds, and was not found at all on *Gigartina*. On *Ascophyllum* two species of *Lumbricillus* were not uncommon, *L. scoticus* which was originally described from a similar habitat at Millport, and *L. pumilio* which was a new species. These two were the only oligochaetes identified (by the late Dr J. Stephenson), but there were certainly two or three other species on the *Laminaria* holdfasts.

SIPUNCULOIDEA. Only one species was found, *Phascolosoma minutum*, which occurred in seven samples distributed among *Fucus vesiculosus*, *F. serratus*, *Gigartina* and *Laminaria*. It was never common, 43 in G 4 being the largest catch.

OSTRACODA. Ostracods were found in all weeds except *Pelvetia* and *Lichina*, but were quite scarce except in *Ascophyllum*. Here they were the most numerous group, with an average of 353.3 and a maximum of 1480 per 100 g. Those collected in 1930 and 1931 were not identified, but in April 1939 I collected about 150 from *Ascophyllum* which were examined by Mr A. G. Lowndes; they were all *Xestoleberis aurantia*.

COPEPODA. Like the ostracods, copepods were not found in either *Pelvetia* or *Lichina*, but except in *Ascophyllum* they were by far the more abundant of the two groups in the other weeds. They constituted the largest group in *Fucus vesiculosus*, *F. serratus* and *Gigartina*, and the second largest in *Fucus spiralis* and *Ascophyllum*. They form a dominant part of the fauna over a wide range in height, from +0.7 m. or a little below high-water neaps down to

-2 m. which is about mean low-water springs. Altogether 36 species of copepod have been identified.

CIRRIPEDIA. Since this survey was made chiefly on the weeds themselves, rock-dwelling barnacles were not generally collected. They were scraped off in fair numbers with *Lichina*, however, and *Verruca stroemia* is quite common on *Laminaria* holdfasts, and occasional on *Gigartina*. 4 species were found.

TANAIDACEA. There were four species of this small group, of which *Tanais* cavolini was found in two samples of *Ascophyllum* and the others on *Laminaria*. None were found anywhere else and they were never at all common.

ISOPODA. The isopods were more numerous and were found in all the weeds. There were 12 species, but the specific make-up differed widely on different parts of the shore; the dominant species were: Ligia oceanica on Pelvetia; Campecopea hirsuta on Lichina; and Naesa bidentata and Idotea granulosa on Fucus vesiculosus, Ascophyllum, Fucus serratus and Gigartina. Campecopea hirsuta was the only abundant isopod, but it was confined to Lichina where its average number was no less than 2886.

AMPHIPODA. 23 species of amphipod were found, of which only one, Hyale nilssoni, was at all common above the level occupied by Gigartina. Hyale nilssoni was a conspicuous member of the populations of Pelvetia, Fucus spiralis and Ascophyllum, in which it occurred in all samples and where it was often the only amphipod present. It was less numerous in Fucus serratus and was not found below Gigartina. Hyale nilssoni has an unusually extensive range for an intertidal animal, from below mean high-water springs down to about mean low-water springs; on Church Reef this represents a vertical range of more than 3.5 m. Apherusa jurinei and Amphithöe rubricata are widely distributed below mean sea-level and also live below tide-marks. Jassa falcata, found on Gigartina and Laminaria, was abundant in one sample (248 in G I), and several species, notably Elasmopus rapax, are not infrequent on Laminaria holdfasts but are not found higher up the shore. On the average, amphipods were most numerous on Laminaria (125.3), followed by Gigartina (83.8), Ascophyllum (48.1), Fucus spiralis (46.3) and Lichina (35).

DECAPODA. Decapod crustacea were not common. There was an occasional young crab or megalopa of *Carcinus maenas* and *Xantho incisus* on the fucoid algae, and several *Pilumnus hirtellus* on *Laminaria*.

PYCNOGONIDA. These were equally scarce. Only one species, Ammothea echinata, was identified, which occurred occasionally on Ascophyllum and Laminaria.

ACARINA. This is a very numerous intertidal group which has not yet been properly examined at Plymouth. Mr J. N. Halbert has identified 4 species from samples of *Ascophyllum* and *Fucus serratus*, but there are certainly more species than this; those found on *Laminaria* holdfasts appear to be all different from those found higher up. There were no acarines in *Pelvetia* and but few in *Fucus spiralis*, though they occurred in all the samples of the latter. In *Lichina*, *Fucus vesiculosus*, *Ascophyllum*, *Fucus serratus* and *Gigartina* they

were usually or at any rate sometimes abundant. The largest single catch was in *Lichina* (1480) in C I, but on an average they were most plentiful in *Gigartina* (758.8); next came *Lichina* with an average of 436, *Ascophyllum* (222.4), *Fucus vesiculosus* (135.7) and *F. serratus* (75.6). There is a very marked drop in these numbers to only 7.3 on reaching the *Laminaria* holdfasts. The great majority of them belong to two truly intertidal species, *Rhombognathus pascens* and *R. seahami*; *Halacarus basteri* is not uncommon in *Ascophyllum*.

INSECTA. Insects of one kind or another were found on all the weeds except Gigartina and Laminaria, and at all levels between +2.01 m. and -1.95 m. or from below mean high-water springs down to about mean low-water springs. The collembolan Lipura maritima and the thysanuran Petrobius maritimus were found occasionally above mean sea-level, and in one sample of Ascophyllum (E 12) there were one or two pupae and adults of beetles and flies. The great bulk of the insect collection, however, consisted of the larvae of diptera; these were found at all times at which collections were made, but were common only on Lichina and Ascophyllum. On the former weed the dominant species was Geranomyia unicolor, a large, brown larva 12 mm. long, which makes a rather tenuous tube, and on Ascophyllum the majority were (probably) Clunio marinus and Thalassomyia frauenfeldi. Although the larvae were always to be seen I have not found any of their pupae among the weeds examined.

PELECYPODA. No bivalves were found on *Pelvetia*, *Fucus spiralis* or *F*. *vesiculosus*, and they were very scarce on *F*. *serratus*. Young specimens of *Mytilus edulis* were found above high-water neaps, and were sometimes common on *Lichina*, *Gigartina* and *Laminaria*, while *Anomia ephippium* and *Hiatella arctica* were usually both to be found in rather small numbers on the holdfasts of *Laminaria*. The only really numerous bivalve was *Lasaea rubra*, which occurs in such astonishing numbers on *Lichina*.

GASTROPODA. As shown in Table XIX, gastropods were found in every sample except A 5 (*Pelvetia*), and were often numerous especially on *Lichina* and *Ascophyllum*. Below low-water neaps there were *Patina pellucida*, *Gibbula cineraria*, *G. umbilicalis* and the young forms of other species, but for the most part the gastropods consisted of the young of littorinids.

BRYOZOA. 12 species of bryozoa were identified, of which 9 were found only on Laminaria holdfasts. The other three species, Membranipora pilosa, Alcyonidium hirsutum and Flustrella hispida, did not occur on any Laminaria holdfasts but were all common on Gigartina. Alcyonidium hirsutum was found only on Gigartina, Membranipora pilosa was not uncommon on the lowest samples of Fucus serratus as well, while Flustrella hispida was found twice on Ascophyllum, even as high as +0.73 m., or just below high-water neaps; this last species is perhaps confined between tide-marks, but the others are also sublittoral.

TUNICATA. Colonial tunicates are not uncommon on some Laminaria

holdfasts, though they are by no means present on all of them. Four species were found on one holdfast, and a few very small simple ascidians were sometimes present. The group did not occur elsewhere.

LIST OF SPECIES, FOUND AMONG INTERTIDAL SEAWEEDS, NOT RECORDED IN THE PLYMOUTH MARINE FAUNA

The following is a list of those species recorded in this paper whose names are not in the *Plymouth Marine Fauna*, 2nd edition, 1931. This does not imply that they have not already been recorded at Plymouth by other workers since 1931. The number in brackets after each sample number is the number of animals found. A reference to a good description is given for each species.

PORIFERA

Haliclona macandrewii Bowerbank [1866, p. 284].

On Laminaria. H6 (4). Dr Burton thinks that this species may be identical with Chalina cinerea (Grant) in the Plymouth Marine Fauna (1931).

NEMATHELMINTHA

Anticoma limalis Bastian [Stekhoven, 1935]. On Ascophyllum. E3 (2). May be numerous.

Leptosomatum sp.

On Laminaria. H6. (Immature.)

?Linhomoeus sp. On Laminaria. H3.

Oncholaimus brachycercus de Man [Stekhoven, 1935]. On Ascophyllum. E3. May be numerous.

Pontonema (Paroncholaimus) ?ditlevseni de Connick & Stekhoven [Ditlevsen, 1928, p. 224].

On Fucus serratus. F3 (immature, numerous).

Symplocostoma longicolle Bastian [Stekhoven, 1935]. On Ascophyllum, Fucus serratus and Laminaria. F3 (few), H6 (1).

Thoracostoma figuratum (Bastian) [Stekhoven, 1935]. On *Ascophyllum* and *Laminaria*. H 3, H 6.

ANNELIDA

POLYCHAETA

Syllis (Ehlersia) ferrugina Langerhans [Fauvel, 1923, p. 269]. On Laminaria. H6 (1).

Eusyllis lamelligera Marion & Bobretsky [Fauvel, 1923, p. 294]. On *Gigartina*. G4 (2).

178

Exogone brevipes (Claparède) [Fauvel, 1923, p. 306]. On Laminaria. H6 (1).

Exogone verrugera (Claparède) [Fauvel, 1923, p. 307]. On Laminaria. H2 (1).

Polydora giardi Mesnil [Fauvel, 1927, p. 50].

On Laminaria. H₃ (399), H₄ (20), H₆ (53). This appears to be the commonest species of *Polydora* in *Laminaria* holdfasts; the worms bore into the calcareous alga *Lithophyllum incrustans* which cements the holdfast to the rock.

Heterocirrus alatus (Southern) [Fauvel, 1927, p. 99]. On *Laminaria*. H6 (1).

Capitellides giardi Mesnil [Fauvel, 1927, p. 157]. Occasionally common on *Laminaria*. H3 (4), H4 (108).

OLIGOCHAETA

Lumbricillus scoticus Elmhirst & Stephenson [1926, p. 469].

Fairly common on Ascophyllum, particularly among tufts of Polysiphonia, associated with Lumbricillus pumilio. E1, E2, E3 (20), E4 (20), E5 (4), E8 (3), E9 (14), E10 (17), E11 (3), E12 (2).

Lumbricillus pumilio Stephenson [1932, p. 902].

On Lichina, and in association with Lumbricillus scoticus on Ascophyllum and Polysiphonia. CI (27), C2 (8), C3 (7). EI, E2, E3 (45), E4 (26), E5 (4), E6 (17), E7 (1), E8 (7), E9 (10), EI0 (6), EII (19), EI2 (40).

CRUSTACEA

COPEPODA

HARPACTICOIDA

Harpacticus uniremis Kröyer [Sars, 1911, v, p. 51].

On Fucus vesiculosus and Ascophyllum. DI (2). E5 (16), rather above mean lowwater neaps.

Idya ensifera (Fischer) [Sars, 1911, v, p. 90] On *Laminaria*. H3 (1), H6 (6).

Idya gracilis Scott [Sars, 1911, v, p. 94]. On Ascophyllum. E3 (1).

Aspidiscus littoralis G. O. Sars [1911, v, p. 79].

On Fucus serratus, Gigartina and Laminaria. FI (1), F5 (239), F7 (159), FIO (27). GI (585), G2 (2), G3 (6), G4 (32). HI (6), H5 (13). In F5, 26. vii. 30 and F7, 28. viii. 30, four-fifths were young stages. In GI, 26. v. 30, there were also 3930 nauplii of this species and of *Psamathe longicauda*. There were 3 Aspidiscus littoralis on frond of Laminaria, 5. iv. 39.

Machairopus minutus G. O. Sars [1911, v, p. 86]. On Fucus vesiculosus. D1 (17).

12-2

Thalestris purpurea G. O. Sars [1911, V, p. 109]. On Fucus vesiculosus and Ascophyllum. D1 (2), D2 (83).

Ameira tenuicornis Scott [Sars, 1911, v, p. 217]. On Ascophyllum. E5 (156).

Laophonte brevirostris (Claus) [Sars, 1911, v, p. 256]. On Ascophyllum. E4 (20).

Laophonte littoralis Scott [Sars, 1911, v, p. 255].

On *Fucus spiralis* and *Ascophyllum*. B2 (I). E4 (20). The sample B2 was just below mean high-water neaps, E4 just above mean sea-level.

TANAIDACEA

Heterotanais oerstedi Kröyer [Sars, 1899, II, p. 14]. On Laminaria. H3 (4), H4 (16), H6 (1).

ISOPODA

Gnathia dentata G. O. Sars [Monod, 1926, p. 516; Sars, 1899, 11, p. 54]. On *Laminaria*. H4 (16). Male, female and young stages all present, 27. viii. 30.

Idotea granulosa Rathke [Collinge, 1917, p. 742; Sars, 1899, 11, p. 82].

On Fucus spiralis, F. vesiculosus, Ascophyllum, Fucus serratus, Gigartina and Laminaria. BI (I). D2 (I). EI (IO), E2 (IO), E3 (I), E4 (6), E6 (I), E7 (2), E8 (I3), E9 (54), EIO (75), EII (97), EI2 (IO). FI (2), F2 (I), F3 (6), F5 (2), F6 (5), F7 (I), F8 (20), FIO (3). GI (56), G2 (37), G3 (I6), G4 (9). H6 (I). This is the only common idoteid living among algae on Church Reef. Its distribution is almost identical with that of Naesa bidentata, with the addition of an individual in H6 from -2.7 m. or below low-water springs. The January samples of Ascophyllum, E9, EIO and EII, contained many young forms.

AMPHIPODA

Leucothöe incisa D. Robertson [Chevreux & Fage, 1925, p. 123]. On Laminaria. H6 (2).

Biancolina cuniculus (Stebbing) [Chevreux & Fage, 1925, p. 342]. On *Fucus serratus*. F1 (1).

ARACHNIDA

ACARINA

Hydrogamasus littoralis (G. and R. Canestrini) [Halbert, 1920, p. 120]. On Ascophyllum. E4, E5. Not common.

Rhombognathus pascens (Lohmann) [Viets, 1927*a*, p. 106; 1927*b*, p. 11]. Apparently always associated with *R. seahami* (q.v.).

180

Rhombognathus seahami (Hodge) [Viets, 1927*a*, p. 107; 1927*b*, p. 12].

Apparently always associated with *R. pascens*. These two species are common or abundant in most samples from just above mean sea-level down to low-water springs. They were scarce in *Fucus spiralis* and the three higher samples of *Lichina*, absent from *Pelvetia* and *Laminaria*, common or abundant in *Fucus vesiculosus*, *Ascophyllum*, *Fucus serratus* and especially in *Gigartina*; apparently least abundant during the summer but there were 1273 in G2 on 28. viii. 30. C1 (1481). D1 (17), D2 (29), D3 (338). E3 (36), E4 (278), E5 (42), E6 (62), E7 (173), E8 (148), E9 (195), E10 (251), E11 (248), E12 (678). F4 (42), F5 (46), F6 (21), F7 (31), F8 (198), F9 (194), F10 (18). G1 (117), G2 (1273), G3 (422), G4 (1209).

Halacarus basteri (Johnston) [Viets, 1927b, p. 18].

On *Fucus serratus* and *Ascophyllum*; not uncommon on the latter, where it appears to make up about one-tenth of the mite population.

INSECTA

DIPTERA (Larvae)

Thalassomyia frauenfeldi Schin. [Chevrel, 1903, as *Scopelodromus isemerinus*, larvae on pp. 16–23. Edwards, 1926, p. 786, considers this to be identical with *Thalassomyia frauenfeldi*.]

Larvae (probably this species) common on Ascophyllum, associated with those of Clunio marinus.

Geranomyia unicolor Hal.

Larvae common on *Lichina* in January, March and September. C1 (46), C2 (175), C3 (64), C4 (104).

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(Porifera) (Nemathelmintha) (Polychaeta) (Oligochaeta) (Ostracoda) (Copepoda) (Crustacea) (Acarina) (Diptera) (Pelecypoda) (Bryozoa, Tunicata) (Calcareous Alga).

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SUMMARY

This paper gives an account of a survey of the invertebrate populations (omitting Protozoa) of eight species of seaweeds on Church Reef, Wembury Bay, extending over the entire intertidal range.

Above high-water neaps the faunas are poor, except for that in *Lichina pygmaea* which is the richest in individuals on the shore.

Between high-water neaps and low-water springs the most numerous groups are copepods, acarines, young littorinids and (in *Ascophyllum* only) ostracods.

In the holdfasts of *Laminaria digitata* polychaetes are very abundant and make up the majority of the population.

The intertidal faunas are compared with those in the soil on land, and prove to be far more abundant. Even the most plentiful group in the soil, the insects, is rarely as numerous as it is in *Ascophyllum* around mean sea-level.

Altogether 177 species are recorded, of which 35 are not in the *Plymouth* Marine Fauna (1931).

REFERENCES

- BAWEJA, K. D., 1939. Studies of the soil fauna, with special reference to the recolonization of sterilized soil. *Journ. Anim. Ecol.*, Vol. VIII, No. 1, pp. 120-61.
- BOKENHAM, N. A. H, NEUGEBAUER, F. L. M. & STEPHENSON, T. A., 1938. The vertical distribution of certain intertidal marine gastropods in False Bay, with notes on

the development of two of them. Ann. Natal Mus., Vol. IX, part I, pp. 113-37. BOWERBANK, J. S., 1866. A monograph of the British Spongiadae. Ray Soc. Publ.,

Vol. 11, pp. 1–388.

CAMERON, A. E., 1917. The insect association of a local environment complex in the district of Holmes Chapel, Cheshire. Trans. Roy. Soc. Edinb., Vol. LII, No. 2, pp. 37-78.

CHEVREL, RENÉ, 1903. Scopelodromus isemerinus. Genre nouveau et espèce nouvelle de Diptères Marins. Arch. Zool. Exp. Gén., Series 4, Vol. I, pp. 1-28.

CHEVREUX, E. & FAGE, L., 1925. Amphipodes, in Faune de France, pp. 1-488.

COLLINGE, W. E., 1917. A revision of the British Idoteidae, a family of marine Isopoda. *Trans. Roy. Soc. Edinb.*, Vol. LI, pp. 721–60.

- COLMAN, JOHN, 1933. The nature of the intertidal zonation of plants and animals. Journ. Mar. Biol. Assoc., Vol. XVIII, pp. 435-76.
- DITLEVSEN, H., 1928. Free-living marine Nemetodes from Greenland waters. Medd. om Grønland, Copenhagen, XXIII, Supp. pp. 201-50.
- EDWARDS, F. W., 1926. Marine Chironomidae. Proc. Zool. Soc. Lond., 1926, Part 2, pp. 779-806.
- ELMHIRST, R. & STEPHENSON, J., 1926. On Lumbricillus scoticus n.sp. Journ. Mar. Biol. Assoc., Vol. XIV, pp. 469-73.

ELTON, CHARLES, 1927. Animal Ecology. London. Pp. 1-207.

FAUVEL, P., 1923. Polychètes errantes. Faune de France, Vol. v, pp. 1-488.

— 1927. Polychètes sédentaires. Faune de France, Vol. XVI, pp. 1-494.

Ford, J., 1935. The animal population of a meadow near Oxford. *Journ. Anim. Ecol.*, Vol. IV, pp. 195-207.

--- 1937. Fluctuations in natural populations of Collembola and Acarina. Journ. Anim. Ecol., Vol. VI, pp. 98-111.

— 1938. Fluctuations in natural populations of Collembola and Acarina. Part 2. Journ. Anim. Ecol., Vol. VII, pp. 350–69.

GURNEY, ROBERT, 1933. Notes on some Copepoda from Plymouth. Journ. Mar. Biol. Assoc., Vol. XIX, pp. 299-304.

HALBERT, J. N., 1920. The Acarina of the seashore. Proc. Roy. Irish Acad., Vol. XXXV B, pp. 106-52.

IMMS, A. D., 1923. (Chapter 9 in Russell, 1923, q.v.)

LINKE, O., 1933. Morphologie und Physiologie des Genitalapparates der Nordseelittorinen. Wiss. Meeresuntersuch., Vol. XIX, Part 5, pp. 1-60.

MARINE BIOLOGICAL ASSOCIATION, 1931. Plymouth Marine Fauna (2nd Edition).

MONOD, TH., 1926. Les Gnathiidae. Essai monographique. Mém. Soc. Sci. Nat. Maroc, Vol. XIII, pp. 1–668.

MOORE, HILARY B., 1935. The biology of Balanus balanoides. IV. Relation to environmental factors. Journ. Mar. Biol. Assoc., Vol. XX, pp. 279-307.

MORRIS, H. M., 1920. Observations on the insect fauna of permanent pasture in Cheshire. Ann. Appl. Biol., Vol. VII, pp. 141-55.

— 1922. The insect and other invertebrate fauna of arable land at Rothamsted. Ann. Appl. Biol., Vol. IX, pp. 282–305.

ORTON, J. H., 1929. Observations on *Patella vulgata*. Part III. Habitat and habits. Journ. Mar. Biol. Assoc., Vol. XVI, pp. 277-88.

PERCIVAL, E., 1929. A report on the fauna of the estuaries of the River Tamar and the River Lynher. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 81-108.

RUSSELL, J., 1923. The micro-organisms of the soil. London.

SARS, G. O., 1899. An Account of the Crustacea of Norway. Vol. II, Isopoda, pp. 1–270.
 — 1911. An Account of the Crustacea of Norway. Vol. v, Copepoda Harpacticoida, pp. 1–449.

STEKHOVEN, J. H. S., 1935. Nematoda Errantia. Tierwelt. Nord- u. Ostsee, Lief. 28, Teil v B, pp. 1-173.

STEPHENSON, J., 1932. Oligochaeta from Australia, North Carolina and other parts of the world. *Proc. Zool. Soc. London*, 1932, pp. 899–941.

THIENEMANN, A., 1915. Zur Kentniss der Salzwasser-Chironomiden. Arch. Hydrobiol. Plankt., Supp. Bd. II, pp. 443-71.

VIETS, K., 1927a. Die Halacaridae der Nordsee. Zeit. wiss. Zool., Vol. CXXX, pp. 84-173.

--- 1927b. Halacaridae. Tierwelt Nord- u. Ostsee, Lief. 10, Teil XI C, pp. 1-72.

Note

The lengths of whole traverses given in metres in Table I are conversions of the total lengths in feet, and not the sum of the component sections in metres. There is inevitably a slight error involved in converting from one scale to another, and this error may be quite large when accumulated from one section to another.

In the later tables, the total numbers of animals per 100 g. are converted directly from the total numbers per sample, and are therefore not necessarily the same as the sum of the component numbers.