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TIDE POOLS OF CARRIGATHORNA AND BARLOGE CREEK†

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[Plate 1]

CONTENTS

An ecological account is given of tide pools on the remote promontory of Carrigathorna, formed of Devonian slates on edge, on the open Atlantic coast, and on a sheltered but otherwise similar slate reef nearby. Both sites are at the entrance to Lough Ine, County Cork, Republic of Ireland. In addition to its immediate ecological

† This is paper no. 21 in the series 'The ecology of Lough Ine'; the earlier parts were published elsewhere.

concern, this study is intended to provide a basis for comparison in the future, in case of climatic or other environmental change. The pools have been charted, and their levels and dimensions are specified. They range from 0.3 to 5 m in depth, and the largest holds over 100 m^3. The highest studied are only replenished by wave-wash, and the lowest are never completely disconnected from the sea.

As is generally recognized, various environmental conditions are subject to wider fluctuations in tide pools than in the sea. Examples are shown of diurnal and tidal changes in temperature and pH, and some readings of oxygen content and salinity are given. The deeper pools remain cool below even when their upper waters are warmed, and this is probably important in permitting the survival of *Laminaria* forest within them. Temperatures of over 25 °C were attained in high-level pools, and pools with much of the green alga *Enteromorpha* reached pH 10. Salinity ranged up to 40‰ in the highest pools, and oxygen tensions to nearly twice the saturation level.

Five ecological facies characterized the tide pools of the open coast, from high level downwards: *Enteromorpha* scrub, smooth encrusting coralline alga scoured by limpets, *Corallina* scrub (extending into *Laminaria* forest as undergrowth), *Laminaria* forest, and *Dictyota* scrub (with other non-calcareous algae). *Enteromorpha* covered the bottoms of tide pools just above the highest tides, where the number of species present was small but in some cases the number of individuals very large. The extension of *Enteromorpha* to lower pools is largely prevented by limpets, themselves probably limited upwards by extreme conditions of temperature, pH, salinity etc. The extension of limpets in any numbers to lower pools is probably limited by the tough calcareous alga *Corallina officinalis*. *Laminaria* forest takes over in mid-tidal pools where the water is deep enough, and *Corallina* gives way at depth to *Dictyota* and other algae, possibly in relation to reduced illumination. The small *Laminaria*-eating limpet *Patina pellucida* reaches higher numbers in the shelter of tide pools than in the sublittoral *Laminaria* forest of the nearby open coast.

The fauna associated with *Corallina* has been studied by means of 0.20 m × 0.15 m quadrats taken from many of the pools. Quantities of epiphytic coralline algae, spirorbid tube-worms, and epizoic Bryozoa have been assessed from 10 g aliquots of *Corallina*, and numbers of other species have been determined from the complete quadrat collections. Many progressive changes from high-tidal to low-tidal pools are described.

One aberrant pool at Carrigathorna drains by slow leakage over the period of neap tides, and is occupied by a blanket of a blue-green alga (*Lyngbya confervoides*) populated by larvae of *Halocladius fucicola* (Diptera, Chironomidae). It is to be expected that *L. confervoides* (like other blue-green algae) can survive considerable desiccation.

A pool on the more sheltered reef ('Urchin Reef') in the mouth of Barloge Creek contains much of the brown alga *Cystoseira nodicaulis*, which together with *Corallina* accommodates extremely large numbers of individuals of many invertebrate species. This sheltered pool, replenished on every tide, acts as a rich marine aquarium. Crevices in the bottom hold over 100 of the sea urchin *Paracentrotus lividus*, of which only a few specimens are found on the open coast. The hard slate probably does not allow this urchin to burrow, so that it probably cannot resist storms on the open coast. A large population exists in Lough Ine in shallow places where the water warms up in summer, and this population possibly provides larvae for settlement.

The occurrence is recorded of 111 species of algae and of 198 species of animals in the tide pools.

1. Introduction

It is our purpose, in the present study of tidal rock pools near Lough Ine, County Cork, to describe the important topographical features, to survey the plants and animals together and intensively, and to leave a record which can be used as a basis for comparison in the future. These rock pools are pre-eminently suitable for such an undertaking. Those on the headland of Carrigathorna (Ordnance Survey 1901) are distributed over the whole tidal range, and some are large and deep. They are fully exposed to Atlantic waves, so that for comparison we have also included pools on 'Urchin Reef' (our name), within the mouth of Barloge Creek and relatively sheltered (figure 1). Carrigathorna is nearly separated from the mainland by a vertical cleft, and Urchin Reef projects into Barloge Creek from the foot of a cliff. Both sites are difficult to reach and are therefore unlikely to be disturbed. We wish also to compare

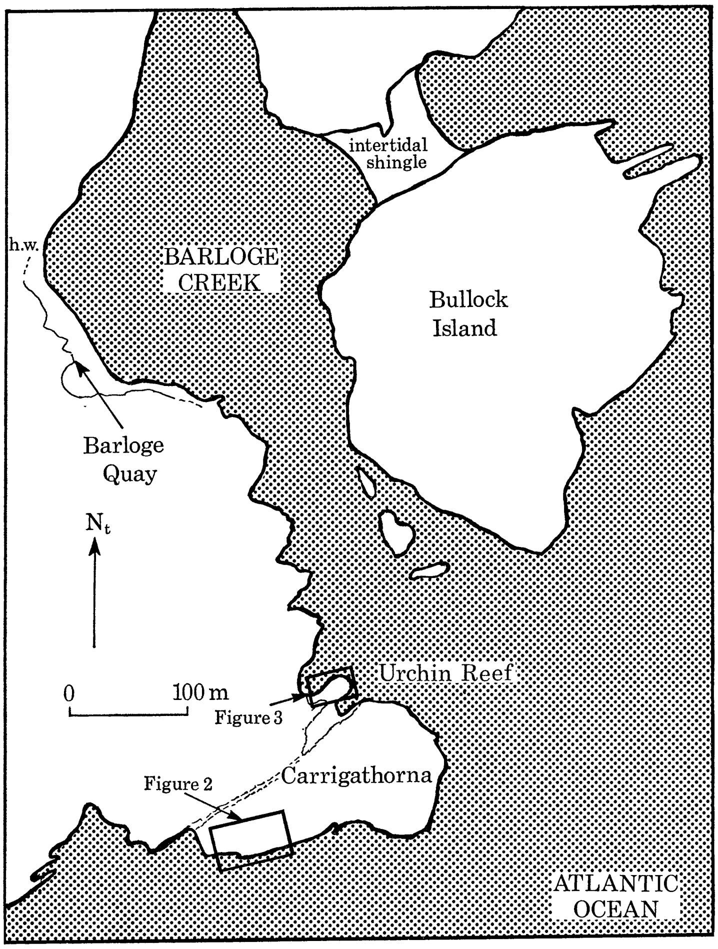

FIGURE 1. Map of Barloge Creek and Carrigathorna.

the flora and fauna of these tide pools with the flora and fauna of the adjacent sublittoral region of the open coast, already described (Norton *et al.* 1977), in order to see to what extent tide pools are inhabited by communities otherwise characteristic of the sublittoral region, and thus act as sublittoral aquaria. Our survey does not so far take account of seasonal changes, although visits were made by one of us (J.A.K.) at various times of year. The investigation of seasonal changes could best be confined to a very few selected pools.

Although there have been many previous studies of tide pools, few combine a botanical and a zoological approach, and few have been carried out on a scale appropriate to the magnitude and complexity of the problems involved. For Atlantic tide pools, important botanical surveys have been described by Johnson & Skutch (1928) for Mt Desert Island, Maine, and by de Virville (1934, 1935) for the coasts of France. Pyefinch (1943) has described the flora and fauna

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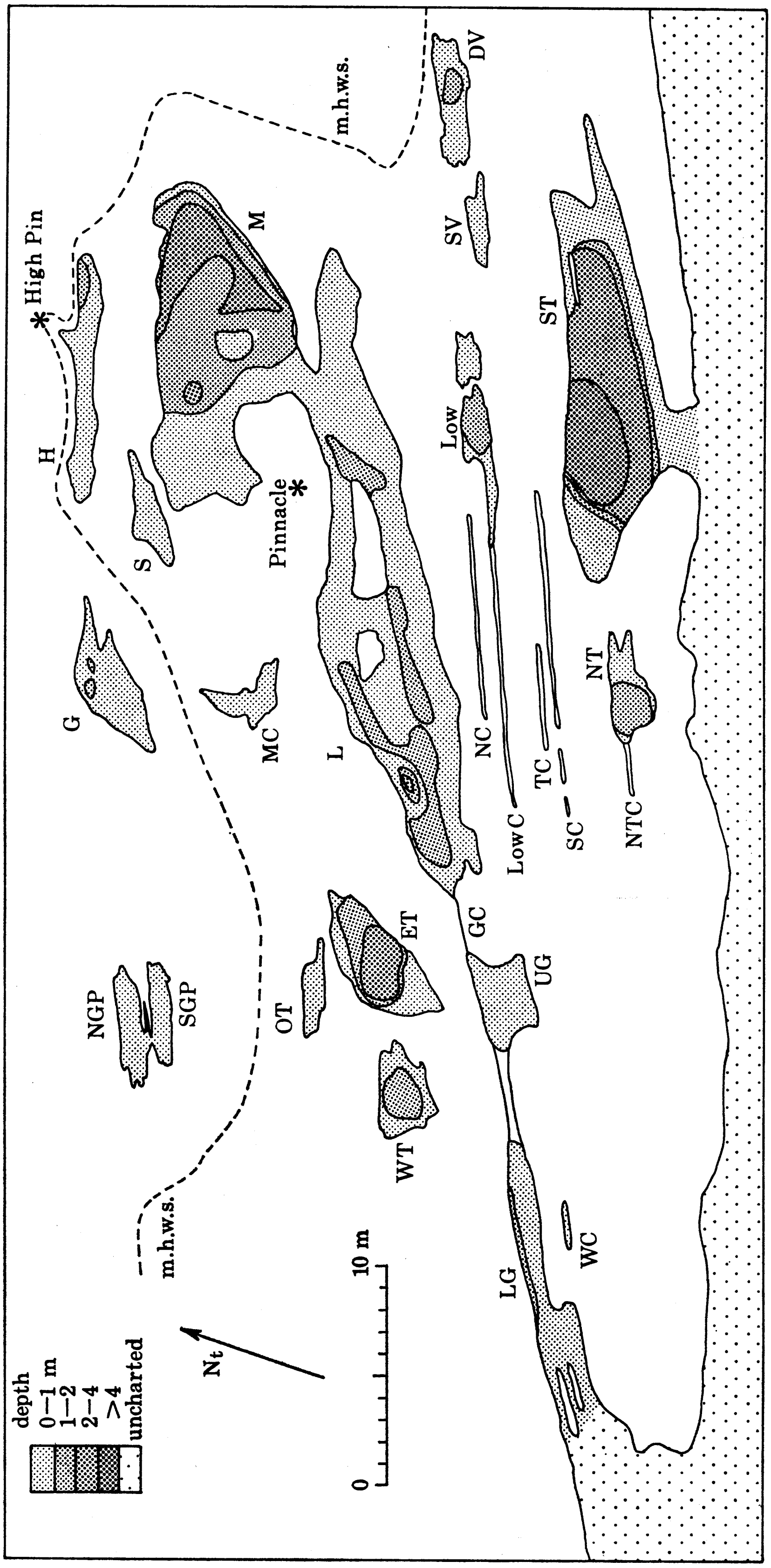

FIGURE 2. Plan of Carrigathorna tide pools. A broken line indicates the approximate position of mean high water of spring tides. Abbreviations for pool names are given in appendix B.

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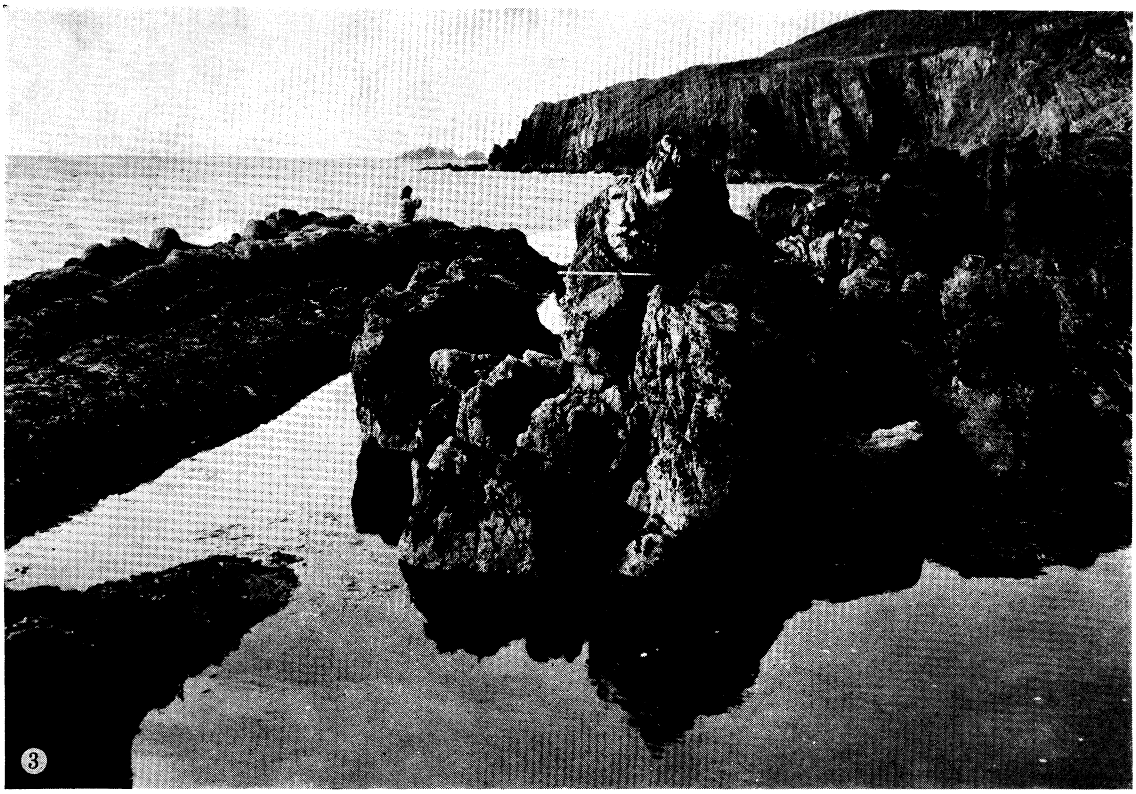

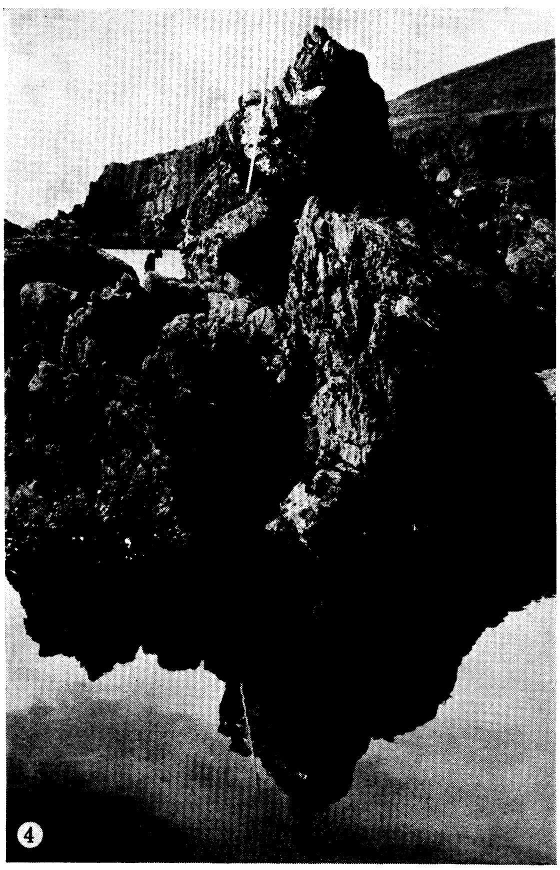

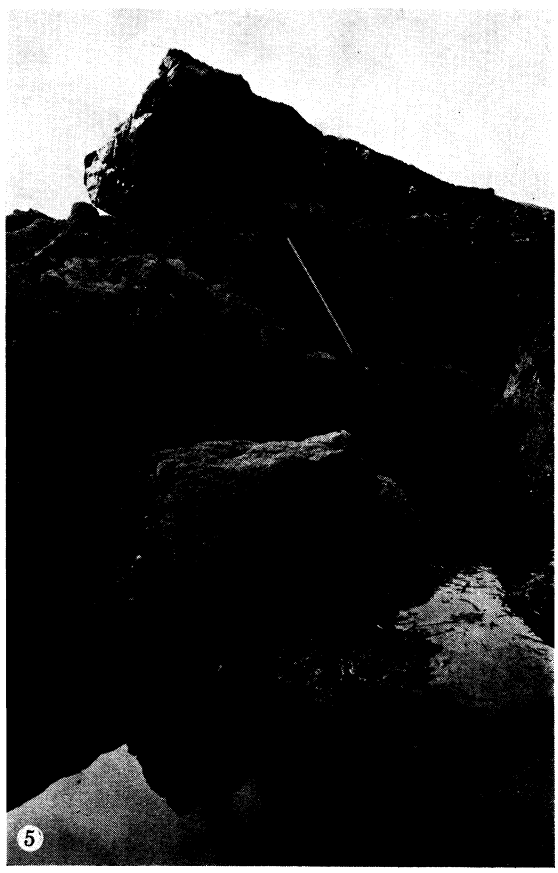

FIGURES 3–5. For description see opposite.

(*Facing p.* 5)

of tide pools on Bardsey Island, North Wales, but the number of species reported is small compared with that found in the present survey. All these authors have usefully surveyed the physical conditions, such as temperature, pH, oxygen content, and salinity, characteristic of tide pools. Here again, however, there is no detailed record throughout the year.

2. Methods

(a) *Topographical survey*

The plan of the Carrigathorna tide pools (figure 2) is based on 'Pinnacle' a conspicuous high point in the middle of the main tide pool area (figures 3, 4, and 5; plate 1). Levels of pools were related to convenient pool water level survey points, situated a little above the edge of each pool, and the levels of these points were related to Pinnacle with an automatic level. A reserve levelling point 'High Pin' was established in a gully above the north side of High Pool, and was marked by the head of a stout stainless steel pin driven in until flush with the rock surface. High Pin is 0.35 m below Pinnacle. Mapping and levelling was also carried out on Urchin Reef (figure 6).

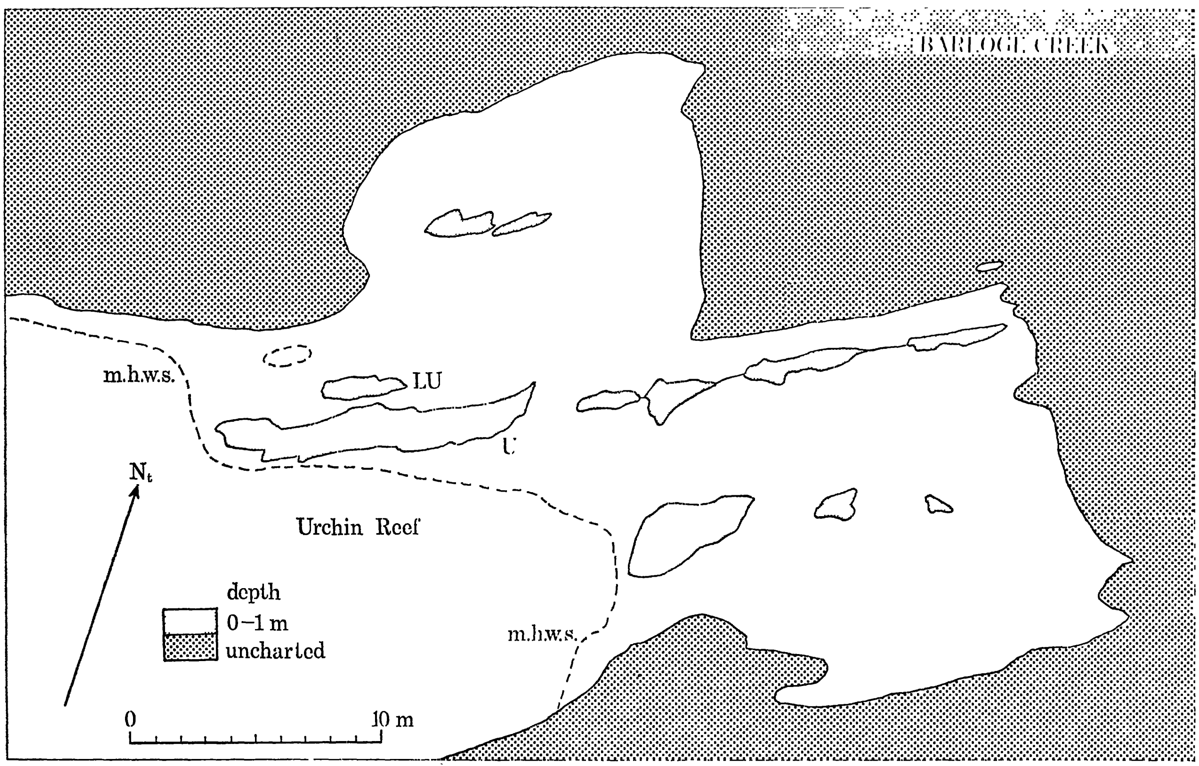

Figure 6. Plan of Urchin Reef. A broken line indicates the approximate position of mean high water of spring tides. The location of Urchin Reef in the mouth of Barloge Creek is shown in figure 1. LU, Little Urchin Pool; U, Urchin Pool.

Description of plate 1

Figure 3. View from east across Main Pool (right and centre) connected with Long Pool (left) to Pinnacle (upper centre). Nearly vertical strata of Devonian slates are seen in background cliff. A 1 m rule shows the scale.

Figure 4. Pinnacle from the east (with 1 m rule).

Figure 5. Pinnacle from the north (with 1 m rule).

Depth contours for each of the major pools were drawn from soundings taken along a series of transects. To estimate the volume of a pool, the areas between adjacent pairs of depth contours were measured, multiplied by the average depth of the enclosing contours, and added up. The mean depth of the pool was obtained by dividing this estimate of volume by the surface area of the pool.

(*b*) *Tide levels*

We wished to correlate the Urchin Reef pools with those at Carrigathorna, and to estimate the mean levels of high and low water of spring and neap tides in relation to a standard level, namely Pinnacle. Our correlations are based on observations of water level taken at short intervals over the period of high water in calm weather. Simultaneous records were made at Carrigathorna and at Barloge Quay (in the shelter of Barloge Bay), and at Urchin Reef and Barloge Quay. We estimate from these observations that the mark on Barloge Quay is 1.23 m below Pinnacle.

For estimating mean levels of high and low water of spring and neap tides at Barloge, we have assumed that tides there are the same as at the nearby port of Baltimore, and we have used the tidal predictions and corrections published by the Admiralty (1977). We have used five series of observations taken at Barloge Quay over the period of high water to estimate from the prediction for Baltimore the level on Barloge Quay of mean high water of spring tides (0.61 m below our mark). We have then assumed that the depths below this of mean levels of high water of neap tides, low water of neap tides, and low water of spring tides are the same as those given by the Admiralty (1977) for Baltimore. Although there are likely to be small differences between Baltimore and Barloge, and the levels of individual tides may differ from predictions, our results (range 0.48–0.70 m) are sufficiently constant to give confidence.

(*c*) *Water temperature*

Water temperature was measured sometimes with a mercury thermometer, read *in situ*, but more usually with an electric resistance thermometer.

(*d*) *Percentage saturation with dissolved oxygen*

A Mackereth oxygen probe was used, and was agitated while readings were being taken. We have not studied oxygen content intensively because repeated agitation of the probe in a small pool would have changed the conditions being measured.

(*e*) *Hydrogen ion concentration*

Indicators (thymol blue or thymol violet) were used to measure pH. After the determination of the temperature at the site, the sample was collected by means of a pipette fitted with a suction bulb. It was discharged to a marked level into a test tube, and the indicator was added. The stoppered tube was then inverted to mix and immediately transferred to a bucket of water holding the comparison tubes, made up freshly from Palitzsch borax-boric acid buffer (Harvey 1945) or Clark and Lubs boric acid–sodium hydroxide or Sørensen's glycine–sodium hydroxide buffers (Clark 1928). Readings were corrected for salt error, and for change in temperature of the sample, and for the temperature of the comparison tubes, as described by Harvey (1945). In July the temperature of the comparison tubes was always close to the standard 18 °C.

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(*f*) *Salinity*

Samples for determination of salinity were collected directly into medicine bottles, which were wiped, tightly stoppered, and sent to the Fisheries Laboratory at Lowestoft. Salinity was determined there with the inductively coupled salinometer.

(*g*) *Systematic authorities*

Nomenclature follows Parke & Dixon (1976) for algae and the Marine Biological Association (1957) for most animals. Any deviations are noted in appendix A, which lists fully all species identified.

(*h*) *Survey of flora and fauna*

The distribution of conspicuous organisms such as *Enteromorpha*, *Corallina*, large brown algae, Anthozoa, sea urchins (*Paracentrotus*) and starfish was observed directly.

Low growing algal cover, such as *Enteromorpha* or *Corallina*, was sampled by means of quadrats measuring 0.20 m (horizontal) × 0.15 m. These were scraped with a triangular-headed paint scraper into a net bag having the mouth fastened around a stiff wire frame of these dimensions. The bag was drawn rapidly through the water so as to trap any motile fauna dislodged from the seaweed, although some fast swimmers such as shrimps and fish might have escaped. Quadrats were normally taken from between 0.1 and 0.5 m below pool water level, and on upward facing rather than on vertical or overhanging surfaces. Inevitably the sites were chosen for convenient accessibility.

Quadrat samples were either partly sorted fresh and then preserved or immediately preserved in 6 % formaldehyde solution. In either case they were fully sorted after preservation. Protozoa, scraps of Porifera, unsegmented worms, and micro-Crustacea (Ostracoda and in most cases Copepoda) and Acarina were wholly or partly ignored either because of their small size or because of systematic difficulties, but other material was sorted and identified as fully as possible. Because of their extreme abundance in the Green-Pair Pools, the numbers of Copepoda in samples taken from there were estimated from aliquots of copepod suspension sufficient to give a total of not less than 1000 in each such count. *Corallina* was weighed after preservation and 10 g aliquots were separated for estimation of certain epibiotic species. Colonies of up to three species of Bryozoa were present in these aliquots and were counted separately. Spirorbid tube-worms were also counted as dextral (anti-clockwise) or sinistral. Many of the worms were removed from their tubes and mounted, and of these all the dextral specimens proved to be *Janua pagenstecheri* and all the sinistral specimens from *Corallina* agreed in structure with *Spirorbis corallinae*, so that the spirorbid worms from *Corallina* have been listed under whichever of these two specific names is appropriate. The calcareous encrusting epiphytes *Mesophyllum lichenoides* and *Dermatolithon corallinae* were virtually confined to the axes and main branches of *Corallina* and were rarely found on the pinnate laterals. Accordingly their quantities were expressed as the percentage of the total axis length invested with either species. The plants were spread out over a black cloth and flattened under glass, and the total lengths of axes and the lengths invested by each species were determined with a map measurer. Each measurement was made twice, and the readings never differed by more than 2.5 %.

Laminarian algae were collected from Main Pool and Springtide Pool by snorkel diving, and some scrape sampling of smaller algae was also carried out in this way. Motile animals would have escaped, but epiphytic algae and animals attached or adhering to the laminarians

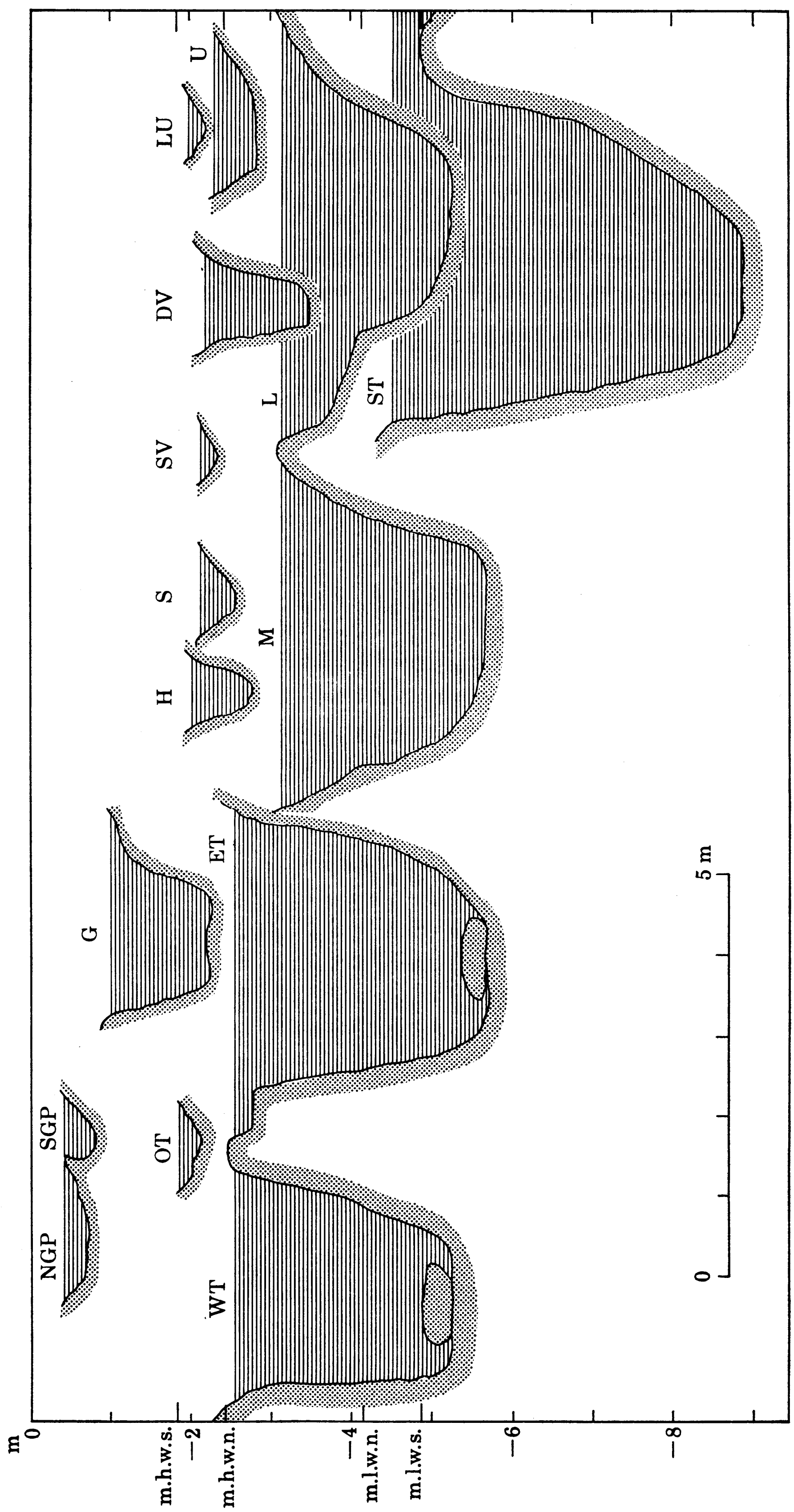

FIGURE 7. Diagrammatic profiles of the tide pools, to natural scale. Levels are shown with reference to Pinnacle (= 0 m). Abbreviations for pool names are given in appendix B.

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or their epiphytes were retained. Complete collections of *Laminaria* were made from 1 m × 1 m squares, and the age of the plants was determined from growth lines in the holdfast, as described by Kain (1963). Each dark growth line is laid down during one slow growing phase, normally within the period July–October. Accordingly for plants collected in July the number of growth lines (excluding the surface) is approximately equal to the age of the plant in years. Lamina thickness was measured with a micrometer at 10 cm from the junction of lamina with stipe.

Table 1. Dimensions and levels of tide pools

pool	surface area/m²	volume/m³	mean depth/m	maximum depth/m	height with reference to Pinnacle/m
North Green-Pair Pool	5.3	1.0	0.2	0.5	−0.43
South Green-Pair Pool	3.3	0.6	0.2	0.5	−0.43
Green Pool	11.5	5	0.5	1.4	−0.99
Overtwin Pool	3.8	0.3	0.1	0.25	−1.87
Many-crevice Pool	3.5	0.6	0.16	0.7	−1.89
High Pool	10	5	0.5	1.1	−2.03
Shallow Pool	4.7	1.0	0.2	0.7	−2.20
Shallow Vee Pool	2.3	0.2	0.1	0.3	−2.20
Deep Vee Pool	6.3	4	0.66	1.6	−2.27
East Twin Pool	15.5	19	1.2	2.8	−2.60
West Twin Pool	8	13	1.7	2.6	−2.60
Main Pool	68	85	1.25	2.8	−3.23
Long Pool	88	54	0.6	2.0	−3.23
Springtide Pool	61	122	2.0	5.2	−4.65 (approx.)
Urchin Pool	17	4.6	0.26	0.7	−2.46
Little Urchin Pool	2.0	0.3	0.15	0.3	−2.08

3. Topography

The main features of the Carrigathorna tide pools are depicted in the plan (figure 2), although for the sake of clarity only a few of the depth contours are shown. These pools lie on a rock platform formed of Devonian slates dipping very steeply in a northerly direction at 70°–90°. The pools lie along the strike, and the deeper pools are steep sided. The platform ends abruptly, giving way to open sea about 10 m beyond the left edge of the plan. The main surge of the sea comes from the west and south west, so that the western pools (Green-Pair, Overtwin and the Twin Pools) are subject to more wave-wash than those set far back to the northeast (Green, High and Shallow Pools). The Gully Pools are subject to continuous surge.

Diagrammatic profiles of the Carrigathorna tide pools are shown in figure 7, and table 1 lists their levels and dimensions. The water level of Springtide Pool falls as low as low tide permits, but is usually slightly above the level of the sea because the water surges over its outer bounding rock wall and only flows out through the narrow exit channel.

The following are estimates of tide levels with reference to the level of Pinnacle (P), derived as described in § 2: mean high water of spring tides $= P - 1.84$ m; mean high water of neap tides $= P - 2.42$ m; mean low water of neap tides $= P - 4.13$ m; mean low water of spring tides $= P - 4.86$ m.

The positions of the pools on Urchin Reef are shown on another plan (figure 6). The two pools surveyed are on the northern and more sheltered side of the reef, and like most of the Carrigathorna pools they are elongated from east to west, along the strike of the strata. Their levels and dimensions are also given in table 1.

4. Measurements of the physical environment

(*a*) *Water temperature*

Measurements of water temperature were made at many sites in the Carrigathorna tide pools at intervals throughout the day on 25 July and 29 July 1976. The sky was overcast on 25 July, but on 29 July the sun shone all day without interruption. On each occasion the temperature rose during the day at all the sites, and most especially at those in shallow pools. The temperature fell again suddenly as the rising tide entered the pools in early or mid afternoon on 25 July, but more extreme conditions were encountered on 29 July with the later tide and continuous sunshine (figure 8). On each occasion the rise in temperature was much greater in shallow pools (Shallow Pool, Shallow Vee Pool) than in deeper pools at the same intertidal

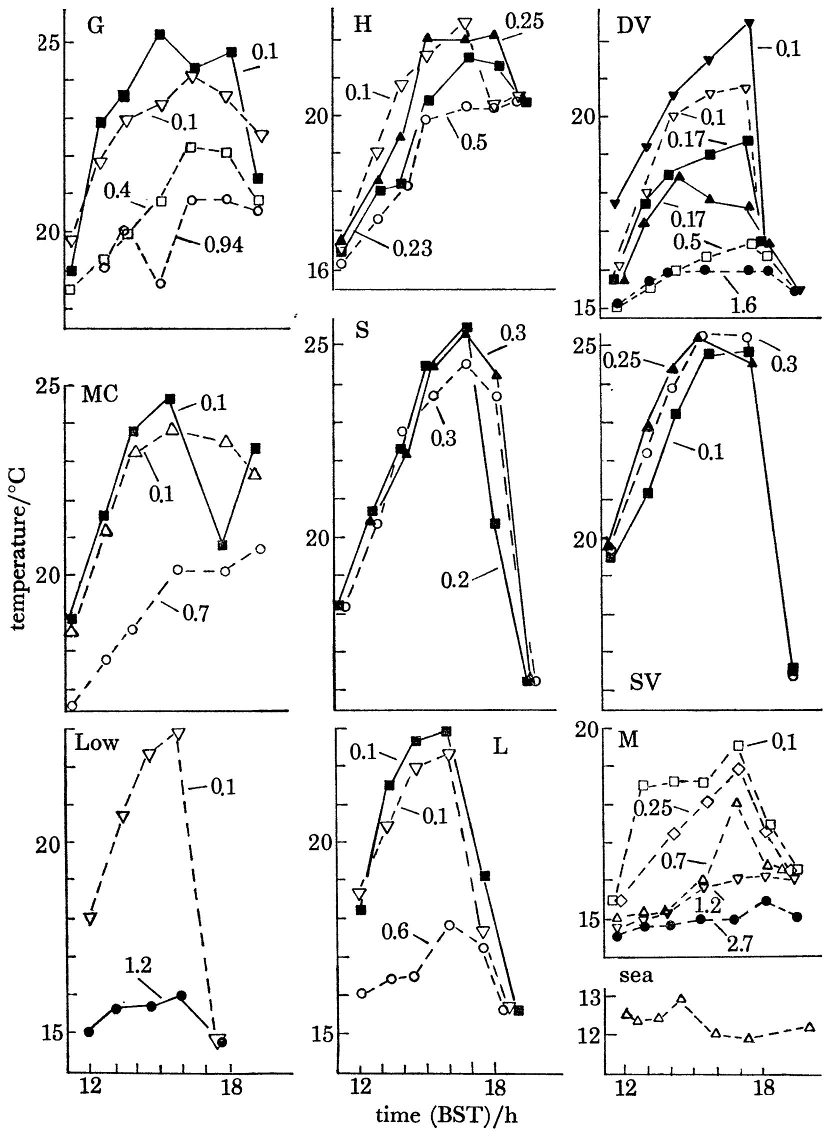

Figure 8. Temperatures in Carrigathorna tide pools on 29 July 1976. Each line represents a separate site. Continuous lines denote sites at the bottom near the edge of the pool, at the depth stated (m). Broken lines denote sites in the centre or over the deepest part of the pool, taken at the depth stated.

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TABLE 2. TEMPERATURES ATTAINED IN AFTERNOON (16–17 h BST) AT SHALLOW SITES IN HIGH-TIDAL POOLS AT CARRIGATHORNA

pool	number of sites	depth of sites/m	28 July 1976			29 July 1976		
			mean/°C	standard error	range	mean/°C	standard error	range
High Pool	6	0.15–0.2	19.9	0.26	18.9–20.4	21.8	0.27	20.8–22.3
Shallow Pool	8	0.1–0.2	22.6	0.07	22.4–22.8	25.25	0.17	24.3–25.9
Deep Vee Pool	4, 6	0.2–0.3	18.3	0.32	17.8–19.0	18.95	0.41	17.7–19.9
Shallow Vee Pool	9	0.05–0.2	24.2	0.16	23.5–24.8	25.4	0.12	24.9–25.8

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level (High Pool, Deep Vee Pool). In the deeper pools the temperature rose substantially (although never as much as in the shallow pools) near the water surface, but remained low throughout the day at deeper levels. This important feature of deeper pools is illustrated for Low Pool, Long Pool, Main Pool, and Deep Vee Pool in figure 8.

For a further comparison between shallow marginal sites among seaweeds in both shallow and deeper pools, readings were taken at the time of maximum temperature on the afternoons of 28 and 29 July at many additional sites in High Pool, Shallow Pool, Deep Vee Pool, and Shallow Vee Pool. The results of this survey are summarized in table 2; they confirm that higher temperatures were reached in all cases in shallow pools.

TABLE 3. PERCENTAGE SATURATION WITH DISSOLVED OXYGEN IN CARRIGATHORNA TIDE POOLS ON 31 JULY 1935

site	depth/m	% saturation at 16.20–17.25 h	% saturation at 17.55–18.25 h
Green Pool	0.1	174	175
	1.0	175	184
High Pool	0.2	175	172
	0.9	147	182
Shallow Pool	0.25	190	194
East Twin Pool	0.25	165	166
	0.5	139	145
	1.0	135	134
	2.0	121	114
Main Pool	0.25	140	142
	0.5	137	138
	1.0	134	135
	2.0	110	119
Long Pool	0.25	163	156
	0.5	149	144
	1.0	127	128
Sea	1.0	99	94

(*b*) *Dissolved oxygen*

Measurements carried out in the afternoon of 31 July 1975 are summarized in table 3. The sea was no more than saturated, while the tide pools became supersaturated with oxygen, most especially Shallow Pool. This state of affairs continued with little change into the late afternoon.

(*c*) *Hydrogen ion concentration*

Measurements of pH (and temperature) were made in the middle of the day, in early afternoon, and in late afternoon at many sites in the Carrigathorna tide pools on 20 July 1977. Other less extensive surveys were made on 4 April (preliminary survey in many pools), 5 April (a detailed survey in the Vee Pools and east end of Long Pool), 6 April and 16 July (Urchin Pool and Little Urchin Pool), and 7 September (including the Green-Pair Pools), all in 1977. On all these occasions the pools were disconnected from the sea over the middle of the day and afternoon. The sky was overcast all day on 16 July and 7 September, and on the other occasions in the afternoon. Many of the results are shown graphically in figure 9 (Vee Pools survey), figure 10 (Urchin Reef pools) and figure 11 (general survey at Carrigathorna). Data for separate sites in a pool are indicated by separate lines. The same sites were used for the April Vee Pools survey and in later surveys (20 July and 7 September) and for these sites the symbols in the graphs (figures 9 and 11) correspond.

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On all these occasions and in all the pools examined there was a progressive rise in pH during the day (figures 9, 10, and 11). The pH reached 10.0 or over in Overtwin Pool (pH 10.2 on 7 September), the Green-Pair Pools (pH 10.2 at all six sites in early and late afternoon on 7 September) and Shallow Vee Pool (figure 11). These are all high level (supra-tidal or high-tidal) pools of small depth ('shallow' or 'intermediate' in terms of the definitions given on page 16) and contained much *Enteromorpha* at the time. Green Pool, filled with *Enteromorpha*, but deep, reached pH 9.6 on 4 April, but only pH 9.2 on 20 July when all the *Enteromorpha* in a

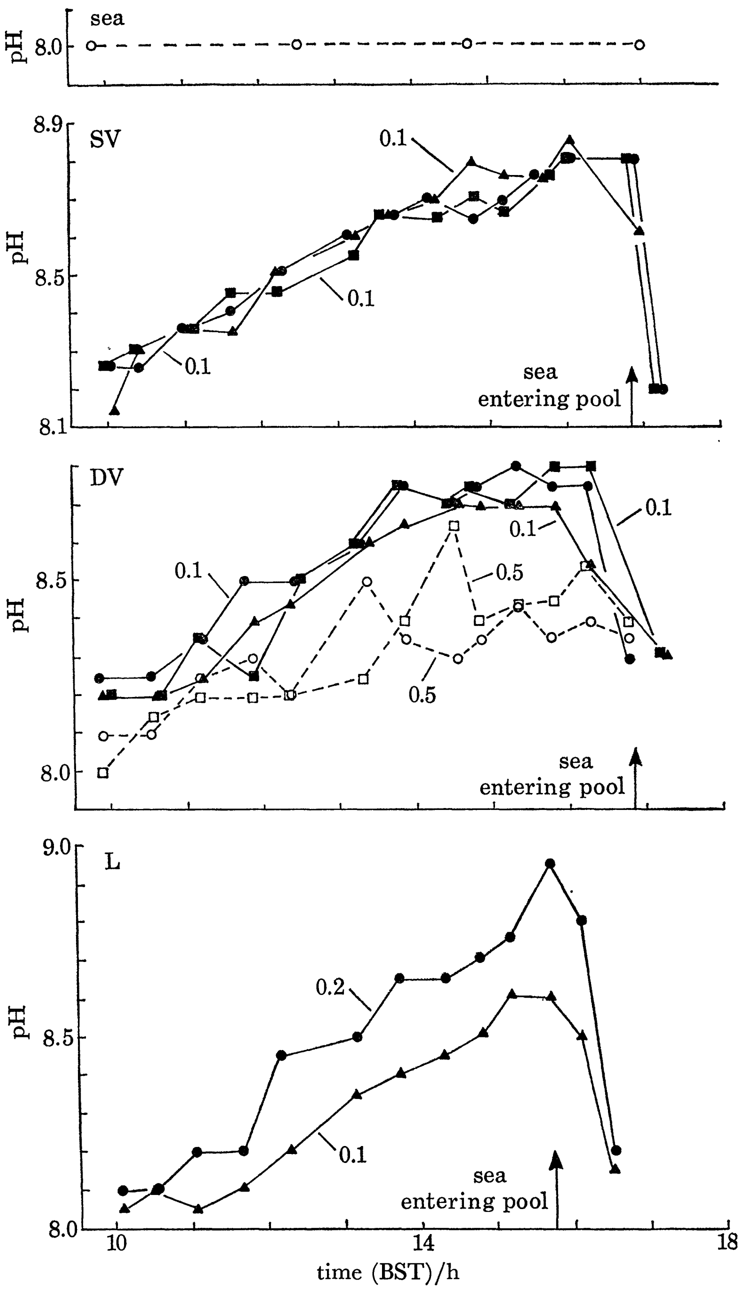

FIGURE 9. Records of pH in the Vee Pools group, taken on 5 April 1977. Continuous lines denote sites at the bottom near the edge of the pool, at the depth stated (m). Broken lines denote sites in the centre or over the deepest part of the pool, taken at the depth stated.

wide zone around the margin was dead. Shallow sites in all the other pools examined reached pH 8.5–9.0, including the shallow alga-filled east end of Long Pool and a *Corallina* covered site in Main Pool. A site on the *Corallina* covered north shelf of East Twin Pool reached pH 9.1. The deeper water of the deeper pools (Deep Vee Pool, Main Pool, East Twin Pool) only reached about pH 8.5. Sea water collected from the edge of the shore ranged from pH 8.0 to pH 8.3; these samples were collected from sites close to littoral or sublittoral vegetation.

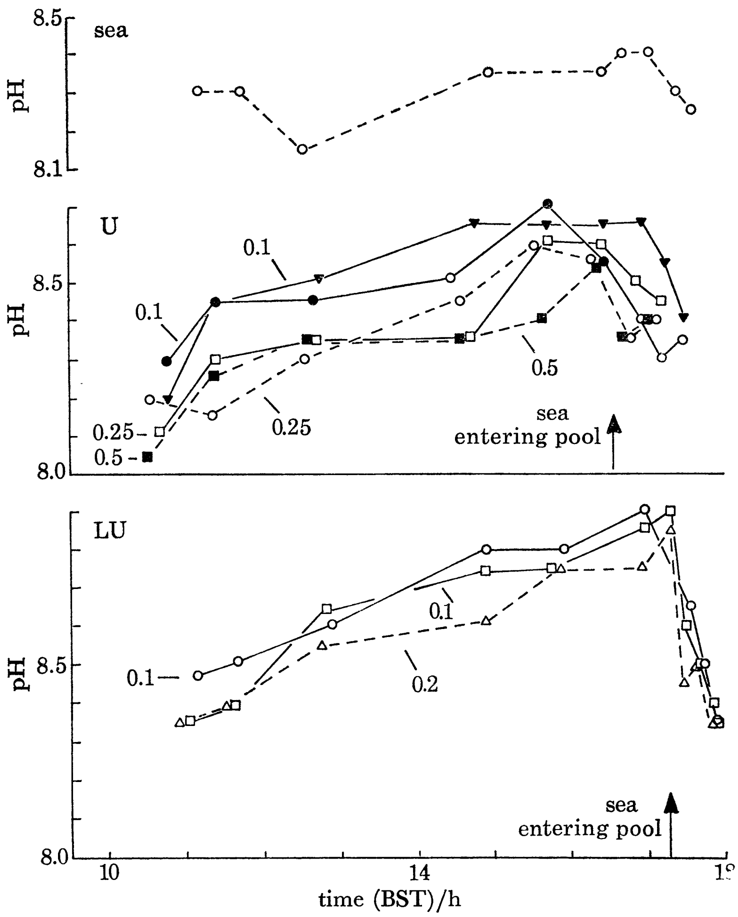

FIGURE 10. Records of pH in the Urchin Reef tide pools, taken on 16 July 1977. Continuous lines denote sites at the bottom near the edge of the pool, at the depth stated (m). Broken lines denote sites in the centre or over the deepest part of the pool, taken at the depth stated.

(*d*) *Salinity*

Salinity samples taken on 31 July 1975, close to neap tides, gave results of 34.60‰ at a depth of 2.0 m and 35.14‰ at 0.5 m in Springtide Pool. Samples from Main, High, Shallow and Green Pools ranged between 34.61‰ and 34.82‰, so that on that occasion salinity was close to that of the sea. However on 12 July 1977, again at neap tides, much higher salinities were obtained in Overtwin, Shallow, Many-crevice and Green Pools (table 4), all at a depth of 0.1 m. Overtwin Pool gave a value of 41‰. High-tidal pools (Deep Vee and Shallow Vee Pools) close to the sea, and therefore more liable to wave-wash, remained at approximately normal salinity. Two samples taken from Green Pool on 7 September 1976 gave 38.94‰ and 39.01‰. The water level was low, presumably owing to evaporation, and there was a band of

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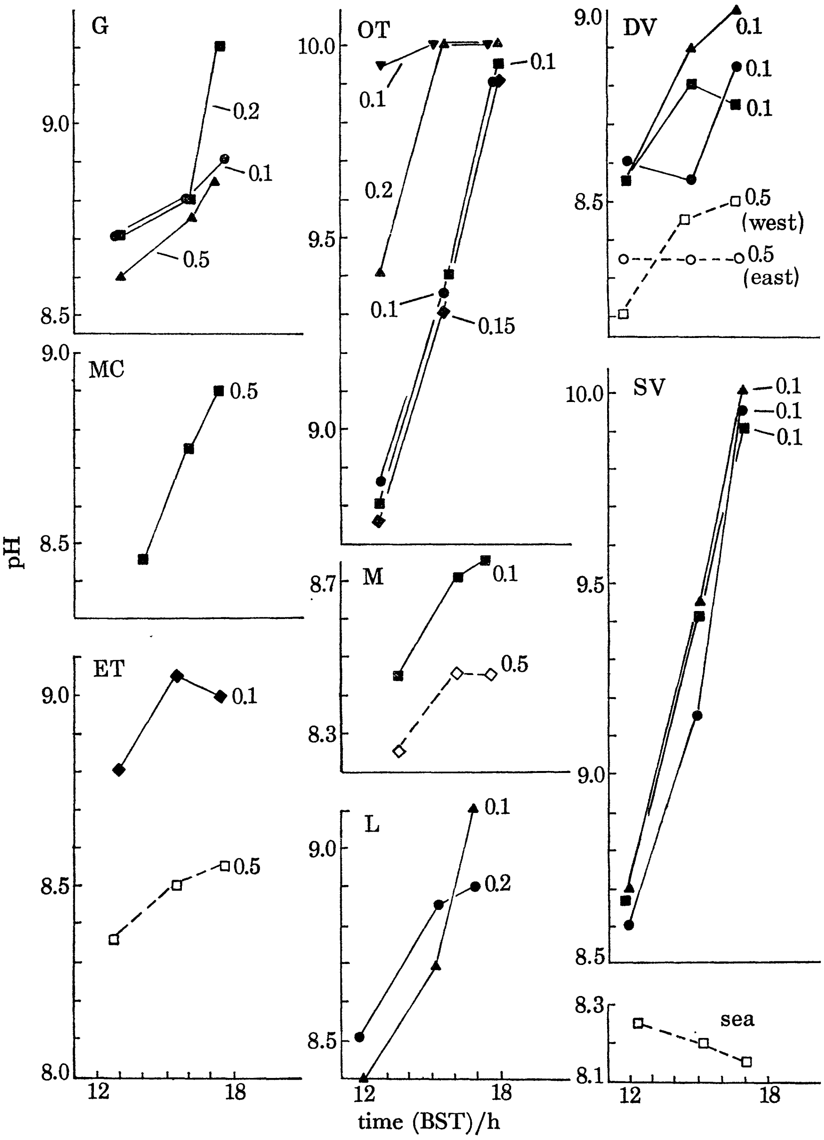

Figure 11. Records of pH in the Carrigathorna tide pools, taken on 20 July 1977. Continuous lines represent sites at the bottom near the edge of the pool, at the depth stated. Broken lines denote sites in the centre or over the deepest part of the pool, taken at the depth stated (m). The same sites were used for the Vee Pools group (SV, Shallow Vee Pool; DV, Deep Vee Pool and the eastern arm of (L) Long Pool) as on the occasion represented in figure 9, and the symbols for these sites correspond.

TABLE 4. SALINITIES IN CARRIGATHORNA TIDE POOLS ON 12 JULY 1977 AT DEPTH OF 0.1 m

site	*S* (‰)	site	*S* (‰)
Green Pool	37.04	Shallow Pool	38.16
Green Pool	36.72	Shallow Pool	38.11
Overtwin Pool	40.95	Shallow Vee Pool	34.92
Overtwin Pool	41.22	Deep Vee Pool	35.03
Many-crevice Pool	37.44	East Twin Pool	34.88
High Pool (west end)	35.43	Main Pool	35.05
High Pool (centre)	35.46	Sea	34.87

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whitened *Enteromorpha* around the margin. By the time the samples were collected a considerable amount of spray had entered, so that the salinity must have risen even higher.

We have no information about the salinity of the tide pools after heavy rain, but the surface salinity is likely to fall considerably, especially in High Pool, which receives drainage from adjacent rock surfaces. A general lowering of salinity is also to be expected in shallow pools.

5. Survey of flora and fauna

(*a*) *Characterization of tide pools*

For purposes of description, pools will be classified arbitrarily by wave-exposure, level, and mean depth. Carrigathorna is very exposed to waves and Urchin Reef moderately sheltered. The subdivisions by level are described as follows: *supratidal* as above the level of high water of spring tides but replenished with sea water in rough weather; *high-tidal* as flooded at high water of spring tides but not (in calm weather) at high water of neap tides; *mid-tidal* as flooded on every tide; *low-tidal* as isolated from the sea at low water of spring tides but not of neap tides; *subtidal* as never completely isolated from the sea. There are obviously borderline cases, but a more precise definition could not be justified in view of the uncertainty introduced by wave-wash. Subdivisions by mean depth are as follows: shallow < 0.25 m; intermediate in depth < 0.5 m; deep > 0.5 m; very deep > 1.0 m.

(*b*) *Supratidal pools at Carrigathorna*

This section only concerns pools slightly above the levels attained by the highest tides in calm weather. In rough weather they are often replenished. There are other pools higher up, splashed occasionally in rough weather, which we have not investigated.

Green Pool was always densely covered with *Enteromorpha intestinalis*, and five other species of Chlorophyta were found in smaller quantities (detailed in appendix A). The water level fell during the summer, leaving a band of dried-up whitened *Enteromorpha* around the margin. Single quadrats were collected on 2 November 1975 and 7 September 1976, and six on 20 July 1975. Small numbers of the amphipod *Melita palmata* were found in five of the July quadrats and in September. The amphipod *Gammarellus angulosus* was found in two quadrats (July, September) and isopods of the *Jaera albifrons* group in four quadrats (July, September). *Palaemon* larvae occurred in five of the July quadrats. A substantial number (37) of the gastropod *Skeneopsis planorbis* was taken in September, but none were found on the other occasions. A few specimens were taken of various other Crustacea and Mollusca, as detailed in appendix A. The complete species list amounted to seven algae and 18 invertebrates and, apart from *Enteromorpha* and on one occasion *Skeneopsis*, the quantities were all very small.

The Green-Pair Pools are shallow, and although slightly higher than Green Pool, are more accessible to wave-wash from the west, and are probably more frequently replenished. They also were completely clothed with *Enteromorpha intestinalis*, and there was some underlying encrusting coralline alga, conspicuous around the margins. Their fauna was totally different from that of Green Pool. Our data for the six quadrats collected on 7 September 1977 are summarized in table 5, and include altogether seven algal and 14 invertebrate species. The copepod *Tigriopus fulvus* was present in extremely large numbers, averaging 21.6×10^3 per quadrat, or 720×10^3 per m^2. This implies a total population of over 6 million among the *Enteromorpha* in these two pools. Larvae of *Halocladius fucicola* (Diptera) averaged 400 per quadrat, and young mussels (1–2 mm long) were also fairly numerous. *Monocelis lineata* (Turbellaria) occurred in substantial numbers in all samples, and *Macrostomum hystricinum* (Turbellaria) – too small to have been collected quantitatively – was also present. Other species occurred casually or even accidentally.

Table 5. Quadrats (0.20 × 0.15 m) from Green-Pair Pools (7 Sept. 1977)

	SGP 1	SGP 2	SGP 3	NGP 1	NGP 2	NGP 3
Algae						
Enteromorpha intestinalis (g) with *E. compressa* and *E. prolifera*	61	68	71	50	62	52
Blidingia minima	–	–	+	–	–	–
Scytosiphon lomentaria	–	–	–	–	+	–
Corallina sp.	+	+	–	–	–	+
encrusting coralline	+++	+++	+++	+++	+++	+++
Turbellaria						
Monocelis lineata	44	25	11	31	21	10
Polychaeta						
Janua pagenstecheri	1	1	–	–	–	–
Copepoda						
Tigriopus fulvus, 10^3	10.2	35.2	28.9	16.3	24.8	14.4
Amphipoda						
damaged, unidentified	2	–	1	1	–	1
Isopoda						
Idotea sp., < 3 mm	–	–	–	–	–	1
Insecta						
Halocladius fucicola (larvae + pupae)	305	346	286	717	690	506
Lamellibranchia						
Mytilus spp. 1–2 mm	91	111	50	41	38	48
Gastropoda						
Littorina saxatilis (small, agg.)	5	–	3	5	1	10
Littorina littorea (small)	2	–	–	1	–	–
Odostomia eulimoides	1	–	–	–	–	–
Rissoa parva	–	1	–	1	–	2
Skeneopsis planorbis	–	–	–	–	1	1
unidentified, small	1	–	–	–	–	–

The minute turbellarian *Macrostomum hystricinum* was present but not separated quantitatively.

(*c*) *High-tidal pools at Carrigathorna*

Shallow Pool, Overtwin Pool and Shallow Vee Pool are shallow. Their whole rock surfaces were covered with encrusting coralline alga, with a few patches of *Corallina officinalis*, many *Actinia equina* (Anthozoa), and many limpets. Of the two limpet species, *Patella aspera* predominated in Overtwin and Shallow Vee Pools but *P. vulgata* in shallow Pool, which is less exposed to wave-wash. Limpets of both species carried a tuft of green algae (mainly *Enteromorpha*) on their shells. The *Corallina* in Shallow Pool carried many of the spirorbid tube-worm *Janua pagenstecheri* (table 6). *Sagartia elegans* var. *miniata* (Anthozoa) lined crevices in Overtwin Pool, and a few were present in a crevice in Shallow Pool. Shallow Vee Pool also contained extensive patches of well-grown mussels (*Mytilus* spp.) up to 2 cm in length and considerable numbers of a tanaid *Tanais cavolini*. A single well grown *Paracentrotus lividus* (Echinoidea) occupied an overhung crevice on the north side of Shallow Vee Pool.

High Pool is of intermediate depth, and like Shallow Pool lies well back from the low water line. Its surface displayed a patchwork distribution of encrusting coralline alga with *Actinia* and limpets (both species) and of tufts of *Corallina*. The *Corallina* was pink in April but turned white from July onwards. In September 1977 there were at its eastern end three short and

Table 6. Quantities of encrusting coralline algae, spirorbid tube-worms and Bryozoa found in 10 g aliquots of *Corallina*

sample number	month collected	*Mesophyllum lichenoides* (axis cover %)	*Dermatolithon corallinae* (axis cover %)	*Janua pagenstecheri* (individuals)	*Spirorbis corallinae* (individuals)	*Celleporella hyalina* (colonies)	*Celleporina hassallii* (colonies)	*Electra pilosa* (colonies)
Shallow Pool								
S1	July	—	—	97	—	—	—	—
S2	July	—	—	65†	—	—	—	—
High Pool								
H1	March	—	< 1	24	2	—	—	—
H2	March	—	< 1	—	12	—	—	—
H3	July	—	—	69	37	—	—	—
H4	July	—	4.7	111	105	—	—	—
H5	Nov.	—	11	12	13	—	—	—
H7	Nov.	—	2.8	29	20	—	—	—
H8	July	—	—	72	1	—	—	—
Deep Vee Pool								
DV1	July	3.2	3.4	18	40	—	—	—
DV2	July	—	< 1	—	118	—	—	—
DV3	July	2.9	2.0	6	159	—	—	—
East Twin Pool								
ET1	April	—	< 1	—	13	20	—	—
ET2	July	—	—	—	78	6	—	—
West Twin Pool								
WT1	April	< 1	< 1	—	4	8	—	—
Main Pool								
M1	April	3.8	13.8	—	378	—	—	—
M3	July	8.4	9.8	—	1254	1	—	—
M4	Nov.	1.6	8.1	—	610	3	1	3
Long Pool								
L1	March	2.6	7.4	—	1	3	1	3
L2	April	4.7	13.6	—	45	3	—	—
L3	July	—	1.6	—	218	3	—	1
L4	July	—	11.4	—	217	12	—	2
L5	Nov.	2.6	5.7	—	413	1	1	1
L6	Nov.	—	1.8	—	351	23	1	10
Upper Gully Pool								
UG1	March	2.6	2.1	—	30	98	4	1
UG2	March	—	< 1	—	61	18	2	—
UG3	March	—	< 1	—	94	30	1	—
UG4	March	—	7.6	—	931	79	11	—
Lower Gully Pool								
LG1	March	—	< 1	—	—	10	1	—
LG3	March	—	1.9	—	—	100	1	—
Springtide Pool								
ST1	March	—	3.6	—	13	326	26	6
Urchin Pool								
U1	April	18.9	—	—	3	—	—	—
U2	July	11.6	< 1	33	25	—	—	—
U3	July	10.2	—	48	56	—	—	—

† Sample contains only 9 g of *Corallina*; this figure has been scaled up appropriately.

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poorly grown plants of *Himanthalia elongata* with reproductive straps and therefore in their second year and three other wretched specimens with buttons only, small, swollen and yellow. In High Pool the encrusting coralline alga *Dermatolithon corallinae* formed jackets around the main stems of the *Corallina*. The *Corallina* also carried many spirorbids of two species (*Spirorbis corallinae* and *Janua pagenstecheri*) and mussel spat (*Mytilus* spp.), and accommodated a considerable population of motile species, including especially *Platynereis dumerili* (Polychaeta), *Stenothoe monoculoides* (Amphipoda), *Asterina gibbosa* (Asteroidea) and *Amphipholis squamata* (Ophiuroidea). A small shoal of young grey mullet (*Crenimugil labrosus*) was present in July 1976.

The Vee Pools derive their name from a horizontally directed hole or miniature cave with a V-shaped roof situated a short distance to the east of them. Deep Vee Pool, deep, narrow, and close to the low water line, was almost fully covered with *Corallina officinalis* which carried much epiphytic *Ceramium rubrum* by July. Small rounded bare stones lay on the bottom, and the pool lacked laminarian or other large brown algae. The *Corallina* also carried encrusting corallines, *Spirorbis corallinae*, some *Janua pagenstecheri* and many *Mytilus* spat, but no Bryozoa were found in aliquots (table 6). There was a rich fauna of motile animals, including especially *Platynereis dumerili*, *Gammarellus angulosus* (Amphipoda), *Stenothoe monoculoides*, *Asterina gibbosa*, *Amphipholis squamata*, and many *Rissoa parva* (Gastropoda). In April 1977 Deep Vee Pool contained five *Asterias rubens* (Asteroidea) and twelve *Tealia felina* (Anthozoa).

The analysis of aliquots of *Corallina* is reported in table 6, the distribution of the commoner animals in quadrats from all the pools in table 7, and records of distribution, including rarer species, are summarized in appendix A.

One further entirely unusual high-tidal pool remains to be described. Many-crevice Pool is a shallow pool which drains very slowly through the enclosing slates, so that if the weather is calm much of the water runs out during the week of less extreme tides. The bottom of the pool, always under water, was covered with *Enteromorpha prolifera*, but the sides, which are liable to dry out, were fully clothed with the filamentous blue-green alga *Lyngbya confervoides*. The pool also contained large numbers of the larvae of *Halocladius fucicola* (Diptera), but very little else. In a quadrat collected from the *Lyngbya* zone in July 1976, after several days of desiccation, most of the larvae were dried up and appeared dead.

(*d*) *Mid-tidal pools at Carrigathorna*

East Twin Pool, West Twin Pool and Main Pool are all very deep, and Long Pool just falls within the 'deep' category (table 1). They all have some very large boulders on the bottom. Main Pool connects by a channel with Long Pool, and while the tide is low there is a slow continuous drainage of water from Long Pool to the sea through Gully Cleft. In all these pools *Laminaria digitata* formed a marginal zone extending vertically about 0.5–0.6 m, and *Laminaria hyperborea* formed a dense forest below it on the sides of the pools and wherever the bottom is stable. Within the *L. hyperborea* forest there were scattered plants of *L. digitata* and *Laminaria saccharina*, and patches of *L. saccharina* were conspicuous on parts of the bottom and on the north wall of Main Pool. *Halydrys siliquosa* (Phaeophyta) was present on the north side of all these pools, and there were a few plants centrally in Main Pool. *Himanthalia elongata* occurred in the channel between Main and Long Pools, and quite extensively in Long Pool, but not in East or West Twin Pools. *Corallina* formed an extensive undergrowth in all these pools, and carried many *Spirorbis corallinae* but no *Janua pagenstecheri*, as determined from aliquots (table 6). A few

Table 7. Quantities of commoner animals in 0.20 × 0.15 m quadrats

pool ...	Shallow			Shallow Vee		High								Deep Vee			Twin Pools			Main			
quadrat number ...	S1	S2	S3	SV1	SV2	H1	H2	H3	H4	H5	H6	H7	H8	DV1	DV2	DV3	ET1	ET2	WT1	M1	M2	M3	M4
date of collection ...	27 July 1976	27 July 1976	27 July 1976	27 July 1976	27 July 1976	27 Mar. 1975	30 Mar. 1975	13 July 1975	13 July 1975	13 Nov. 1975	16 Nov. 1975	18 Nov. 1975	27 July 1976	20 July 1976	21 July 1976	27 July 1976	2 Apr. 1975	24 July 1975	2 Apr. 1975	2 Apr. 1975	17 July 1975	24 July 1975	16 Nov. 1975
least depth/m ...	0.15	0.15	0.04	0.1	0.1	0.1	0.05	0.3	0.2	0.1	0.1	0.25	0.1	0.1	0.15	0.15	0.08	0.2	0.03	0.2	1.4	0.04	0.2
(1) *Corallina officinalis* (g)	11	9	0.5	—	—	18	17	—	14	16	13	30	26	43	63	27	44	84	24	31	9	17	22
(2) *Corynactis viridis*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	33	—	1	9	12	—
(3) *Amphiglena mediterranea*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—
(4) *Nereis pelagica*	—	—	—	—	—	7	—	—	1	—	—	1	—	—	—	—	—	3	5	—	1	1	1
(5) *Platynereis dumerili*	29	25	—	1	—	5	1	1	12	—	3	2	10	12	9	4	—	3	1	28	—	—	1
(6) Syllidae	—	1	—	7	—	—	—	—	—	1	1	10	—	2	—	7	8	8	6	10	—	—	2
(7) *Verruca stroemia*	—	—	—	1	—	—	—	—	—	—	—	—	—	1	—	—	10	—	2	1	—	—	—
(8) *Amphithoe neglecta*	2	2	2	—	—	—	—	—	—	—	—	2	1	2	—	1	—	—	—	—	1	9	—
(9) *Apherusa jurinei*	—	—	—	—	—	—	—	—	—	—	—	3	—	—	—	—	—	—	2	—	—	—	2
(10) *Dexamine thea*	—	1	—	—	—	1	—	—	11	—	—	5	—	28	1	9	—	—	—	2	1	—	—
(11) *Gammarellus angulosus*	—	—	—	1	2	—	6	—	1	10	2	—	—	60	30	1	—	—	14	40	—	—	50
(12) *Hyale pontica*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	1	—	—	—	1
(13) *Parajassa pelagica*	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—
(14) *Stenothoe monoculoides*	3	—	1	—	—	7	2	—	2	1	—	5	3	29	3	—	15	—	1	1	—	6	—
(15) *Tanais cavolini*	—	1	1	33	5	2	1	—	1	—	1	5	—	1	—	5	—	—	—	—	—	—	—
(16) *Dynamene bidentata*	—	—	—	—	—	—	—	—	—	—	—	—	—	10	1	—	—	—	—	1	4	10	1
(17) *Idotea granulosa*	—	—	—	1	—	6	—	—	—	2	3	1	—	3	1	2	5	7	1	20	1	2	9
(18) *I. pelagica*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	2	—	1	—	—	—	—
(19) *Idotea* < 3 mm	—	—	—	—	—	—	2	—	—	—	—	1	1	6	5	—	33	1	2	29	—	—	4
(20) *Clunio marinus*	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	1	—	—	1	—	—	—	—
(21) *Halocladius fucicola*	—	3	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
(22) *Heteranomia squamula*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	—	3	3	1	—
(23) *Hiatella arctica*	—	—	—	—	1	—	1	1	—	—	2	—	—	2	2	15	4	15	18	—	—	9	1
(24) *Modiolula phaseolina*	1	1	—	9	4	—	—	1	—	—	1	—	—	12	2	4	1	39	—	2	7	3	4
(25) *Mytilus* spp. (small)	18	105	14	369	87	60	19	1	10	1	5	11	49	259	111	382	363	58	116	411	10	23	11
(26) *Cingula semicostata*	—	—	—	—	—	—	—	1	—	—	—	—	1	7	—	—	—	—	—	5	—	—	—
(27) *Cingulopsis fulgida*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	—	1	—	—	1	—	—
(28) *Hydrobia ? ventrosa*	—	1	—	—	—	—	—	—	—	—	—	—	—	14	2	11	—	2	—	—	—	5	—
(29) *Lacuna vincta*	—	—	—	1	1	—	—	—	—	—	—	—	—	12	1	8	—	—	—	2	5	1	—
(30) *Omalogyra atomus*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	—	—	—	—	—	—	—
(31) *Patina pellucida*	—	—	—	—	—	—	—	—	—	—	—	—	—	1	3	—	—	—	—	—	—	3	1
(32) *Rissoa parva*	2	4	—	2	2	2	—	—	1	—	—	—	2	196	41	86	—	4	3	112	11	189	2
(33) *Skeneopsis planorbis*	—	1	2	—	—	2	—	—	—	—	—	—	—	4	5	10	4	—	—	—	—	—	—
(34) *Asterina gibbosa*	5	2	—	—	—	2	8	8	7	1	—	11	—	15	7	51	—	1	—	16	4	61	1
(35) *Amphipholis squamata*	1	1	—	9	3	—	—	7	8	—	—	7	3	15	6	8	1	1	—	17	15	11	2

TABLE 7. *continued*

pool ...	Long						Upper Gully					Lower Gully				Little Urchin		Urchin		
quadrat number ...	L1	L2	L3	L4	L5	L6	GC1	UG1	UG2	UG3	UG4	LG1	LG2	LG3	ST1	LU1	LU2	U1	U2	U3
date of collection ...	27 Mar. 1975	2 Apr. 1975	24 July 1975	31 July 1975	16 Nov. 1975	18 Nov. 1975	30 Mar. 1975	27 Mar. 1975	29 Mar. 1975	29 Mar. 1975	30 Mar. 1975	29 Mar. 1975	30 Mar. 1975	30 Mar. 1975	27 Mar. 1975	30 July 1977	30 July 1977	18 Apr. 1976	16 July 1976	16 July 1976
least depth/m ...	0.1	0.1	0.07	0.27	0.2	0.2	0.1	0.08	0.35	0.33	0.2	0	0.1	0	0	0.2	0.2	0.1	0.2	0.2
(1) *Corallina officinalis* (g)	18	35	72	26	10	28	11	35	10	20	20	27	20	16	9	2	2	104	82	46
(2) *Corynactis viridis*	—	2	4	1	16	23	5	19	—	—	5	1	18	6	8	—	—	—	—	—
(3) *Amphiglena mediterranea*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	6	4
(4) *Nereis pelagica*	7	3	6	2	1	4	10	7	—	1	2	12	4	8	—	—	—	—	2	—
(5) *Platynereis dumerili*	—	4	—	1	2	—	—	—	—	—	—	—	—	—	—	1	4	34	172	48
(6) Syllidae	1	1	5	—	3	5	1	1	2	—	—	2	1	3	—	1	—	47	88	15
(7) *Verruca stroemia*	—	1	3	35	8	43	—	8	1	7	11	1	37	1	9	—	—	11	—	—
(8) *Amphithoe neglecta*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	4	2
(9) *Apherusa jurinei*	—	1	4	1	2	3	5	1	1	1	9	1	2	2	—	—	—	—	1	—
(10) *Dexamine thea*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	20	—
(11) *Gammarellus angulosus*	3	—	2	—	20	7	17	77	43	17	58	17	27	41	25	—	—	—	2	1
(12) *Hyale pontica*	1	—	—	1	—	—	5	18	—	9	8	7	3	10	4	—	—	—	—	—
(13) *Parajassa pelagica*	2	2	4	—	1	—	33	12	5	5	13	18	12	15	11	—	—	—	—	—
(14) *Stenothoe monoculoides*	—	3	2	—	—	1	2	—	1	—	—	—	—	—	—	—	—	10	9	5
(15) *Tanais cavolini*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	—
(16) *Dynamene bidentata*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
(17) *Idotea granulosa*	8	32	9	2	7	9	4	1	—	—	1	1	—	—	3	—	—	1	—	—
(18) *I. pelagica*	6	—	3	—	—	—	11	7	—	2	1	3	2	2	1	—	—	—	—	—
(19) *Idotea* < 3 mm	7	22	13	7	—	9	4	6	1	—	1	1	3	4	5	—	—	—	—	—
(20) *Clunio marinus*	—	2	1	—	—	—	—	—	—	—	—	—	—	—	—	2	—	4	4	66
(21) *Halocladius fucicola*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	2	—	5	5
(22) *Heteranomia squamula*	1	1	—	4	4	3	—	4	—	1	—	1	—	5	2	—	—	—	5	4
(23) *Hiatella arctica*	1	6	5	16	5	13	10	21	—	3	2	8	10	1	3	—	—	11	23	15
(24) *Modiolula phaseolina*	2	20	2	—	2	7	—	1	1	1	18	1	2	1	—	1	1	48	60	37
(25) *Mytilus* spp. (small)	736	484	524	102	12	133	180	309	140	169	186	286	328	421	252	22	7	24	75	17
(26) *Cingula semicostata*	2	1	11	10	—	1	—	—	—	—	—	—	—	—	—	1	—	49	10	8
(27) *Cingulopsis fulgida*	3	—	1	1	—	—	—	—	—	—	—	—	—	—	—	2	5	90	41	6
(28) *Hydrobia ? ventrosa*	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	5
(29) *Lacuna vincta*	—	—	45	24	—	1	—	—	—	—	—	—	—	—	—	—	—	1	1	1
(30) *Omalogyra atomus*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	15	10	—	8	—
(31) *Patina pellucida*	—	4	16	6	5	—	—	1	—	1	—	—	1	1	—	—	—	3	—	—
(32) *Rissoa parva*	30	20	642	243	2	25	5	6	3	3	—	1	4	7	5	—	—	51	15	3
(33) *Skeneopsis planorbis*	3	1	1	—	—	—	—	—	—	—	—	—	—	—	—	2	—	5	51	7
(34) *Asterina gibbosa*	2	3	5	4	—	3	—	—	—	—	—	—	—	—	—	—	—	45	26	21
(35) *Amphipholis squamata*	1	2	3	4	3	1	—	1	—	—	—	—	—	—	—	10	2	309	90	295

Table 8. Population density and characteristics of *Laminaria hyperborea* in Main Pool

(Numbers, ages and sizes of *Laminaria hyperborea* plants in two horizontal metre squares. Measurements are given as mean ± standard error, or as mean and range for small numbers.)

age (number of growth lines)	metre square No. 2, depth 0.75 m, 18 July 1977						metre square No. 1, depth 1.5 m, 8 July 1977					
	number of plants	stipe length mm	lamina length mm	lamina thickness mm	lamina weight g	stipe weight g	number of plants	stipe length mm	lamina length mm	lamina thickness mm	lamina weight g	stipe weight g
0	11	35 ±3	183 ±27	0.22 ±0.07	2.9 ±0.07	0.37 ±0.06	20	17.2 ±3.7	71 ±18	0.18 ±0.02	0.7 ±0.2	0.4 ±0.3
1	6	63 ±8	250 ±28	0.32 ±0.02	5.2 ±0.9	0.96 ±0.3	20	81 ±9	285 ±18	0.43 ±0.02	7.4 ±1.3	1.0 ±0.3
2	1	95	340	0.38	12.5	2.5	12	168 ±23	360 ±43	0.55 ±0.04	26 ±6	7.2 ±1.1
3	1	175	650	0.51	202	13	7	185 ±17	629 ±77	0.77 ±0.05	111 ±26	13 ±2.9
4	6	296 ±22	593 ±48	0.79 ±0.03	170 ±38	37 ±8.7	10	218 ±16	617 ±54	0.80 ±0.18	134 ±32	18 ±2.1
5	9	316 ±20	602 ±49	0.83 ±0.04	192 ±26	42 ±4.9	3	275 250–315	555 435–740	0.83 0.7–1.0	176 116–220	23 20–25
6	3	328 310–345	683 510–860	0.83 0.79–0.84	276 168–335	57 31–72	3	235 210–275	640 620–670	0.96 0.8–1.0	133 40–220	21 10–38
7	2	323 315–330	610 560–660	0.88 0.81–0.94	234 200–268	67 55–78	3	267 240–300	582 525–620	0.86 0.8–1.0	153 58–210	26 14–38
	(+1 not aged)						(+2 not aged)					

colonies of Bryozoa (mainly *Celleporella hyalina* but a few also of *Electra pilosa* and *Celleporina hassallii*) also grew on the *Corallina*. As seen from quadrats (table 7), the undergrowth of *Corallina* accommodates a rich fauna, including many species already noted in the high-tidal pools. However some species showed a marked increase in numbers (*Nereis pelagica*, *Apherusa jurinei*, *Idotea pelagica*, *Hiatella arctica*, *Rissoa parva*) or first appeared at this level (*Hyale pontica*

Table 9. Numbers of *Patina pellucida* on laminae of *Laminaria hyperborea*

(Estimates are given for linear regressions ($y = a+bx$) of numbers of *Patina* (y) against lamina mass (x) and (from these regressions) for numbers of *Patina* per standard 100 g lamina, all ± standard error. Data for open sea sublittoral are based on collections made by Norton *et al.* (1977) in July 1972.)

station	number of plants	regression a	regression b	estimated number of *Patina* per 100 g lamina
Main Pool, metre square no. 2, depth 0.75 m	39	0.48 ± 2.38	0.187 ± 0.015	19.2 ± 1.7
Main Pool, metre square no. 1, depth 1.4 m	80	1.84 ± 0.83	0.159 ± 0.009	17.8 ± 0.8
open sea sublittoral, depth 3 m	57	1.08 ± 0.45	0.017 ± 0.003	2.7 ± 0.4
open sea sublittoral, depth 6 m	42	1.05 ± 0.57	0.019 ± 0.006	3.0 ± 0.6
open sea sublittoral, depth 13 m	26	0.49 ± 0.41	0.027 ± 0.007	3.2 ± 0.5
open sea sublittoral, depth 17 m	24	0.27 ± 0.30	0.022 ± 0.014	2.4 ± 1.2

Table 10. Quantities of animals in samples of *Cystoseira* from Urchin Pool

(Reference numbers of species are the same as for table 7. No specimens were found of those species listed in table 7 but not in this table.)

sample number ...	Cy1	Cy2	Cy3	Cy4	Cy5	Cy6	Cy7
data of collection ...	18 Apr. 1976	16 July 1976	16 July 1976	16 July 1976	8 Apr. 1977	8 Apr. 1977	8 Apr. 1977
Cystoseira nodicaulis (g)	188	170	76	255	44	43	39
(5) *Platynereis dumerili*	16	330	7	50	—	1	1
(6) Syllidae	11	1	1	5	3	—	—
(8) *Amphithoe neglecta*	11	348	366	1146	—	1	1
(9) *Apherusa jurinei*	60	96	8	76	7	2	3
(10) *Dexamine thea*	2	231	6	28	—	—	—
(11) *Gammarellus angulosus*	—	—	—	—	25	176	67
(14) *Stenothoe monoculoides*	53	73	287	23	35	7	10
(15) *Tanais cavolini*	—	1	—	1	—	—	—
(16) *Dynamene bidentata*	2	33	32	37	1	8	—
(17) *Idotea granulosa*	18	12	—	2	33	40	11
(19) *Idotea* < 3 mm	—	8	—	1	6	4	2
(20) *Clunio marinus*	—	34	4	28	5	—	—
(21) *Halocladius fucicola*	—	114	3	39	—	—	—
(24) *Modiolula phaseolina*	—	—	—	1	—	—	—
(25) *Mytilus* spp. (small)	—	14	14	1	—	3	—
(26) *Cingula semicostata*	—	—	1	—	—	—	—
(27) *Cingulopsis fulgida*	—	68	38	44	—	—	1
(28) *Hydrobia ? ventrosa*	—	2	—	13	—	—	—
(29) *Lacuna vincta*	—	25	18	5	—	—	—
(30) *Omalogyra atomus*	—	8	2	2	4	—	—
(31) *Patina pellucida*	—	—	2	—	4	—	—
(32) *Rissoa parva*	3	118	12	29	—	—	1
(33) *Skeneopsis planorbis*	—	67	48	23	—	—	—
(34) *Asterina gibbosa*	—	—	—	15	—	—	—
(35) *Amphipholis squamata*	—	—	—	32	—	—	—

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(Amphipoda) and the lamellibranch *Heteranomia squamula*). Others were less numerous or were missing from the quadrats (*Tanais cavolini*, *Dexamine thea*, *Halocladius fucicola*). There were many *Tealia felina* (Anthozoa) on the north side of Long Pool, and a few in the other three mid-tidal pools. A conspicuous green band around the margins of Main Pool and Long Pool marked the rock surfaces exposed to air by slow leakage of water through Gully Cleft. Its vertical extension measured 0.12–0.17 m and it consisted mainly of *Enteromorpha intestinalis* and *Ulva lactuca*, with occasional plants of *Gigartina stellata*, *Fucus* sp., and *Corallina officinalis*.

Information about the growth characteristics and standing crop of *Laminaria* in Main Pool was obtained from complete collections from two horizontal 1 m × 1 m squares from depths of 0.75 and 1.5 m. Some additional information was also provided by samples of *L. hyperborea* from a depth of about 2 m in the northeast sector of the pool. *L. hyperborea* predominated in both these metre squares. The oldest collected had seven growth lines, although 0–1 year old plants were the most numerous (table 9). In both these features the collections from Main Pool resembled those from the shallow sublittoral (3 m) of the nearby open coast (Norton *et al.* 1977). *L. digitata* made a substantial contribution to the collection from 0.75 m, but none exceeded three lines and most were younger. Laminae and stipes of *L. hyperborea* were weighed and measured for a comparison with sublittoral populations, and the results are also summarized in table 9. In fact comparisons are only possible between age groups sufficiently well represented in both habitats. *L. hyperborea* grew as long and heavy a lamina in Main Pool as at any depth, age for age, in the nearby sublittoral, and lamina thickness was also within the range of sublittoral populations at 3–6 m (Norton *et al.* 1977). However, from the age of four or five lines the stipes were shorter in Main Pool than in the sublittoral, and there is little evidence of any substantial growth of the stipes from Main Pool beyond the age of four lines. The holdfasts were not weighed because many were slashed when the plants were collected, but after an allowance for these (of about 20 % of lamina + frond weights) the standing crop of *Laminaria* spp. in the 2 m squares in Main Pool is estimated as 7.3 and 5.9 kg, or about 7.5 and 6 kg with epiphytes.

The laminae of *Laminaria* spp. from Main Pool were almost completely clean of epiphytes and encrusting animals. No *Membranipora membranacea* (Bryozoa) was found on any of them, and only two laminae (both from the metre square at 1.5 m) carried a trace of what was probably *Obelia geniculata* (Hydrozoa). Both these species are normal epibionts of the laminae of *L. hyperborea* and were present although not abundant in the sublittoral region (Norton *et al.* 1977, table 4). There were many more of the limpet *Patina pellucida* on *Laminaria hyperborea* in Main Pool (table 10) than in the adjacent sublittoral.

The stipes of *Laminaria digitata* from Main Pool sometimes bore *Palmaria palmata* (Rhodophyta), while those of *L. hyperborea* with three or more growth lines carried many different epiphytes. (In all 20 are recorded in appendix A.) The commonest were *Palmaria palmata* and *Cladophora rupestris* (Chlorophyta), followed by *Sphacelaria cirrosa* (Phaeophyta), and *Membranoptera alata*, *Phycodrys rubens*, and the encrusting forms *Dermatolithon pustulatum* and *Melobesia membranacea* (all Rhodophyta). Of these commonly occurring epiphytes only *Cladophora rupestris* and *Sphacelaria cirrosa* were also found on the adjacent rock. Many of the stipes were encrusted with *Electra pilosa* (Bryozoa).

(*e*) *Low-tidal and subtidal pools at Carrigathorna*

Upper and Lower Gully Pools together form a surge channel open to the west. Upper Gully Pool is disconnected from the sea briefly at low water of spring tides, but Lower Gully Pool – within our experience – is subject to constant replenishment. *Corallina* covered much of their surfaces, and it reached up to 0.5–0.75 m above low water of spring tides along both sides of Lower Gully Pool. At the western end of Lower Gully Pool *Corallina* was replaced by *Alaria esculenta* (Phaeophyta) and *Laminaria digitata*, characteristic of the sublittoral fringe of the open coast.

The fauna associated with *Corallina* in low tidal pools continued and extended the trends already noted in comparing mid-tidal with high-tidal pools. *Spirorbis corallinae* was the only spirorbid, but this was totally missing from quadrats and other specially collected samples from Lower Gully Pool. Colonies of Bryozoa were more numerous (table 6), *Nereis pelagica* now wholly replaced *Platynereis dumerili*, the chief amphipod was *Gammarellus angulosus*, and *Idotea pelagica* (Isopoda) now exceeded *I. granulosa*. As in the mid-tidal pools, there were large numbers of *Mytilus* spat, mostly 1–2 mm in length. Small gastropods were scarce, and we found no asteroids or ophiuroids. The populations of common animals are summarized in table 7.

Springtide Pool is the deepest of the pools, reaching a depth of over 5 m below its lowest water level at spring tides. It connects by a narrow channel with the sea even at the lowest tide. The pool has a mixed marginal zone of *Laminaria digitata* and *Alaria esculenta*, with *Alaria* especially abundant along the wave-beaten north side and around the entrance. *Corallina* also covered much of the rock in shallow water. *Laminaria hyperborea* and the related annual *Saccorhiza polyschides* formed a forest at the sides of the pool below *L. digitata*, thick for the first 0.5 m, but then thinning out down to 1–2 m. *Corallina* formed a dense undergrowth in shallow water, and *Chondrus crispus*, *Ceramium rubrum* and *Ulva lactuca* were conspicuous. Below 0.5 m as the *Laminaria* thinned out there appeared *Dictyota dichotoma*, *Desmarestia ligulata* (both Phaeophyta) and *Dilsea carnosa* and *Delesseria sanguinea* (both Rhodophyta), while *Chondrus crispus* (Rhodophyta) and *Corallina* persisted. Below 2 m there were no laminarians, *Dictyota* prevailed, and *Desmarestia viridis* (Phaeophyta) and *Phyllophora crispa*, *Nitophyllum punctatum* and *Cryptopleura ramosa* (all Rhodophyta) formed with it a mixed scrub. This assemblage of algae continued all down the steep sides of the pool to the boulder-strewn bottom. The Anthozoa *Corynactis viridis* and *Sagartia elegans* were conspicuous in places on the sides, and a number of starfish (*Asterias rubens* and a single *Marthasterias glacialis*) were seen on the floor of the pool. The fauna associated with *Corallina* in Springtide Pool agreed closely with that in the Gully Pools, but included larger numbers of colonies of Bryozoa (table 6).

A collection of 12 *Laminaria hyperborea* plants was made from a depth of about 0.5 m in Springtide Pool on 11 July 1975. The oldest plants had six growth lines (excluding the surface). The lamina of seven of the plants (including all the older ones) had some *Obelia geniculata*, three had small colonies of *Membranipora membranacea*, and all except for one young (two line) plant had *Patina pellucida*. None of the three plants in the 1–2 line age group had any *Obelia* or Bryozoa on its lamina. *Palmaria palmata* was abundant on the stipes of nearly all the older plants, and was itself heavily infested with *Patina pellucida*. Counts of *Patina* on *Palmaria* from six separate stipes averaged 162 (range 75–252) per 100 g of *Palmaria*. Other epiphytes present in small quantities on a few stipes included *Membranoptera alata*, *Phycodrys rubens*, *Polysiphonia urceolata*, and *Rhodophysema elegans*. *Electra pilosa* (Bryozoa) was present on eight stipes and covered 20 % or more of the available surface of five of them. Other animal species were only occasional. There was a complete absence of hydroids from the stipes. The holdfasts carried a variety of animals on or among their haptera, especially *Mytilus* spat, *Corynactis viridis* (Anthozoa), and occasional *Pomatoceros triqueter* (Polychaeta), *Hiatella arctica* and *Heteranomia squamula* (Lamellibranchia), the limpet *Patina pellucida*, *Verruca stroemia* and *Balanus* sp. (Cirripedia), and *Membranipora membranacea* (Bryozoa). There were no hydroids except possibly for some dead *Tubularia* stems.

A collection was made in Springtide Pool on 17 July 1975 of nine *Saccorhiza polyschides* from a depth of about 0.4 m (below the level of low water of spring tides in the pool) and 11 plants from about 1.2 m. Lamina weights ranged up to 3250 g. The deeper plants had longer stipes. All except the smallest carried many specimens of *Patina pellucida*, which were large and had sunk into the laminae. Hundreds of the amphipod *Jassa falcata* inhabited tubes attached to the frilly margins of the stipes. The *Saccorhiza* was free from epiphytes except for occasional plants of *Giffordia hincksiae* on lamina or stipe.

(*f*) *Mid-tidal and low-tidal crevices at Carrigathorna*

Gully Cleft is exposed to air at low water, but it is so narrow that it is almost continuously shaded, and its walls are kept damp over the period of low water by the continuous outflow of water through it from Long Pool. Gully Cleft contained colonies of the hydroids *Sarsia eximia*, *Tubularia bellis*, and *Tubularia indivisa*, and large patches of *Corynactis viridis*. The amphipod *Parajassa pelagica* was abundant in a quadrat taken at the opening of Gully Cleft into Upper Gully Pool (GC1). *Nereis pelagica* was also present, but the quadrat contained no *Platynereis dumerili*.

West Crevice, a continuation of Low Pool Crevice, contains a slit-like pool (West Crevice Pool) the walls of which carried sheets of the anemone *Corynactis viridis* and the hydroid *Tubularia indivisa*.

Other crevices are mainly mid-tidal, and have small narrow pools distributed along their length. They had numerous *Tealia felina* and *Sagartia elegans* var. *venusta* (both Anthozoa), as detailed in appendix A. *Actinia equina* (Anthozoa) was abundant in places out of water at low tide. In April 1977 there were six *Paracentrotus lividus* (Echinoidea) deep in Top Crevice.

(*g*) *Pools on Urchin Reef*

We studied two pools on Urchin Reef, which lies within the mouth of Barloge Creek and is sheltered from all directions except the east. Little Urchin Pool is high-tidal and shallow. It was covered with encrusting coralline alga. It contained a few clumps of *Corallina officinalis* scattered along the south side in its eastern half, and at its western end one clump of *Cystoseira nodicaulis* (Phaeophyta) surrounded by *Cladophora rupestris* (Chlorophyta). There were many limpets (*Patella vulgata* and *P. aspera*), and *Enteromorpha intestinalis* and *Cladophora rupestris* grew on their shells. There were no sea urchins but many copepods.

Urchin Pool, of intermediate depth, lies close to but just below mean high water of neap tides. Its sides had patches of *Corallina* and tufts of *Cystoseira nodicaulis* and areas of encrusting coralline alga with limpets. Numerous tubes of a sinistral spirorbid, believed to be *Spirorbis inornatus*, covered the older parts of the *Cystoseira*. The *Corallina* was heavily encrusted with a bracket-like coralline alga – *Mesophyllum lichenoides* – found in smaller quantities in mid-tidal pools at Carrigathorna. The *Corallina* also carried the spirorbids *Spirorbis corallinae* and *Janua* *pagenstecheri* but no Bryozoa. The *Corallina* (table 7) and *Cystoseira* (table 8) held a motile fauna richer both in variety and in numbers of individuals than were found in any other pool in this investigation. *Modiolula phaseolina* spat was more abundant than *Mytilus* spat. *Platynereis dumerili* and Syllidae (Polychaeta), *Stenothoe monoculoides* (Amphipoda), *Cingula semicostata*, *Cingulopsis fulgida*, *Rissoa parva*, and other Gastropoda, *Asterina gibbosa* and *Amphipholis squamata* abounded. The amphipod *Amphithoe neglecta* occurred in very large numbers (> 4000 per kg) among *Cystoseira*. Acarina were plentiful; several were found attached to host animals, including the polychaete *Amphiglena mediterranea*. Grooves in the bottom of Urchin Pool were occupied by the sea urchin *Paracentrotus lividus*. Counts taken on 18 April 1976, 6 April 1977, and 6 April 1978 gave 137, 119 and 106 specimens respectively. No *Paracentrotus* were found in any of the other pools on Urchin Reef.

(*h*) *Clearance of limpets*

Defined areas at the west ends of Shallow Pool and Overtwin Pool were completely cleared of limpets on 28 and 29 July 1975. Before clearance these areas were covered with bare smooth encrusting coralline alga, but the limpets carried tufts of filamentous algae, mainly *Enteromorpha prolifera* and *E. intestinalis*, with other species as listed in appendix A. All of the 47 limpets removed in the test area in Shallow Pool were *Patella vulgata*. A total of 27 *P. vulgata* and 176 *P. aspera* were removed from the test area in Overtwin Pool. When re-examined on 20 September 1975, both areas were covered with *Enteromorpha* growing directly on the rock, while the adjacent untreated (and much larger) areas of these two pools appeared the same as originally.

(*i*) *Clearance of* Corallina

An area of *Corallina* in Deep Vee Pool was scraped clean on 27 July 1976. The area measured about 0.5 m (horizontally) × 0.25 m, and its upper edge coincided with the upper margin of the *Corallina* scrub, at about pool water level. The area was re-examined on 6 September 1976, was found to be covered with *Enteromorpha*, and was rescraped. By April 1977 the area had been very thickly overgrown by various soft algae, including *Ceramium*. Algal cover was less by 7 September 1977, and limpets were observed in the experimental area. All limpets were therefore collected. They amounted to five *Patella vulgata* (1.0–1.7 cm in length) and eight *P. aspera* of which four measured 3.7–4.0 cm and the remainder 1.5–2.4 cm. The largest limpets had probably walked onto the area. All except the four smallest limpets had *Ulva* or *Enteromorpha* growing on their shells.

6. Discussion

During the period of separation from the sea, tide pools are subject to wider fluctuations in a number of environmental conditions: temperature, oxygen and carbon dioxide content of the water, pH, and salinity. These can rise above or sink below the levels found in the adjacent coastal water, depending on weather, time of day, and season. In addition, there is protection from wave action while the tide is out, although turbulence can probably be just as severe during high water as in the shallow sublittoral. Irradiance also differs from that in the adjacent shallow sublittoral of the sea: the depth of water through which radiation has to penetrate is less, but tide pools may be shaded by the rock which encloses them or by the adjacent shore.

The higher a tide pool is situated, the longer is it separated from the sea. The duration of continuous separation is critical. In tide pools separated only at low water of spring tides we may expect a close approach in flora and fauna to the shallow sublittoral. In deep mid-tidal pools, with replenishment at every tide, those species of the sublittoral flora and fauna which are not geographically close to their limits of tolerance may be expected to survive, and some species may even find encouragement from the shelter and other special conditions. Much greater changes in flora and fauna may be expected in those pools which are continuously separated for several or more cycles of the tide. The situation is closely comparable with that illustrated by Lewis (1964, fig. 11) for the open shore. Exceedingly severe aquatic conditions, and in some cases desiccation, affect the supratidal pools, and limit their flora and fauna drastically; the death and decomposition of algae (as in Green Pool) may make matters even worse. Nevertheless a few species able to tolerate such conditions may multiply and reach a high density of population, as found in the Green-Pair Pools (table 5). *Enteromorpha intestinalis* is notably resistant to variations of temperature, salinity and pH (Biebl 1959; Black 1971; Ganning 1971; Jones & Babb 1968; Kylin 1927); the enormously abundant copepod *Tigriopus fulvus*, predominant in other high-tidal pools (Fraser 1936*a*), can endure very high concentrations of sea water (Fraser 1936*b*); and the turbellarian *Monocelis lineata* is also able to tolerate a wide range of habitats and conditions (Boaden 1963, 1977; Karling 1974; Straarup 1970). High-tidal pools may also suffer during calm weather at neap tides, as seen in High Pool in the bleaching of *Corallina* during the summer.

A series of major dominant growth types or facies may be recognized in the Carrigathorna tide pools, giving character to the pools and distributed in accordance with their altitude and depth. These are: *Enteromorpha* scrub, sheets of encrusting coralline alga dotted with limpets, *Corallina* scrub or undergrowth, *Laminaria* forest, and *Dictyota* scrub or undergrowth. These provide accommodation for many other organisms, plant and animal; and in some cases they also provide food for animals, although many of the animals feed on plankton produced either in the tide pools or (more probably) in the adjoining coastal waters. The distribution both of the dominant growth types and of the plants and animals inhabiting them is determined by a combination of abiotic and biotic environmental conditions which approach those of the shallow sublittoral at the lowest intertidal levels. Corresponding facies are found in pools on the north and west coasts of France (de Virville 1934, 1935).

The growth type highest in altitude on the shore is a scrub or blanket of *Enteromorpha*. *E. intestinalis* covers the supratidal pools (Green and Green-Pair Pools). It is able to tolerate extremes of pH (as well as of other conditions), and in fact to generate them (de Virville 1935). Pools filled with *Enteromorpha* reached pH 10 both at Carrigathorna and on the coasts of France, and high pH values were also attained at Carrigathorna where the limpets carried much *Enteromorpha*, as in Shallow Vee Pool in the summer. In shallow high-tidal pools *Enteromorpha intestinalis* (in company with *E. prolifera*) is restricted to the backs of limpets. This is the only habitat in these pools where *Enteromorpha* is safe from limpets. It also grows quickly on the encrusting coralline alga if the limpets are removed, so that we must conclude that the lower limit of the *Enteromorpha* blanket is determined by the upper limit of limpets. Thus *Enteromorpha intestinalis* does not occupy the whole of its potential niche, but by reason of its speedy growth it can colonize temporarily sites which are newly available but from which it will ultimately be excluded. Winkles control *Enteromorpha* in some tide pools in New England (Lubchenco 1978).

Smooth encrusting coralline alga scoured by limpets covers Overtwin Pool, Shallow Pool and Shallow Vee Pool. Encrusting coralline alga with limpets is mixed with patches of *Corallina* in High Pool, no doubt because this pool is deeper although at the same altitude, and thus lies at the environmental boundary between these two facies. The upper limit of the limpet and encrusting coralline facies is probably set by a combination of physical and chemical conditions.

At its lower limit the encrusting coralline-limpet facies encounters the *Corallina* scrub. It is possible to suppose that *Corallina* prevails here either because some unspecified condition, either abiotic or biotic, prevents the downward extension of limpets, which would otherwise destroy the *Corallina*, or because some condition or combination of conditions, such as high temperature or pH, prevents the upward extension of *Corallina*, which itself resists limpets and restricts their grazing area. The bleaching of *Corallina* in High Pool during the summer, and the growth of limpets in Deep Vee Pool in an area from which the *Corallina* had been removed, both favour the second interpretation. It seems likely that calcification affords important protection against grazing. *Corallina* scrub extends as an undergrowth into the *Laminaria* forest, but (in Springtide Pool) eventually gives way to non-calcareous scrub-forming algae.

Laminaria forest occupies all firm upward facing and even vertical surfaces down to a depth of 2–3 m in mid-tidal, low-tidal and subtidal pools, except for shallow marginal areas, which are occupied only by *Corallina* scrub. There are no small *Laminaria* sporophytes on such areas, so that it is difficult to explain the lack of *Laminaria* in terms of insufficient depth for growth. It seems more likely that the greater extremes of temperature, pH, etc. found in such places may prevent the development of *Laminaria* at an early stage. At the depths at which *Laminaria* grows in tide pools, the temperature rises in summer far less than it does near the surface (figure 8), and no doubt other physical and chemical conditions fluctuate much less, at any time of year, in the deeper water. Kain (1964, 1969) has pointed out that environmental factors may determine the success or failure of laminarians by action at an early stage in their development. For instance young sporophytes of *L. hyperborea* appeared unhealthy at 18 °C in culture, and none were produced at 20 °C. Both *L. digitata* and *L. hyperborea* are northern species. The reproductive period of *L. hyperborea*, extending from autumn to spring in the British Isles, offers a wide range in the environmental conditions available in tide pools, so that it is not possible to reach any conclusion at present. *L. digitata* transplanted by Sundene (1964) from northern Norway to the Oslo fjord grew well during April, but died during an exceptionally hot summer, as the temperature rose to 22–23 °C at the site in question. The situation in tide pools is further complicated by the possibility that intermittent high temperature, pH, etc., interrupted by the regular tidal flushing of the pool, may be less destructive than continuous exposure to extreme conditions, so that comparisons between localities are difficult.

The *Laminaria* population of Main Pool, like that of the adjacent very shallow sublittoral region, was characterized by a predominance of very young plants. Calm conditions which obtain while pools are isolated from the sea may encourage the settlement of spores, and turbulence during high water may remove older plants selectively, as has been suggested by Kain (1971) for the shallow sublittoral. Adult plants of *L. hyperborea* are similar in size, age for age, to those in the adjacent shallow sublittoral except that from the age of 4–5 years onwards the plants in Main Pool had shorter stipes. At intermediate depths in the sublittoral there is less turbulence than in shallow water or in pools, so that larger plants can survive, and as in a forest there is intense competition for light, so that long stipes are advantageous. In contrast, on the relatively shallow horizontal surfaces in Main Pool there is plenty of light to permit good growth, but long stipes might bring the laminae into very shallow water where less favourable conditions might destroy the plant. We do not know to what extent the plant can respond to various environmental conditions by modification of the growth form.

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The total standing crop of algae in Main Pool (7.5 kg m^{-2}) is close to that found in the the shallow sublittoral off the southeast point of Carrigathorna (8 kg m^{-2}; Norton *et al.* 1977, table 3), but is less than at depths of 6–10 m (12 kg m^{-2}) because of a lack of large plants.

With increasing depth in Springtide Pool, changes take place which seem to parallel the transition to the infrasilvan zone on the open coast. The *Laminaria* forest dwindles and disappears, and *Corallina* scrub gives way to *Dictyota dichotoma* mixed with various red algae. These changes may be attributed largely to a decrease in illumination. They occur over a depth range of about 12–18 m in the sublittoral of the open coast, but at 2–3 m in Springtide Pool. The difference may be due to the very steep sides of Springtide Pool, which lead to shading by the rock and also by the projecting *Laminaria* forest itself. Mechanical and other factors may also make the steeper slope less favourable. At the same time the decrease in turbulence with depth may be telescoped in the protective enclosure of a tide pool, although the absence of a film of sediment from the rock surface in Springtide Pool such as was found by Hiscock (Norton *et al.* 1977) to cover all surfaces at the foot of the sublittoral cliff indicate that turbulence must periodically disturb Springtide Pool to the bottom.

One aberrant growth facies covers the sides of Many-crevice Pool: a blanket of the blue-green alga *Lyngbya confervoides*. The *Lyngbya* covers those parts of the pool which dry out by slow leakage during neap tides. The permanently wet bottom is covered by *Enteromorpha*. No doubt the *Lyngbya* possesses a capacity to recover after desiccation and the osmotic stress indicated by the crystallization of salt on the plants as they dry out. Although little is known of the ecology of *L. confervoides*, the blue-green algae as a group are renowned for their tolerance of environmental extremes. Several species are known to tolerate very high salinities, and *Lyngbya aestuari* is a common contaminant of the evaporating pans in salt works (Hof & Frémy 1933). Many species can withstand prolonged desiccation and *Nostoc commune* has been successfully revived from an 87-year-old herbarium specimen (Lipman 1941). On the shore blue-green algae including *Lyngbya* spp. are usually only abundant on the upper shore in the spray zone where they are habitually subjected to prolonged desiccation. In Many-crevice Pool the *Lyngbya* is inhabited by numerous larvae of *Halocladius fucicola* (Diptera, Chironomidae), which also occurs in other high-tidal and supratidal pools, where its tolerance of extreme conditions is no doubt advantageous. It would be interesting to know how well these larvae can tolerate osmotic stress and loss of water. Only one insect larva – a chironomid – is known to survive complete desiccation (Hinton 1951). Many-crevice Pool, although topographically high-tidal, is functionally supratidal and abnormal.

Although most of the tide pools at Carrigathorna are obviously dominated by one of the major growth types, it is possible for a pool of intermediate or heterogeneous physical characteristics to support more than one facies. High Pool has already been cited as intermediate (p. 28). East Twin Pool is uniformly deep except for a narrow horizontal shelf along its north side with a depth of only 0.1–0.2 m. The sides of this pool are covered with *Laminaria* forest but the north shelf carries only *Corallina* scrub. Many-crevice Pool also contains two facies, associated with different physical conditions.

The flora and fauna of the tide pools are essentially subaquatic. Fucoids and the two common intertidal barnacles are missing from the pools, and very few species inhabit both tide pools and the open unshaded intertidal. There are a few notable exceptions: all species tolerant of a wide range of conditions. The limpets *Patella vulgata* and *P. aspera* are genuinely intertidal, although spat may use damp places or shallow pools for settlement (reviewed by Fretter &

Graham 1962, p. 501). *P. aspera* tends to occur lower on the shore than *P. vulgata*, but occurs at high levels in tide pools (Ebling *et al.* 1962). Even so, *P. vulgata* predominates in Shallow Pool, which is the least subject to wave-wash of those inhabited by limpets, and *P. aspera* in Overtwin Pool, which is higher in level but more wave-washed. *Mytilus edulis* also tolerates a wide range of conditions. Large numbers of spat settle on *Corallina* and on other substrata in the tide pools (table 8), but even though young *Mytilus* is known to relinquish its first attachment and move to its final mooring at the age of several weeks (Seed 1969) it seems likely that many in tide pools are lost in the process or destroyed by predators. It seems possible that the hairs on the valves of *Modiolula phaseolina* (common as spat in Urchin Pool) afford it some protection against predators. The only pool containing well grown *Mytilus edulis*, similar in size to the rather small specimens which cover the lower intertidal region at Carrigathorna, was Shallow Vee Pool. This shallow pool is subject to severe and frequent wave-wash throughout its depth, and we suggest that this protects the mussels from predators such as crabs or starfish.

Certain features of the tide pool flora and fauna may be ascribed to some degree of protection from wave action, at any rate for much of the summer. For instance *Himanthalia elongata*, characteristic of the sublittoral fringe in rather sheltered but not in fully wave-exposed situations, is present in shallow water in Main and Long Pools. Moreover the stipes and holdfasts of *Laminaria hyperborea* in the tide pools had more species of epiphytes than did those of *L. hyperborea* in the sublittoral of the open coast, and the general flora of the pools was also much richer in number of species than that of the adjacent sublittoral. The number of *Patina pellucida* per 100 g lamina of *L. hyperborea* was much greater in the metre squares in Main Pool than at any depth in the sublittoral (table 9), and was even higher (77.6 ± 12.9 individuals) in a deeper collection from the northeast corner of the pool. This may be compared with the situation in the Rapids, where *Patina* reaches higher population densities on *Saccorhiza polyschides* in moderate rather than very fast current (Ebling *et al.* 1948). *Spirorbis corallinae* was plentiful on *Corallina* in the lower tide pools, but was missing from Lower Gully Pool, which is subject to continual wave-wash. We do not know to what extent the shelter afforded by tide pools benefits certain organisms over their whole life span, or to what extent it operates briefly, as for instance in providing conditions safe for settlement even during a single low tide.

The great wealth of small gastropods such as *Rissoa parva* in certain of the pools recalls the situation at some distance down the sublittoral rock slope, where turbulence is less. Wigham (1971) has suggested that a preference of *Rissoa parva* for filamentous algae may be due in part to the shelter which these afford and in part to the accumulation among algae of detritus upon which the young snails feed. Some gastropods of brief life span may well benefit in summer from the security afforded by tide pools. Urchin Pool provides an outstanding example of the effect of shelter from wave action. It contains many species and an enormous number of individuals. In summer the much-branching brown alga *Cystoseira nodicaulis* harbours very large numbers of amphipods, and there are many polychaetes, mites, insect larvae, small gastropods, and small asteroids and ophiuroids. A severe fall in the population density of various rissoid gastropods in winter has been noted by Fretter (1948). Table 8 strongly suggests that a study of seasonal population changes of many small invertebrates in Urchin Pool would prove instructive. The very large numbers of young specimens of certain species (*Platynereis dumerili*, *Amphithoe neglecta*) also suggest a high early mortality.

The sea urchin *Paracentrotus lividus*, found in the Mediterranean and on the west coast of mainland Europe, extends up the west coast of Ireland in tide pools (Duerden 1895; Ryland

& Nelson-Smith 1975) and is found in a few sheltered shallow sublittoral sites, such as Bantry Bay (Crapp 1973) and Lough Ine. Southward & Crisp (1954) have concluded that a requirement for a sufficiently high summer temperature for breeding may limit it to these habitats and to this geographical range. Although *Paracentrotus* forms close fitting excavations in tide pools in places where the rock is not too hard (Otter 1932), in the pools at Carrigathorna, formed in Devonian slates, it is limited to a very few crevices. It is more successful in Urchin Pool, although still confined to crevices, but there is a large population distributed over the shallow sublittoral of Lough Ine unprotected by crevices although often with empty shells held over them. We may attribute the almost complete failure at Carrigathorna to the hardness and unsuitability of the slates. Excavations – where these are possible – no doubt give snug protection against dislodgement by waves and possibly against predators. These risks are diminished in those parts of Lough Ine which are colonized by *Paracentrotus*, and in summer the water temperature evidently reaches the level required for breeding. We do not even know that the few *Paracentrotus* at Carrigathorna or even the many in Urchin Pool are derived from pool-produced larvae; they may be restocked by larvae from the lough.

Progressive changes in the composition of the population of small invertebrates from high-level to low-level pools have been described in §5. Not enough is known of the habits and requirements of these various species for it to be possible to explain these changes, although we may suspect that in a number of cases upper limits (towards the more adverse conditions) are determined mainly by abiotic conditions, and that predation and competition set lower limits. This generalization seems likely to be true except where the lower limit is less favourable than the upper, as for instance when diminishing irradiance reduces the growth of algae. Species common both in low level pools and in the shallow sublittoral include the Anthozoa *Sagartia elegans* and *Corynactis viridis* and the Amphipoda *Jassa falcata* and *Parajassa pelagica*. These species are all also common in the main stream of the Rapids, either in moderate or fast current (Lilly *et al.* 1953; Sloane *et al.* 1961). *Parajassa pelagica* appears to require a high degree of water turbulence (Dommasnes 1968). The Bryozoa show a striking increase in numbers of colonies and species towards the lower pools (*Membranipora membranacea* on *Laminaria* laminae, and other species on *Corallina*), with a maximum in Springtide Pool. Members of this group have great advantages for use as environmental indicators – there are a large number of species with diverse requirements, they cannot escape during collection, and they are easily preserved.

There remain certain sublittoral species strikingly absent from our tide pool collections: the hydroid *Amphisbetia operculata*, epizoic on stipes of *Laminaria hyperborea* in the sublittoral and abundant on boulders in the fastest current in the Rapids, and various Porifera and Tunicata. It is possible that some species are missing from the tide pools because there is a lack of overhanging surfaces. The vertical walls of Gully Cleft, uncovered briefly at low tide but always damp and dim, had a special and characteristic fauna, sharing an abundance of *Corynactis* with other weakly lit but clean rock surfaces (Muntz *et al.* 1972) and including three hydroids of which *Tubularia bellis* also abounds in the Rapids.

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Appendix A. Records of flora and fauna

Numbers in parentheses, placed after the specific names, refer to specialists who have examined some or all of the material. These specialists are listed at the end of this appendix. Sites are designated by letters as explained in appendix B.

Algae: Cyanophyta

Dermocarpa leibleiniae (Reinsch) Born. et Thur. (1) H
Lyngbya confervoides [C. Ag.] Gom. (1) MC, DV; new record for Ireland
L. epiphytica Kirchn. (1) MC, DV; new record for Ireland
Lyngbya sp. (undetermined) G (on *Cladophora sericea*)
Oscillatoria sp. (1) G; on *C. sericea*
Xenococcus schousbei Thur. (1) G. H, LU; some on *Cladophora rupestris*

Algae: Rhodophyta

Acrosorium uncinatum (Turn.) Kylin ST; on *Corallina*
Apoglossum ruscifolium (Turn.) J. Ag. M; on *L. hyperborea*
Atractophora hypnoides Crouan frat. (2) ST; new record for Ireland
Audouinella floridula (Dillw.) Woelkerling M, U
A. purpurea (Lightf.) Woelkerling M; on *L. hyperborea*
Callithamnion hookeri (Dillw.) S. F. Gray (3) LG
Callophyllis laciniata (Huds.) Kütz. M
Ceramium ciliatum (Ellis) Ducluz. M, U
C. rubrum (Huds.) C. Ag. H, DV, ET, WT, M, GC, UG, ST, U
C. shuttleworthianum (Kütz.) Rabenh. ST
Champia parvula (C. Ag.) Harv. DV
Chondrus crispus Stackh. M (some on *L. hyperborea*), L
Corallina officinalis L. OT, H, S, SV, DV, ET, WT, M, L, GC, UG, ST, LG, LU, U
Cryptopleura ramosa (Huds.) Newton M, ST; mostly on *L. hyperborea*
Delesseria sanguinea (Huds.) Lamour. M (some on *L. hyperborea*)
Dermatolithon corallinae (Crouan frat.) Fosl. (4) H, DV, ET, M, L, UG, ST, LG, U; on *Corallina*
D. littorale (Suneson) Lemoine (4) M; on *Corallina*; new record for Ireland
D. pustulatum (Lamour.) Fosl. (4) M, L, ST; on *Gigartina* and *L. hyperborea*
Dilsea carnosa (Schmidel) Kuntze M, L
Fosliella farinosa (Lamour.) Howe (4) U; on *Cystoseira nodicaulis*
Furcellaria lumbricalis (Huds.) Lamour. M
Gastroclonium ovatum (Huds.) Papenf. H, DV, M, L, LU
Gelidium latifolium (Grev.) Born. et Thur. M
G. pusillum (Stackh.) Le Jol. U
Gigartina stellata (Stackh.) Batt. M (some on *L. hyperborea*), L, ST

Goniotrichum alsidii (Zanard.) Howe LU
Halarachnion ligulatum (Woodw.) Kütz. ST
Hypoglossum woodwardii Kütz. M
Laurencia pinnatifida (Huds.) Lamour. M
Lithophyllum incrustans Phil. (6) OT, H, S, SV, DV, WT, L, UG, LU, U
Lomentaria articulata (Huds.) Lyngb. M; mostly on *L. hyperborea*
Melobesia membranacea (Esper) Lamour. (4) L (on *Gigartina*)
Membranoptera alata (Huds.) Stackh. M, ST; some on *L. hyperborea*
Mesophyllum lichenoides (L.) Lemoine (4) H, DV, ET, M, L, GC, UG, U
Nitophyllum punctatum (Stackh.) Grev. ST
Palmaria palmata (L.) Stackh. M, L, ST; on *L. hyperborea* and *L. digitata*
Peyssonelia atropurpurea Crouan frat. M; on *L. hyperborea*
Peyssonelia sp. (4) M (on *L. hyperborea*), LU
Phycodrys rubens (L.) Batt. M, ST; on *L. hyperborea*
Phyllophora crispa (Huds.) Dixon M, ST
Phymatolithon lenormandi (Aresch.) Adey (6) S, L, LU
P. polymorphum (L) Fosl. (4, 6) H, DV, ET, WT, M, L, ST (on *Corallina*), LG
P. rugulosum Adey (6) DV
Plumaria elegans (Bonnem.) Schm. M; some on *L. hyperborea*
Polyneura hilliae (Grev.) Kylin M; some on *L. hyperborea*
Polysiphonia brodiaei (Dillw.) Spreng. ST, UG
P. denudata (Dillw.) Harv. DV
P. fibrata (Dillw.) Harv. H
P. fruticulosa (Wulf.) Spreng. DV, U
P. urceolata (Dillw.) Grev. M, ST, LG; some on *L. hyperborea*
Pterocladia capillacea (S. G. Gmel.) Born. et Thur. DV, M, L, U
Pterosiphonia parasitica (Huds.) Falkenb. M
Ptilothamnion pluma (Dillw.) Thur. M; on *L. hyperborea*
Rhodomela confervoides (Huds.) Silva ST
Rhodophyllis divaricata (Stackh.) Papenf. M; some on *L. hyperborea*
Rhodophysema elegans (J. Ag.) Dixon M, ST; on *L. hyperborea*
Rhodymenia pseudopalmata (Lamour.) Silva M
Spermothamnion repens (Dillw.) Rosenv. ST

Algae: Phaeophyta

Alaria esculenta (L.) Grev. ST, LG
Asperococcus fistulosus (Huds.) Hook. LU, U
Cutleria multifida (Sm.) Grev. ST
Aglaozonia phase of *C. multifida* M; on *L. hyperborea*
Cystoseira nodicaulis (With.) Roberts LU, U
Dictyota dichotoma (Huds.) Lamour. DV, M, L
Ectocarpus fasciculatus Harv. OT, SV, ST; some on *Saccorhiza*
E. siliculosus (Dillw.) Lyngb. OT, S
Elachista fucicola (Vell.) Aresch. U
Feldmannia simplex (Crouan frat.) Hamel U

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Giffordia hincksiae (Harv.) Hamel ST; on *Saccorhiza* and *L. hyperborea*
Halidrys siliquosa (L.) Lyngb. M, L
Halopteris filicina (Grat.) Kütz. M, ST
Himanthalia elongata (L.) S. F. Gray H, M, L
Laminaria digitata (Huds.) Lamour. ET, WT, M, L, NT, UG, ST, LG; a few on *L. hyperborea*
L. hyperborea (Gunn.) Fosl. ET, WT, M, L, ST
L. saccharina (L.) Lamour. M, L
Leathesia difformis (L.) Aresch. DV, M, U
Myriotrichia filiformis Harv. U
Pilayella littoralis (L.) Kjellm. OT
Saccorhiza polyschides (Lightf.) Batt. ST
Scytosiphon lomentaria (Lyngb.) Link OT
Sphacelaria cirrosa (Roth) C. Ag. DV, M (some on *L. hyperborea*), L, LU, U
S. fusca (Huds.) S. F. Gray M; on *L. hyperborea*
S. plumula Zanard M
Spongonema tomentosum (Huds.) Kütz. U
Taonia atomaria (Woodw.) J. Ag. ST

Algae: Chlorophyta

Blidingia marginata (J. Ag.) P. Dang. MC
B. minima (Kütz.) Kylin SGP, S (on limpets), GC
Chaetomorpha capillaris (Kütz.) Børg. DV, M, SV, U
C. linum (O. F. Mull.) Kütz. G, H, M
Chlorochytrium facciolae (Borzi) Bristol (5) LU; amidst blue-green algae on *Cladophora sericea*, 1st marine record of this species for the British Isles
C. willei Printz (5) MC; on *Blidingia marginata*
Cladophora albida (Huds.) Kütz. (5) OT (on limpets), DV
C. dalmatica Kütz. (5) (*C. oblitterata* form) LU
C. rupestris (L.) Kütz. H, M, L, LU, U; some on *L. hyperborea*
C. sericea (Huds.) Kütz. (5) G, OT (on limpets), MC, DV, LU
C. vagabunda (L.) Hoek (5) DV
Codium fragile (Sur.) Hariot subsp. *tomentosoides* (Goor) Silva H; on a limpet
Enteromorpha clathrata (Roth) Grev. LU
E. compressa (L.) Grev. NGP, SGP, OT, M
E. intestinalis (L.) Link NGP, SGP, G, OT (on limpets), H, SV, DV, M, LG, LU, U
E. prolifera (O. F. Mull.) J. Ag. NGP, SGP, G, OT (on limpets), MC
Monostroma oxyspermum (Kütz.) Doty H
Phaeophila wittrockii (Wille) Nielson G
Pringsheimiella scutata (Reinke) Marchew. G
Rhizoclonium riparium (Roth) Harv. OT, M, LU, U
Spongomorpha arcta (Dillw.) Kütz. DV, M, ST
Ulva lactuca L. OT (on limpets), DV, M (some on *L. hyperborea*), ST
U. rigida (C. Ag.) Thur. OT, H, S, DV, M, L, LU, U

Porifera: Calcarea

(For synonymy see Burton 1963)

Aphroceras cliarensis (Stephens) (7) M (probably this species)
Leuconia johnstonii Carter (7) M
L. nivea (Grant)? (7) M

Porifera: Desmospongiaria

Adocia sp. (7) M
Haliclona sp. ? (7) M
Hymeniacidon perleve (Montagu) (7) S

Coelenterata: Hydrozoa

Diphasia rosacea (L.) LG
Obelia dichotoma (L.) UG, LG
O. geniculata (L.) ST (on laminae of *Laminaria hyperborea*)
Plumularia setacea (Ellis & Solander) LG (on *Corallina*)
Sarsia eximia (Allman) GC
Tubularia bellis Allman (see Hincks 1868) GC, UG, LG
T. indivisa L. GC, WC

Coelenterata: Anthozoa

Actinia equina L. OT, H, S, SV, DV, ET, WT, M, GC, and widely distributed in damp places intertidally, including NC, LowC, TC, SC
Corynactis viridis Allman (8) DV, ET, M, L, GC, UG, LG, WC, ST
Metridium senile (L.) H (1 specimen)
Sagartia elegans (Dalyell) var. *miniata* OT, S, LU; var. *rosea* S (1 specimen); var. *venusta* Low, NT, GC, UG, ST, NC, LowC, TC, SC
Tealia felina (L.) DV, ET, WT, M, L, NT, UG, LowC, TC, SC, NTC; no information for LG or ST

Platyhelminthes: Turbellaria

Macrostomum hystricinum Beklemischev (9) (see Karling 1974) NGP
Monocelis lineata (O. F. Müller) (9) NGP, SGP
Stylochoplana maculata (Quatrefages) (9) M, ST

Annelida: Polychaeta

(Nomenclature follows Knight-Jones & Knight-Jones (1977) for Spirorbidae ,and Hartman (1959, 1965) for other Polychaeta; some specimens were too damaged to be determined.)

Amphiglena mediterranea (Leydig) ET, U; tables 7 and 8
Autolytus sp. WT, UG
Branchiomaldane vincenti Langerhans U (1 specimen)
Brania clavata (Claparède) (some specimens difficult to distinguish from *B. limbata* (Claparède), which is doubtfully separate according to Fauvel (1923); *Grubea* in Plymouth Marine Fauna M, U
Capitellidae L, ET, WT, ST, U
Cirratulidae U
Dodecaceria concharum Oersted H, DV, ET, WT, L, UG, LG, U

Eumida ? *sanguinea* (Oersted) (*Eulalia* in Plymouth Marine Fauna) LG
Eusyllis blomstrandi Malmgren L, U
Fabricia sabella (Ehrenberg) G, H, U
Harmothoe extenuata (Grube) (*Lagisca* in Plymouth Marine Fauna) M, ST
Harmothoe spp. ET, M, L, GC, UG, LG, ST, U
Janua pagenstecheri (Quatrefages) (11) (*Spirorbis* in Plymouth Marine Fauna; *Dexiospira* in Hartman, 1959, 1965; see Knight-Jones & Knight-Jones 1977) SGP, H, S, DV, LU, U; tables 6 and 7
Lepidonotus clava (Montagu) L, LG, ST
L. squamatus (L.) L (1 specimen)
Lumbrinereis sp. (*Lumbriconereis* in Plymouth Marine Fauna) ET
Micronereis variegata Claperède U (in 4 samples, 12 specimens altogether)
Nereis pelagica (L.) H, ET, WT, M, L, GC, UG, LG, U; table 7
Odontosyllis ctenostoma Claparède M, L?, U
Pholoe minuta (Fabricius) H, SV, DV, M, L, UG, LU, U
Platynereis dumerilii (Audouin & Milne Edwards) H, S, SV, DV, ET, WT, M, L, LU, U
Polydora sp. WT (1 specimen)
Pomatoceros triqueter (L.) DV, ET, M, L, GC, LG, ST
Salmacina incrustans Claparède M (on holdfasts of *L. hyperborea*)
Sphaerodorum gracile (Rathke) (*Ephesia* in Plymouth Marine Fauna) L, UG
Sphaerosyllis sp. SV, WT, M, U
Spirorbis corallinae de Silva & Knight-Jones (11) (*Laeospira* in Hartman 1959, 1965; see Knight-Jones & Knight-Jones 1977) H, DV, ET, WT, M, L, UG, ST, U; table 6
S. inornatus L'Hardy & Quievreux (11) (see Knight-Jones & Knight-Jones 1977) U (on *Cystoseira* and presumed to be this species rather than *S. corallinae*)
S. tridentatus Levinsen (see Knight-Jones & Knight-Jones 1977) M (on holdfast of *L. hyperborea*)
Syllis gracilis Grube H, SV, ET, WT, M, L, UG, LG, U
Typosyllis armillaris (Müller) GC, UG?, LG, U
T. Krohnii Ehlers ET, M, L, U
T. prolifera (Krohn) (10) M, U; probably also in other pools
Terebellidae DV, M
Trypanosyllis zebra (Grube) ET, U; undetermined specimens from many pools belong either to this species or to *Typosyllis prolifera*

Arthropoda: Crustacea: Copepoda
(Incompletely collected)

Amphiascus minutus (Claus) (12) LU
Laophonte cornuta Philippi (12) ET, LU, U
L. strömi (Baird) (12) U
Microthalestris forficula (Claus) (12) LU
Parapontella brevicornis (Lubbock) (12) ET
Temora longicornis (O. F. Müller) (12) ET
Tigriopus fulvus (Fischer) (12) NGP, SGP, S, LU, U
Westwoodia pygmaea (T. & A. Scott) LU

Arthropoda: Crustacea: Cirripedia

Balanus balanoides (L.) GC
B. balanus (L.) (see Bassindale 1964) ST (on holdfast of *L. hyperborea*)
Chthamalus stellatus (Poli) UG (on shell of *Patella* sp.)
Verruca stroemia (O. F. Müller) SV, DV, ET, WT, M, L, GC, UG, LG, ST, U

Arthropoda: Crustacea: tanaidacea

Tanais cavolini Milne Edwards (13) G, H, S, SV, DV, M, U

Arthropoda: Crustacea: Isopoda

Dynamene bidentata (Adams) DV, M, U; tables 7 and 8
Idotea granulosa Rathke H, SV, DV, ET, WT, M, L, GC, UG, LG, ST, U; tables 7 and 8
I. pelagica Leach DV, ET, WT, L, GC, UG, LG, ST (Many *Idotea* sp. < 3 mm long were also found in many pools)
Jaera ischiosetosa Forsman (13) (see Naylor 1972) G
J. praehirsuta Forsman (13) (see Naylor 1972) G, OT
Jaera spp. (*albifrons* group, not further determined) G, OT, H, S, SV
Janiropsis breviremis Sars (13) L, UG, LG, ST
Ligia oceanica (L.) ST, U
Munna sp. (13) U

Arthropoda: Crustacea: Amphipoda

Amphithoe (*Pleonexes*) *neglecta* Lincoln (1976) (13) H, S, DV, M, U; tables 7 and 8, and see page 27.
A. rubricata (Montagu) DV, M, L, ST, U
Apherusa bispinosa (Bate) H, M, L, ST, U
A. jurinei (Milne Edwards) H, WT, M, L, GC, UG, LG, ST, U; tables 7 and 8
Caprella acanthifera Leach H, DV, M, L, ST, U
C. acutifrons Latreille ST
Dexamine thea Boeck H, S, DV, M, U; tables 7 and 8
Gammarellus angulosus (Rathke) (13) G, H, SV, DV, WT, M, L, GC, UG, LG, ST, U; tables 7 and 8
Hyale nilssoni (Rathke) (13) OT, H, U
H. nilssoni var. *stebbingi* (13) ET, WT, L, U
H. perieri (Lucas) (13) G, OT, MC, M, U
H. pontica Rathke (13) ET, WT, M, L, GC, UG, LG, ST; table 7
Jassa falcata (Montagu) M, L, ST (tubes with many hundreds, including many young specimens, among the frills of the stipes of *Saccorhiza polyschides*), U (1 specimen)
Lembos websteri Bate single specimens from G, DV, L, U
Lysianassa ceratina (A. O. Walker) (13) single specimens from M, ST
Melita palmata (Montagu) G (29 specimens in 6 quadrats), H, U (1 specimen)
Microdeutopus chelifer (Bate) (13) U (1 specimen)
Orchomene sp. ST (1 specimen)
Parajassa pelagica (Leach) H (1 specimen), L, GC, UG, LG, ST; table 7
Podocerus variegatus Leach (13) U
Stenothoe monoculoides (Montagu) OT, H, S, SV, DV, ET, WT, M, L, UG, U; tables 7 and 8

Arthropoda: Crustacea: Decapoda

Cancer pagurus L. ET, GC, UG, LG
Carcinus maenas (L.) H, LU, U
Galathea sp. ST
Maia squinado (Herbst) ST (1 very small specimen)
Palaemon elegans Rathke G, OT, H, DV
Porcellana longicornis (L.) M, L, UG, ST
Praunus sp. M

Arthropoda: Pycnogonida

Achelia echinata Hodge (14) (*Ammothea* in Plymouth Marine Fauna; see King 1974) ST, U
A. hispida Hodge (14) (see King 1974) ST, U
A. longipes Hodge (14) (see King 1974) U
Anoplodactylus angulatus (Dohrn) U
Endeis spinosa (Montagu) (14) ST
Phoxichilidium femoratum (Rathke) (14) LG, ST
Pycnogonum littorale (Ström) (14) U

Arthropoda: Insecta: Collembola

Lipura maritima (Laboulbène) (*Anurida* in Plymouth Marine Fauna) H, SV, U

Arthropoda: Insecta: Diptera

Clunio marinus Haliday (15) larvae in H, SV, DV, WT, L, U; tables 7 and 8
Halocladius fucicola (Edwards) (15) (*Cricotopus* in Plymouth Marine Fauna; see Hirvenoja 1973) mostly larvae, NGP, SGP, G, OT, MC (130 and 67 in two quadrats), H, SV, LU, U; tables 5, 7 and 8

Mollusca: Amphineura

Acanthochitona crinitus (Pennant) (16) SV, M, L, LG, ST, U
Tonicella rubra (L.) (16) M, ST, U

Mollusca: Castropoda: Prosobranchia

Acmaea virginea (Müller) DV, M, L, U
Alvania crassa (Kanmacher) G (1 shell)
A. punctura (Montagu) (16) M, L, U
Barleeia rubra Adams (16) DV, L, U
Bittium reticulatum (da Costa) U
Calliostoma zizyphinum (L.) M, ST
Cingula alderi (Jeffreys) (16) U (numerous); possibly occasional specimens in the Carrigathorna pools, but shells corroded by preservative
C. cingillus (Montagu) (16) U
C. semicostata (Montagu) (16) H, DV, M, L, ST, LU, U; tables 7 and 8
C. semistriata (Montagu) (16) DV, M
Cingulopsis fulgida (Adams) (16) G, DV, ET, M, L, LU, U; tables 7 and 8
Diodora apertura (Montagu) M (on *L. hyperborea* holdfast)
Gibbula cineraria (L.) H, M, L, UG, U

G. umbilicalis (da Costa) M
Hydrobia sp., probably *H. ventrosa* (Montagu) (16) DV, ET, M, L, ST, U; tables 7 and 8
Lacuna pallidula (da Costa) (16) M, ST, U
L. vincta (Montagu) (16) G, SV, DV, M, L, ST, U; tables 7 and 8
Littorina littoralis (L.) M, L, ST, LU, U
L. neglecta (Bean) (16) M, GC, LG
L. saxatilis group G, H, S, DV, ST
Lunatia sp. (= *Natica*) (probably) DV, M, L, U
Nassarius incrassatus (Ström) DV, M, L, ST
N. pygmaeus (Lamarck) M
Nucella lapillus (L.) G, MC, SV, WT, L, GC, UG, LG, ST
Ocenebra erinacea (L.) U (1 specimen)
Omalogyra atomus (Philippi) (16) DV, LU, U; tables 7 and 8
Patella aspera Lamarck OT, H, SV, ET, WT, LU
P. vulgata L. OT, H, S, SV, LU
Patina pellucida (L.) G, DV, M, L, UG, LG, ST, U; abundant on *Laminaria* spp. (M, ST) and on *Saccorhiza polischides* and *Palmaria palmata* (ST) but also occasionally on other algae
Philbertia linearis (Montagu) M (1 specimen)
Rissoa membranacea (Adams) (16) U (1 specimen)
R. parva (da Costa) (16) NGP, SGP, H, S, SV, DV, ET, WT, M, L, GC, UG, LG, ST, U; tables 7 and 8
Rissoella diaphana (Alder) (16) DV, M, L, LU, U
R. opalina (Jeffreys) (16) DV, M, U
Skeneopsis planorbis (Fabricius) (16) SGP, G, H, S, DV, ET, L, LU, U; tables 7 and 8
Tricolia pullus (L.) G, M, ST

Mollusca: Gastropoda: Opisthobranchia

Archidoris pseudoargus (Rapp) (17) LG (1 specimen)
Coryphella sp. (17) Low (1 specimen)
Elysia viridis (Montagu) (17) U (1 specimen)
Odostomia eulimoides Hanley (16) NGP (1 specimen), SV
O. nivosa (Montagu) (16) M, L
Retusa truncatula (Brugiere) (16) H (1 specimen), U (1 specimen)
Runcina coronata (Quatrefages) (= *Pelta coronata* of Plymouth Marine Fauna) (17) H, WT, UG

Mollusca: Gastropoda: Pulmonata

Otina otis (Brown) (17) ST

Mollusca: Lamellibranchia

Gastrochaena dubia (Pennant) ET (1 specimen under encrusting coralline alga on north shelf)
Heteranomia squamula (L.) (16) DV, ET, WT, M, L, UG, LG, ST, U; table 7
Hiatella arctica (L.) SV, DV, ET, WT, M, L, GC, UG, LG, ST, LowC, U; table 7
Kellia suborbicularis (Montagu) (16) DV, M, L, UG, LG, U
Lasaea rubra (Montagu) (16) H, SV, ET, L, U
Modiolula phaseolina (L.) H, S, SV, DV, ET, M, L, UG, LG, LU, U; tables 7 and 8; spat only
Monia squama (Gmelin) (16) ST (1 specimen)

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Musculus discors (L.) (16) L, U
M. marmoratus (Forbes) (16) S, DV, M, ST, U
Mytilus edulis L. and/or *M. galloprovincialis* Lamarck (many intermediates are reported by Seed (1974) to occur at Carrigathorna) H, S, SV, DV, ET, WT, M, L, GC, UG, LG, ST, LU, U; tables 7 and 10

Bryozoa: Cyclostomata

Crisia eburnea (L.) (18) L, UG, ST
C. ramosa Harmer (18) ST
Crisidia cornuta (L.) (18) UG

Bryozoa: Cheilostomata

Aetea sica (Couch) (19) ST (on *Rhodomela confervoides*)
Callopora lineata (L.) (19) M, ST; on stipes and holdfasts of *L. hyperborea*
Cellepora ria pumicosa (Pallas) (*Cellepora* in Plymouth Marine Fauna; see Ryland 1969) (19) ST
Celleporella hyalina (L.) (19) ET, WT, M, L, GC, UG, LG, ST; on *Corallina*, table 6
Celleporina hassallii (Johnston) (19) M, L, GC, UG, LG, ST; on *Corallina*, table 6
Electra pilosa (L.) (19) M, L, GC, UG, ST; on *Corallina*, table 6
Escharoides coccineus (Abildgaard) ST
Haplopoma impressum (Audouin) ST
Membranipora membranacea (L.) M, ST; on laminae of *L. hyperborea*
Microporella ciliata (Pallas) (19) L, ST
Scruparia chelata (L.) (19) ST
Scrupocellaria reptans (L.) (19) ST
Umbonula littoralis Hastings (19) UG

Echinodermata: Crinoidea

Antedon bifida (Pennant) ST (2 pentacrinoid larvae at depth of 4 m on 11 July 1975)

Echinodermata: Asteroidea

Asterias rubens L. DV, ST
Asterina gibbosa (Pennant) H, S, DV, ET, M, L, ST, U; tables 7 and 8; not separated from the recently described *A. phylactica* (Emson & Crump 1979)
Marthasterias glacialis (L.) DV, ST

Echinodermata: Ophiuroidea

Amphipholis squamata (Delle Chiaje) H, S, SV, DV, ET, M, L, UG, LU, U; tables 7 and 8
Ophiothrix fragilis (Abildgaard) ET, M, L, ST, U

Echinodermata: Echinoidea

Echinus esculentus L. DV (1 specimen), M (1 specimen)
Paracentrotus lividus (Lamarck) SV (1 under overhang on north side), TC (6 specimens)

Chordata: Tunicata

Aplidium proliferum (Milne Edwards) (probably) M, ST, U
Botryllus schlosseri (Pallas) M (1 colony)

Chordata: Pisces

(for nomenclature see Wheeler 1969)

Crenimugil labrosus (Risso) (*Mugil* in Plymouth Marine Fauna) H, S, MC; young specimens only, in small shoals in all these pools

Taurulus bulbalis (Euphrasen) (*Cottus* in Plymouth Marine Fauna) ET (in crab trap)

(1) Identified by Dr B. A. Whitton, University of Durham.
(2) Confirmed by Professor P. S. Dixon, University of California.
(3) Identified by Mr J. H. Price, British Museum (Natural History).
(4) Identified or confirmed by Ms Y. M. Butler, Portsmouth Polytechnic.
(5) Identified or confirmed by Dr E. M. Burrows.
(6) Identified by Mr J. Clokie, Universities Marine Station, Millport.
(7) Identified by Miss S. M. Stone, British Museum (Natural History).
(8) Confirmed by Dr P. F. S. Cornelius, British Museum (Natural History) in consultation with Dr R. L. Manuel, Oxford University.
(9) Identified by Dr T. G. Karling, Swedish Museum of Natural History, Stockholm.
(10) A few identified by Dr J. D. George, British Museum (Natural History).
(11) Some specimens identified or confirmed by Mrs Phyllis Knight-Jones, University College of Swansea.
(12) Identified or confirmed by Dr Brenda Thompson, Ministry of Agriculture, Fisheries and Food, Fisheries Laboratory, Lowestoft.
(13) Some specimens identified or confirmed by Dr R. J. Lincoln, British Museum (Natural History).
(14) Identified or confirmed by Dr P. E. King, University College of Swansea.
(15) Many specimens identified by Dr R. S. Wilson, University of Bristol.
(16) Some specimens identified by Dr J. D. Taylor, British Museum (Natural History), assisted by Miss A. Blake for *Odostomia* and Mrs S. Whybrow for Lamellibranchia, and in consultation with Mr C. P. Palmer for rissoids.
(17) Identified by Dr T. E. Thompson, University of Bristol.
(18) Some specimens identified or confirmed by Professor J. S. Ryland, University College of Swansea.
(19) Some specimens identified or confirmed by Dr P. J. Hayward, University College of Swansea.

Appendix B. Abbreviations for site names

(These abbreviations are used in appendix A, for the numbering of quadrats in tables 5, 6 and 7, and in the figures.)

DV	Deep Vee Pool
ET	East Twin Pool
G	Green Pool
GC	Gully Cleft
H	High Pool
L	Long Pool
LG	Lower Gully Pool
Low	Low Pool
LowC	Low Pool Crevice
LU	Little Urchin Pool
M	Main Pool
MC	Many-crevice Pool
NC	North Crevice
NGP	North Green-Pair Pool
NT	Neap-tide Pool
NTC	Neap-tide Pool Crevice

OT	Overtwin Pool	TC	Top Crevice
S	Shallow Pool	U	Urchin Pool
SC	South Crevice	UG	Upper Gully Pool
SGP	South Green-Pair Pool	WC	West Crevice Pool
ST	Spring-tide Pool	WT	West Twin Pool
SV	Shallow Vee Pool		

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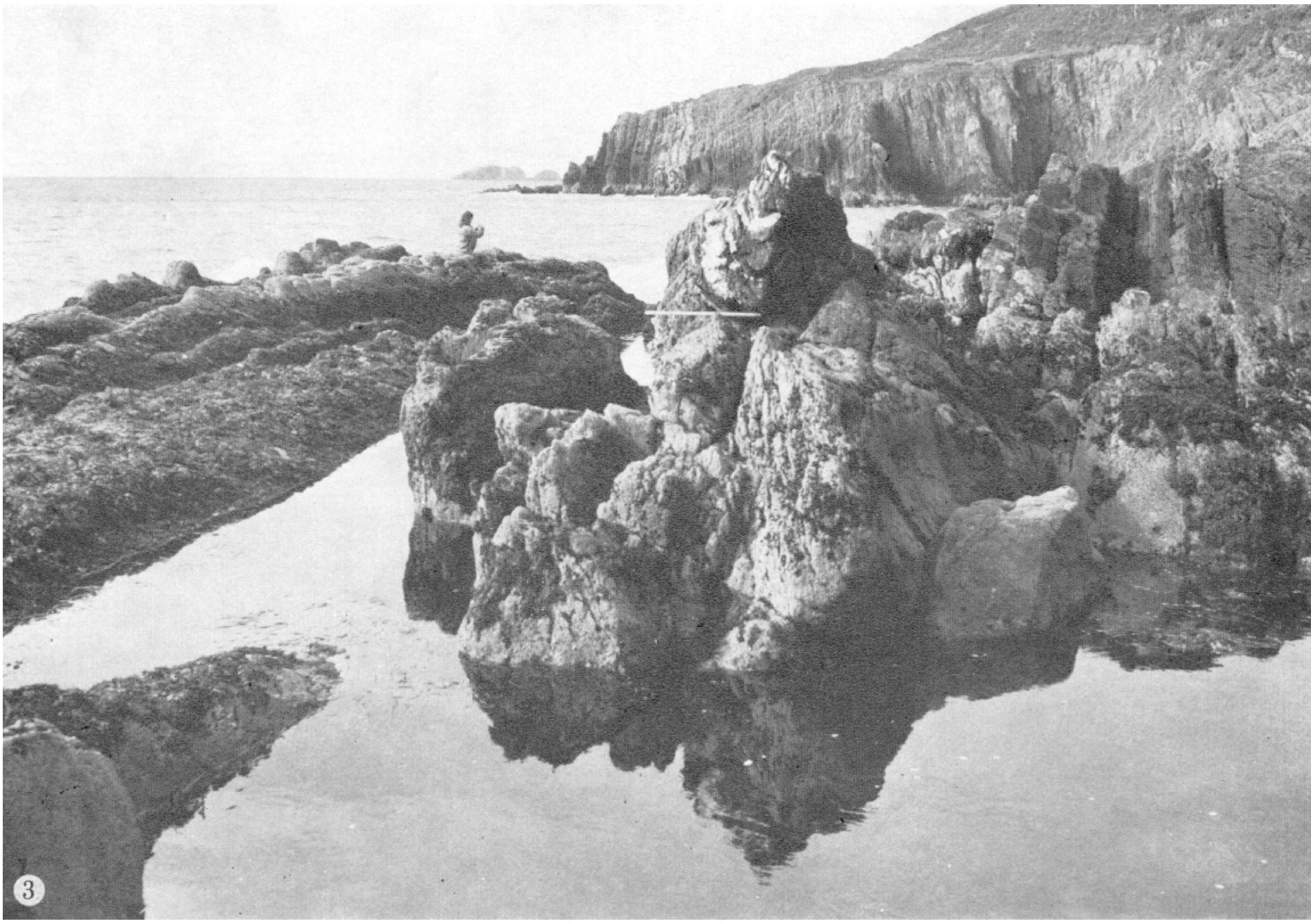

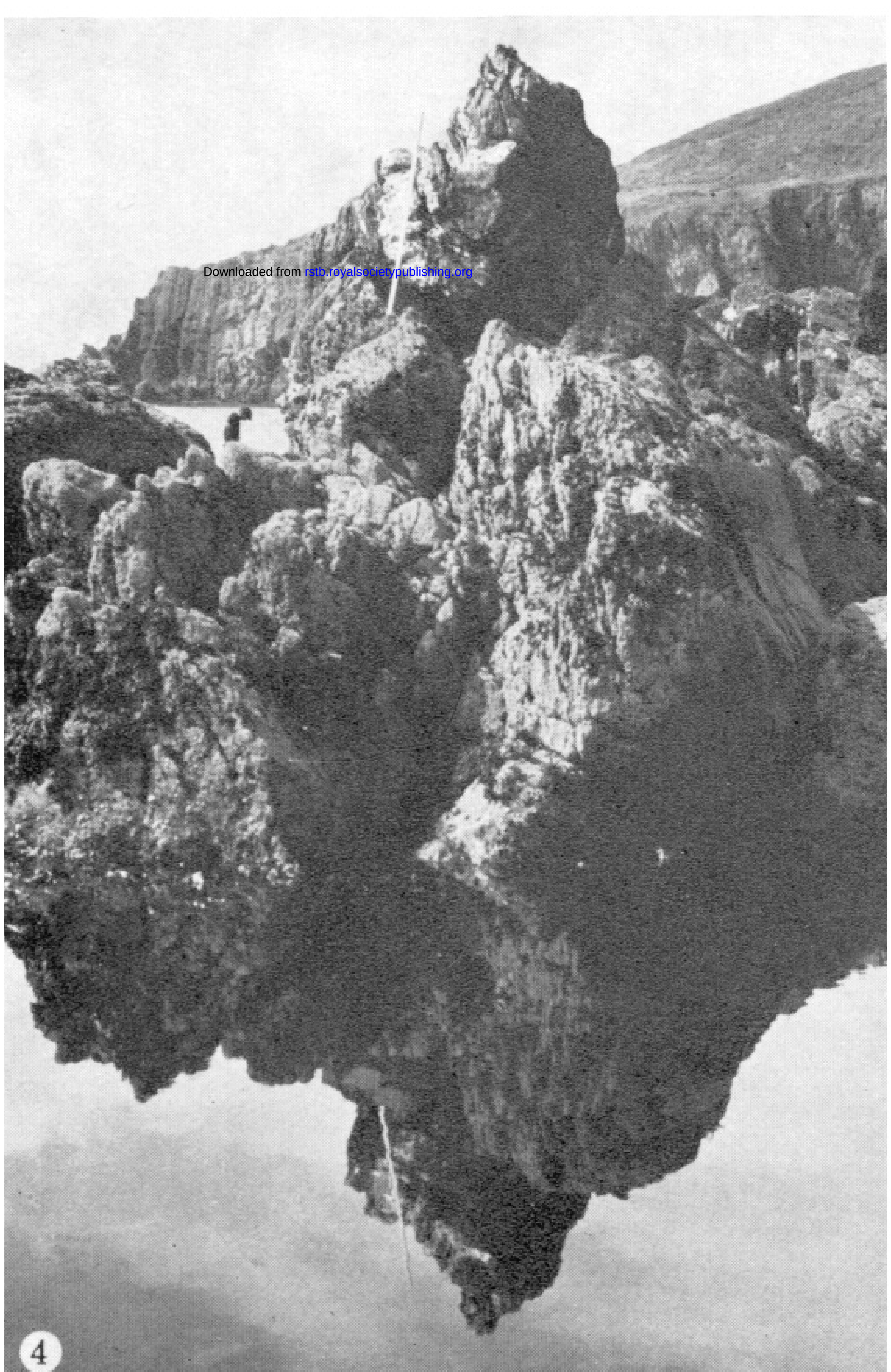

FIGURES 3–5. For description see opposite.