MARINE BIOLOGY OF MILFORD HAVEN: THE DISTRIBUTION OF LITTORAL PLANTS AND ANIMALS

By A. NELSON-SMITH

Department of Zoology, University College of Swansea

Milford Haven is a deep and rocky estuary which is likely to become heavily industrialized in the near future. As part of an ecological study of the entire estuary, shore surveys already carried out around the mouth were extended to the limits of tidal influence in the rivers Cleddau. Distribution maps are given for all the common sessile plants and animals of rocky or stony shores and their vertical zonation has been determined on a selection of such shores throughout the estuary. The patterns of distribution revealed in this way point to three regions as being biologically critical. In each of these the salinity regime or the nature of shore deposits changes markedly within a short distance. Although some forms typical of exposed shores do not penetrate far into the Haven, many other marine species extend for a considerable distance upstream; the factors influencing the extent of their penetration and the significance of changes in their zonation are discussed.

INTRODUCTION

MILFORD HAVEN is situated at the south-western tip of Wales, its mouth forming part of a rocky coastline (Fig. 1) in a region where the ranges of predominantly southern and Arctic forms overlap. Its marine flora and fauna are therefore amongst the most varied in the British Isles. Because of the deep and rocky nature of the inlet, this variety extends far up the Haven and the common estuary of the rivers Cleddau which opens into it. The lower Haven has long been used by fishing vessels, coastal freighters and small naval craft with little effect on its shores, but within the last ten years it has become established as Britain's largest oil port, with four terminals capable of accommodating tankers of over 100,000 tons. Three of these serve adjacent oil refineries and the other a refinery near Swansea by an overland pipeline. The construction of a large oil-fired electricity generating station at the mouth of the Pembroke River is now well advanced and further industrialization is likely to follow. The present study was started during the earliest of these developments and consists mainly of a careful survey of the distribution of common species of plants and animals inhabiting rocky shores throughout the estuary. An account of the physical environment, including comments on the incidence and possible effects of oil pollution, has already been published (Nelson-Smith, 1965) and brings together measurements made during the survey and other data from scattered or obscure sources.

Previous work on the marine biology of Milford Haven has been concerned mainly with the neighbourhood of Dale Fort Field Centre. Full bibliographies

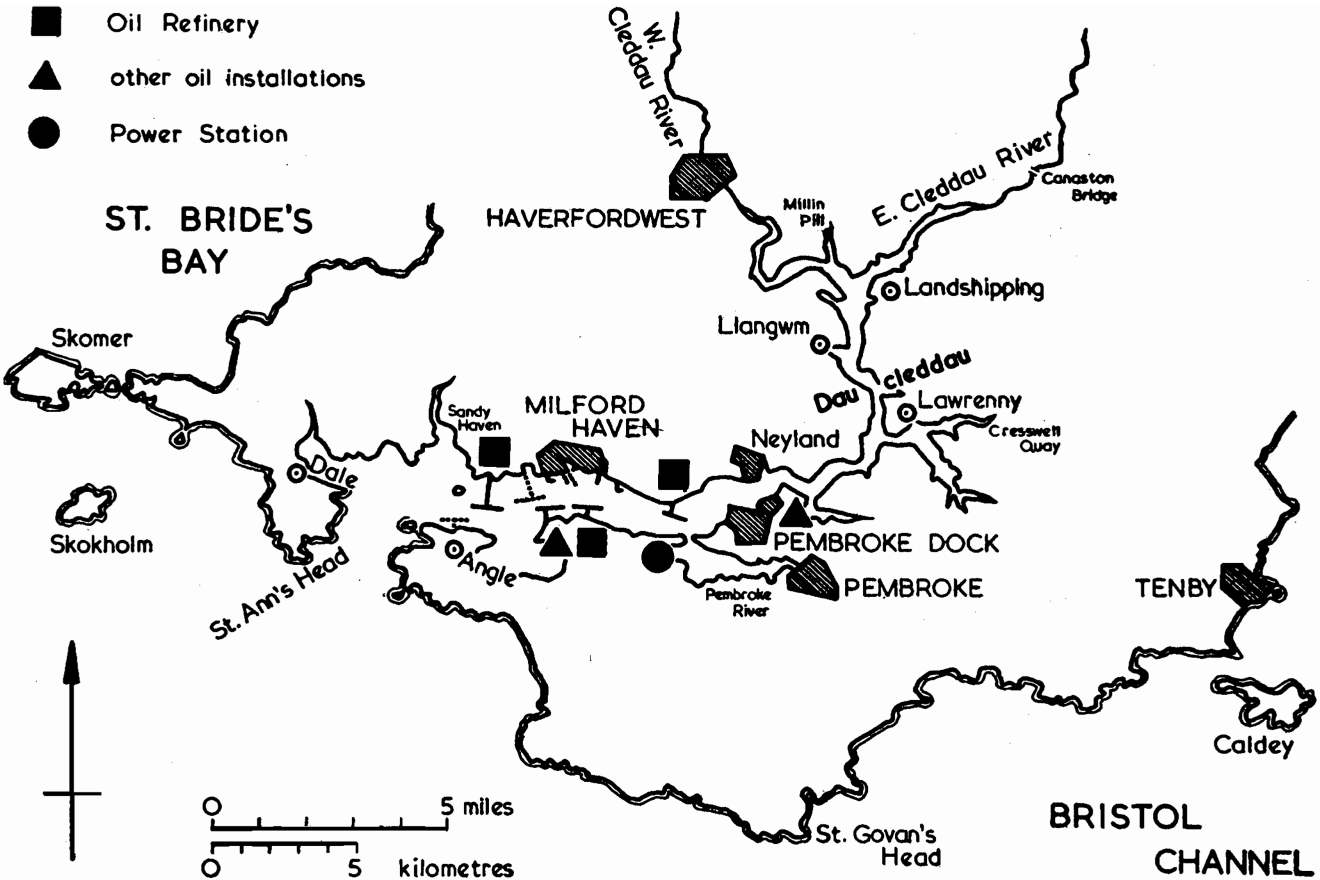

FIG. 1.
Outline map of South Pembrokeshire, showing recent industrial developments in Milford Haven. Broken lines indicate jetties proposed but not yet built.

are cited in Crothers, 1966 and Jones and Williams, 1966. This study extends that work into the estuary of Milford Haven. A careful survey was made of the abundance and zonation of the more common marine or maritime species on nineteen shores scattered throughout the rocky or stony part of the estuary (Fig. 2). The presence or absence of these species was also recorded at intermediate stations and in the tidal reaches of the rivers Cleddau to determine their horizontal distribution throughout the estuary. Finally, more detailed collections made at many of these shores and limited ones from elsewhere have added to the number and extent of records from the area (see Crothers, 1966).

METHODS

At each shore studied in detail a transect was laid down from low water of spring tides to the first few flowering plants at the top of the shore, divided into stations separated vertically by two feet (ca. 0·6 m) using a simple levelling method described by Moyse and Nelson-Smith (1963). In the absence of reliable corrections for other locations in the Haven, levels were based on predictions of the height and time of low water at Newton Noyes Pier, Milford Haven (Admiralty Tide Tables, 1961–63). The mean range of spring tides there is 20·8 ft. (6·3 m) and of neap tides 9·1 ft. (2·8 m). Observations made in the upper reaches during later surveys (Nelson-Smith, 1965) show that these ranges are greater by 2–3 ft at Landshipping Ferry, where the level of high tide lies 1–1·5 ft higher than at Milford Haven; tidal ranges diminish rapidly in the lower reaches of the rivers. The zonation diagrams have not been adjusted because the differences, even at the highest major station (Landshipping Woodhouse; see Fig. 2), are not great enough to distort the general picture of zonation changes.

The general density of each species was recorded over an area about ten feet (ca. 3 m) to each side of a station mark and one foot vertically above and below it. As around Dale the inhabitants of pools, gullies and crevices were ignored in recording vertical zonation except for the few species (such as *Littorina neritoides*) normally found only in crevices. Such occurrences were, however, noted for use in compiling distribution maps. Densities were assessed as abundant, common, frequent, occasional or rare according to criteria appropriate for each species or group of species, following Crisp and Southward (1958), Ballantine (1961) and Moyse and Nelson-Smith (1963). The criterion for "rare" was in every case the discovery of very few specimens in 30 minutes' searching; it was clearly impossible to spend this length of time at any one station, so this grade was used infrequently and rather more subjectively. In preparing distribution maps occurrences at this grade, or known to be very local, were usually ignored.

Moyse and Nelson-Smith applied the biological exposure scale of Ballantine (1961), listing 27 species used in determining the degree of wave exposure of the shores which they surveyed around Dale. This list, showing the degree of abundance of those species typical of each exposure grade to be found in the region, was also used in the present study. The exposure grade of a shore was derived from the maximum density (or the absence) of each indicator species there. It was possible to assign such grades to shores as far up the Haven as Hazelbeach Point (see Table 1) but beyond that station the decreasing number

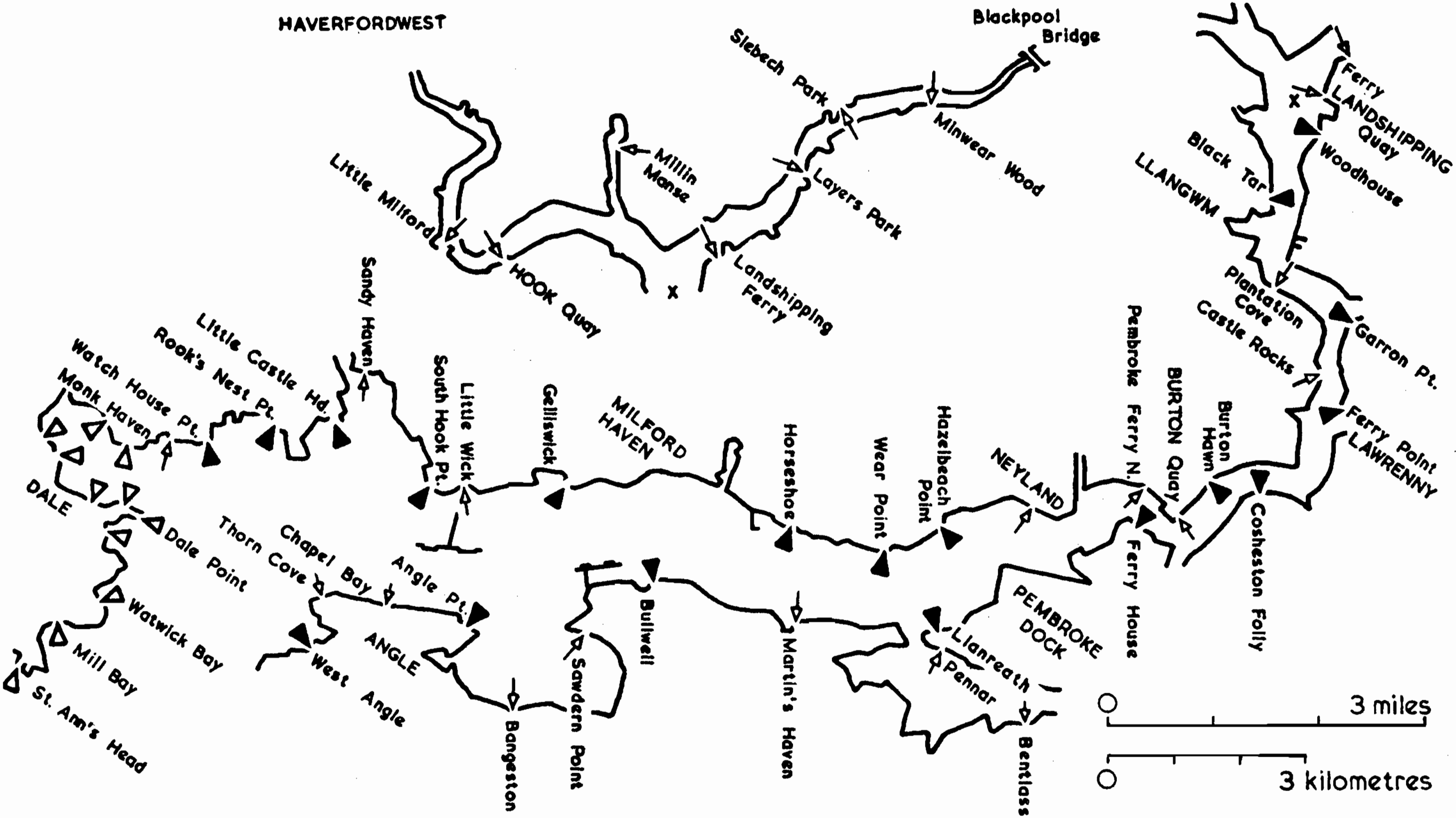

Fig. 2.

The location of biological survey stations in Milford Haven. The rivers north of the mark "X" are shown inset above, to the same scale. Detailed surveys were made at shores marked with solid arrowheads; open arrowheads indicate the sites of similar surveys carried out around Dale by Moyse and Nelson-Smith (1963) and small arrows point to the main subsidiary stations visited. Industrial waterfronts at Milford Haven, Neyland and Pembroke Dock were excluded from the survey.

Table 1. *Shores upon which vertical zonations have been surveyed*

Shore	Abbreviation	Exposure	Aspect	Date Surveyed
St. Ann's Head	StA	2	SW	June 1961
Dale Point	DPt	3	SE	June 1961
South Hook Point	SHk	3	WSW	September 1962
Watch House Point	WHo	3	S	July 1961
Rook's Nest Point	RkN	3	WSW	July 1961
Little Castle Head	LCs	4	S	July 1961
West Angle Bay	WAB	5	WNW	September 1961
Gelliswick Bay	Gwk	6	SW	August 1962
Angle Point	APt	6	NE	September 1961
Bullwell	Bwl	6	N	October 1962
Horseshoe	Hsh	6	SSW	October 1963
Wear Point	WPt	6	SSE	September 1962
Hazelbeach Point	Hzb	6	SSE	October 1962
Llanreath	Lth	—	NNW	May 1963
Pembroke Ferry (Ferry House) ..	PbF	—	NE	October 1962
Burton Hawn	BHn	—	SE	September 1962
Cosheston Folly	Csh	—	N	May 1963
Lawrenny (Ferry Point)	Lny	—	W	August 1962
Garron Point	GPt	—	WNW	September 1962
Llangwm (Black Tar)	Lgm	—	E	September 1962
Landshipping (Woodhouse) ..	Lsh	—	WNW	September 1962

St. Ann's Head and Dale Point were surveyed by Moyse and Nelson-Smith (1963). Abbreviations given as those used in Tables 2 and 3 and zonation diagrams. Biological exposure grades have been allocated where the method is applicable (see p. 437). The aspect shown is of that part of the shore across which the transect was laid. The positions of these transects are indicated in Fig. 2.

of indicators present made it impossible to derive exposure grades by this method. The physical nature of these shores has been described earlier (Nelson-Smith, 1965). Inspection of those above Pembroke Dockyard makes it clear that all are very sheltered (equivalent to grade 7) and some ought probably to be considered as extremely sheltered (grade 8). The order of disappearance of indicator and other species up the estuary is discussed below.

In the zonation diagrams and in Tables 2 and 3, shores around the mouth and up to Gelliswick Bay are arranged in order of their exposure. The remainder have been placed according to their distance up the estuary. Data for St. Ann's Head and Dale Point are included for completeness and were obtained during the survey of the Dale peninsula. It will be seen from Table 1 that most shores were surveyed in the early autumn. Few of the observed differences between shores will thus be purely seasonal; many stations were in any case re-visited at other times of year. Shores near the heated-water outfall of the Pembroke Power Station have been surveyed at regular intervals in recent years so that possible future effects of its effluent may be distinguished from normal seasonal changes. Such changes are rarely very significant amongst the sessile animals and larger algae of rocky shores (see Jones and Williams, 1966). The effects of an abnormally cold winter have been recorded by Moyse and Nelson-Smith (1964).

Fig. 22 gives mean histograms calculated from the survey data for those species whose zonation varies little throughout their range in the estuary.

Table 2. *The distribution of flowering plants along the shores of Milford Haven*

	StA	DPt	SHk	WHo	RkN	LCs	WAB	Gwk	APt	Bwl	Hsh	WPt	Hzb	Lth	PbF	BHn	Csh	Lny	GPt	Lgm	Lsh
Spergularia rupicola ..	61	45	—	47	45	39	33	31	25	—	—	—	—	—	—	—	—	—	—	—	—
Crithmum maritimum ..	61	43	31	45	53	39	—	29	—	—	—	27	29	—	—	—	—	—	—	—	—
Plantago maritima ..	—	47	31	—	45	39	31	27	—	27	31	27	—	25	—	—	—	—	—	—	—
Beta maritima	—	—	—	55	—	—	—	31	—	—	—	27	29	25	—	27	—	—	—	—	—
Festuca rubra	—	45	—	—	45	—	33	27	27	27	31	29	25	25	25	25	27	29	25	27	27
Armeria maritima ..	61	43	31	45	39	37	29	27	25	25	31	27	25	—	23	23	27	29	25	25	27
Limonium humile ..	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	27	—	—	29	29	27
Halimione portulacoides	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	29	29	27
Spartina townsendii ..	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	27	27

The names of shores are abbreviated as in Table 1. Heights shown here are the lowest plants found, in feet above Chart Datum. MHWS lies at 23 ft above CD. The level of the highest station surveyed at each shore is shown in Table 3. A dash (—) indicates absence from the transect.

Table 3. *The distribution of Supralittoral Lichens along the shores of Milford Haven*

	limit	StA	DPt	SHk	WHo	RkN	LCs	WAB	Gwk	APt	Bwl	Hsh	WPt	Hzb	Lth	PbF	BHn	Csh	Lny	GPt	Lgm	Lsh
Highest station surveyed		69	47	37	47	45	39	37	31	27	29	27	33	31	27	27	27	27	29	29	29	27
Pseudophyscia fusca	L	N	45	N	O	O	35	O	N	27	N	N	31	29	N	N	25	N	N	N	N	N
Ramalina spp. ..	U	∧	∧	∧	∧	∧	∧	31	27	25	∧	∧	29	N	∧	∧	∧	25	N	∧	N	N
	L	69	43	35	39	35	31	29	23	25	25	27	27		27	25	25	23		29		
Xanthoria parietina	U	∧	∧	∧	∧	∧	∧	31	29	∧	∧	∧	31	∧	∧	∧	∧	25	∧	∧	25	25
	L	53	41	33	37	35	29	27	23	23	23	25	25	25	27	23	23	23	27	25	23	23
Caloplaca marina ..	U	*	45	35	43	41	33	N	23	N	N	∧	27	25	N	N	23	25	∧	N	25	N
	L		33	33	35	33	27		21			25	23	25			23	23	27		25	
Grey Lichens	U	61	∧	∧	∧	∧	∧	31	29	∧	∧	∧	31	∧	∧	∧	∧	∧	∧	∧	27	∧
	L	55	37	33	36	33	27	27	21	23	23	25	25	25	27	23	23	23	27	25	23	23
"Verrucaria maura"	U	∧	∧	∧	∧	∧	∧	31	27	∧	∧	N	29	∧	O	∧	∧	25	∧	∧	25	∧
	L	19	17	17	9	11	13	17	11	17	19		17	17		21	17	15	23	23	21	21

The names of shores are abbreviated as in Table 1. Heights are shown of the highest station surveyed and the upper (U) and lower (L) limits of species present at each shore studied, in feet above Chart Datum. MHWS lies at 23 ft above CD. ∧ indicates that the upper limit lay above the highest station surveyed. N, absent from transect; O, not recorded; * included with *Xanthoria* here.

Except where otherwise indicated, species are named as in the Plymouth Marine Fauna (Marine Biological Association, 1957) and were identified from the authorities listed there.

THE DISTRIBUTION OF LITTORAL ANIMALS AND PLANTS

FLOWERING PLANTS (Angiospermae)

On the more exposed shores around the mouth of Milford Haven, the supralittoral flowering plants are scattered in a wide zone, merging with the rough grassland or scrub of the cliff-tops in which they are often still abundant. Only the lowest plants were recorded; their distribution and the heights at which they were found are given in Table 2. They were identified from Clapham, Tutin and Warburg (1952). In addition to these, *Cochlearia officinalis* and *Matricaria maritima* were recorded at a low level at Rook's Nest Point and occurred higher than the transect on other shores around the mouth; *Matricaria* was also recorded from Lawrenny. The maritime fern *Asplenium marinum* was recorded at Gelliswick and was seen elsewhere in shaded crevices, whilst the sea campion *Silene maritima* was found a few feet above high water at Wear Point and is widespread at higher levels.

On the sheltered shores of the upper reaches the general level of terrestrial vegetation is low, with scrub or woodland extending down to five or six feet above high water; stranded seaweeds may often be observed caught in overhanging tree-branches. In the tributary pills and above Landshipping there is a patchily-developed marginal saltmarsh. *Spartina townsendii* is the most obvious fringe plant at the head of the estuary, giving way to *Phragmites communis* below Haverfordwest and on the Eastern Cleddau between Slebech Park and Minwear Wood, where the water is nearly fresh at all states of tide.

LICHENS (Lichenes) (Figs. 3–5)

The shores around the mouth of Milford Haven bear a rich flora of supralittoral lichens (see Wade, 1960) but only the lowest and most characteristic were included in this survey. These were identified from Duncan (1959) and their distribution is indicated in Table 3.

Pseudophyscia fusca was seen above the highest surveyed station on several shores where it is shown as absent from the transect, but does not extend above Burton Hawn. *Ramalina* spp. consisted mainly of *R. scopulorum*. The grey encrusting lichens were not separated into species, although *Lecanora atra* was seen to be a constant and conspicuous member. *Verrucaria* was divided as for the Dale peninsula into a black, mainly supralittoral "*Verrucaria maura*" group and greenish littoral forms recorded as "*Verrucaria mucosa*".

The table demonstrates the narrower zones and lower levels at which the supralittoral lichens were found on the more sheltered shores; this is also seen for *Lichina confinis* in Fig. 24. With one exception, *Caloplaca marina* (*Placodium lobulatum*) was recorded only from open, sunlit shores as around Anglesey (Lewis, 1953). *Lichina confinis* extends much further into shelter than in the Tenby areas, where Evans (1949) found it rather more demanding of surf than *L. pygmaea*. Lewis (1953, 1964) suggested that, in shelter, occasional immersion may compensate for lack of spray. His conclusion that *L. confinis* prefers a sunny aspect is in general borne out in Milford Haven. *Lichina pygmaea* is

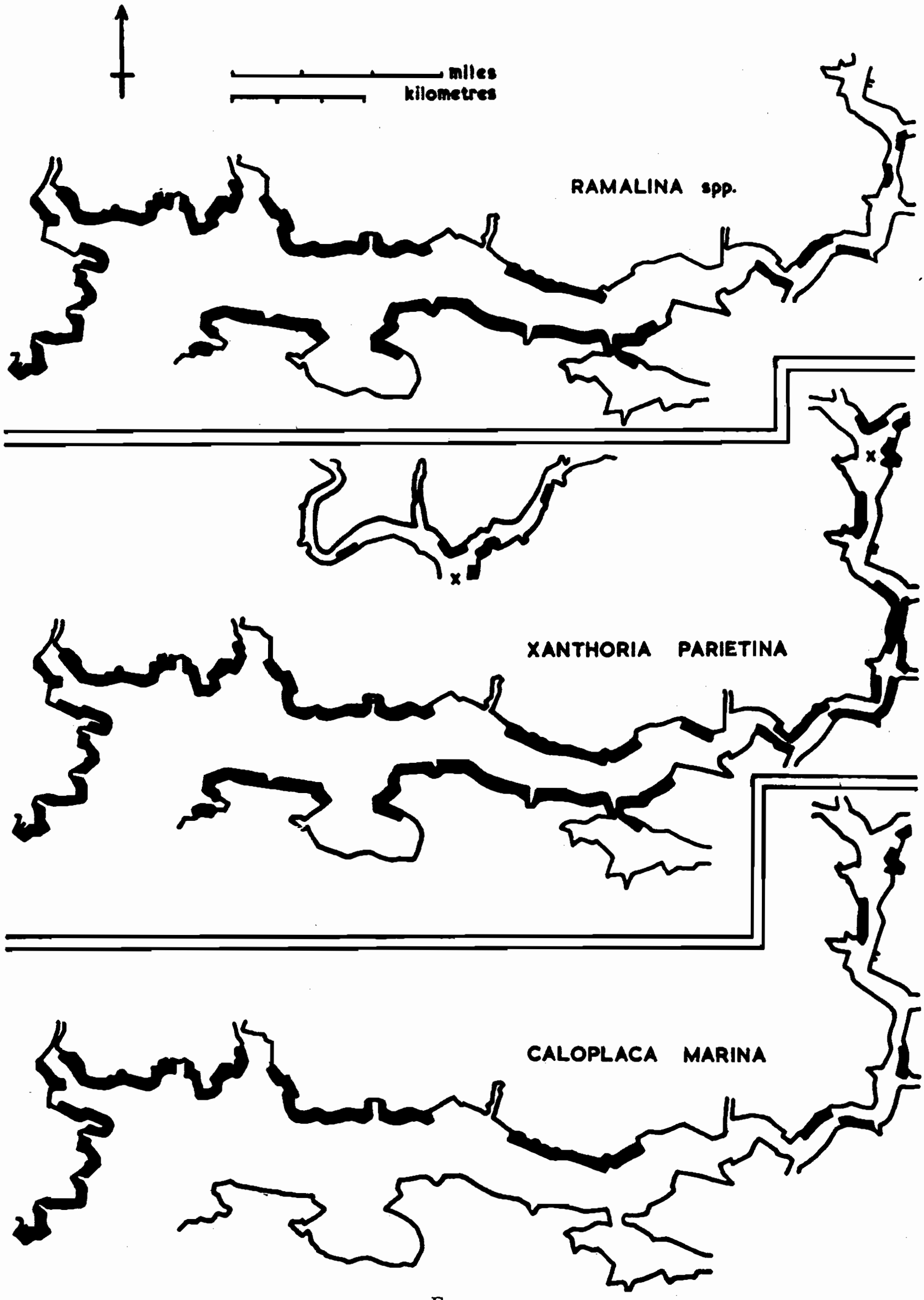

FIG. 3.
The distribution of some supralittoral lichens. *Xanthoria* also occurs on inland structures.

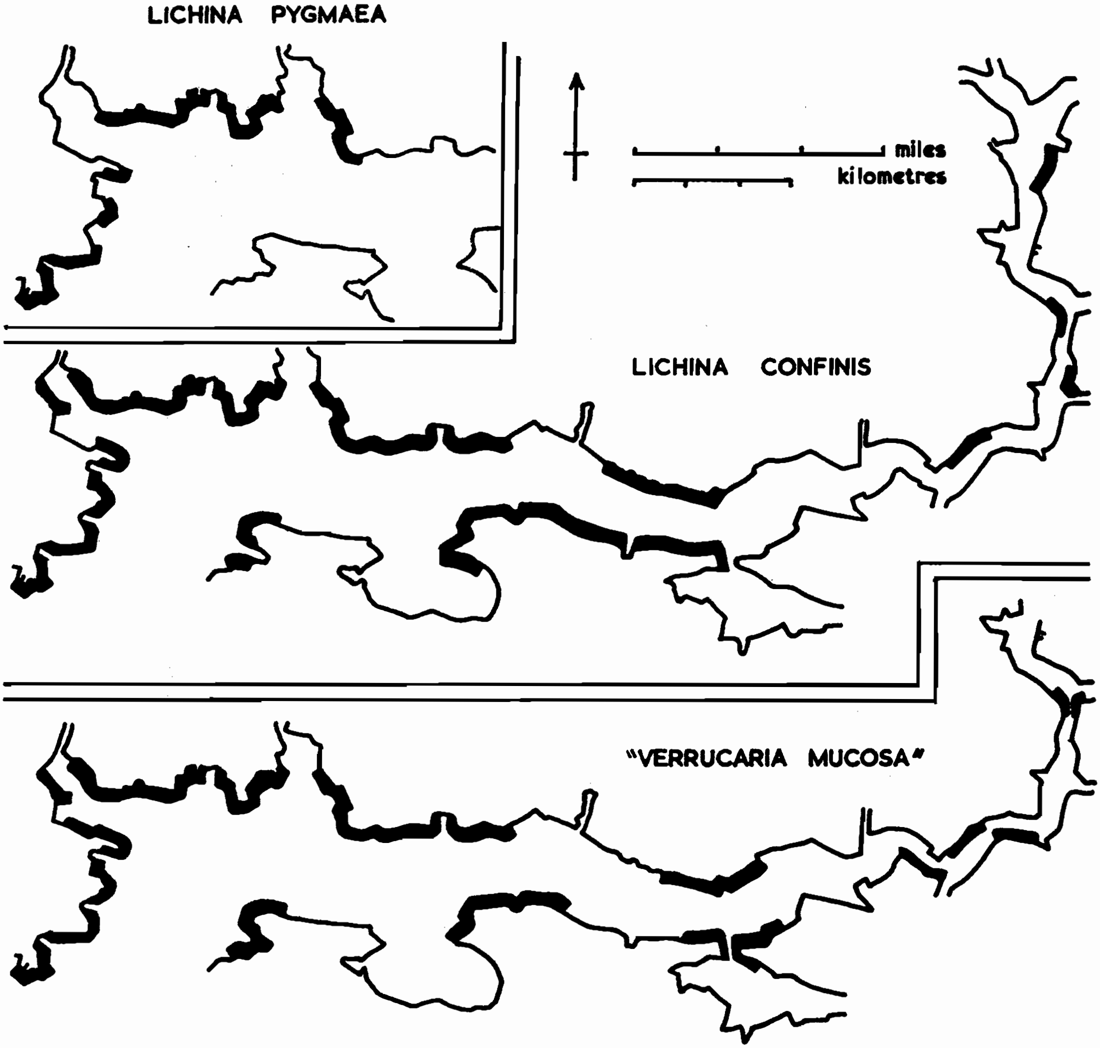

FIG. 4.
The distribution of some marine lichens. *Lichina pygmaea* was seen only on exposed shores around the mouth of the Haven.

restricted to exposed headlands in the mouth of the Haven, where it occupies steep sunlit rock-faces at about MHWN; it sometimes extends down to MLWN, whereas the red alga *Catenella repens* which it superficially resembles was found below MHWN only occasionally and thrives best in shady, sheltered regions.

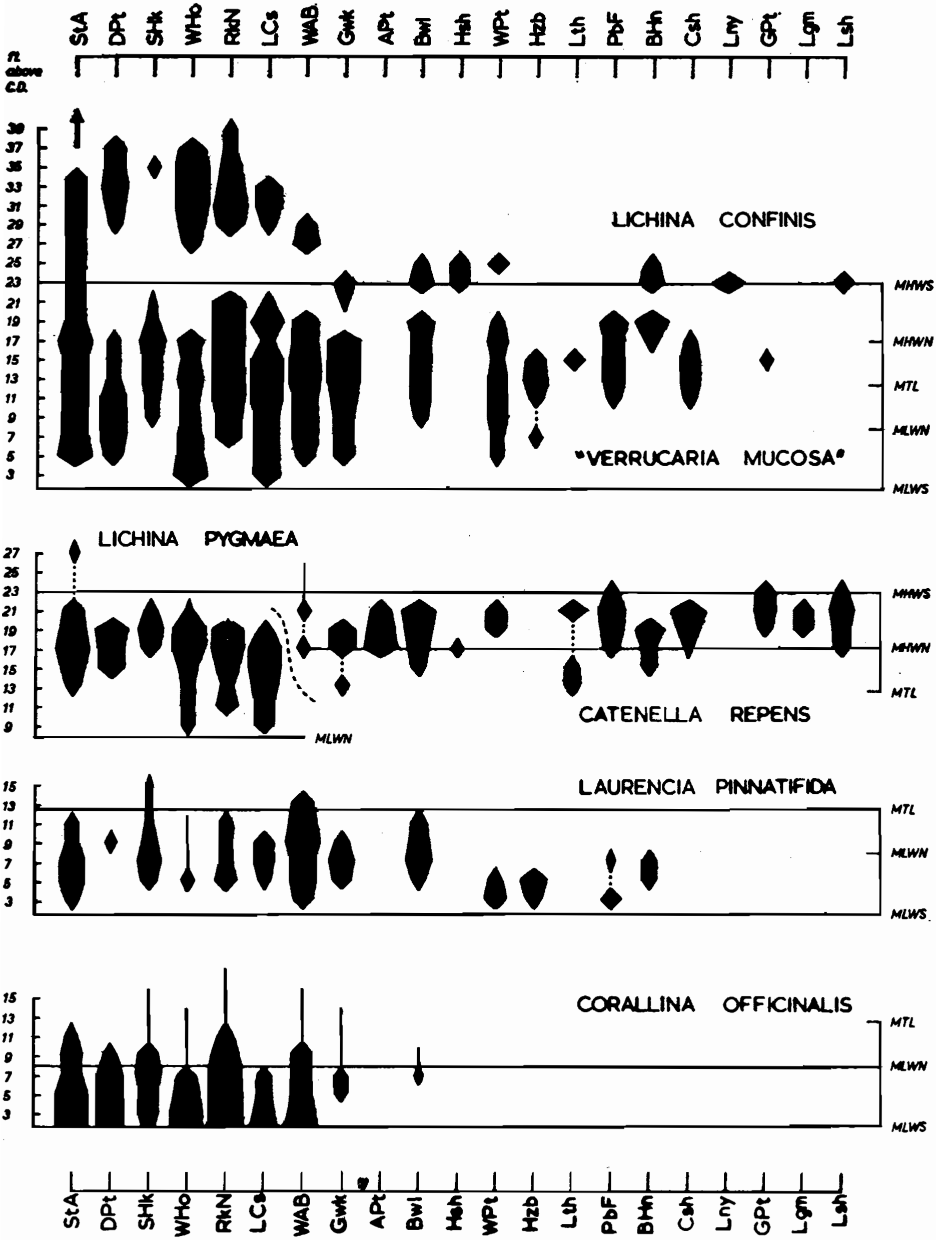

Fig. 5.

The zonation of some lichens (above) and red algae (below). The shores are arranged according to their degree of exposure in the mouth, then in order up the estuary; abbreviations are as in Table 1. St. Ann's Head and Dale Point were surveyed by Moyse and Nelson-Smith (1963). The scale to which the histograms have been drawn is given in Fig. 15. *Lichina confinis* occurs on St. Ann's Head only at levels over 39 ft. above CD; *L. pygmaea* tends to replace *Catenella* on exposed rock surfaces and coincides with it in that habitat only at Rook's Nest Point.

BROWN ALGAE (Phaeophyceae) (Figs. 6–10)

These and other algae were identified from Newton (1931) and Dickinson (1963) and are named in accordance with Parke and Dixon (1964). *Pelvetia canaliculata* is the most widespread of the algae included in this survey, occupying a narrow zone consistently a little below MHWS. The upper limit of this zone is depressed at Lawrenny because of a short stretch of sandy shingle there; *Pelvetia* extends to 23 ft above CD on the nearby Castle Rocks.

Fucus spiralis extends into Millin Pill and a little further up the Eastern Cleddau than *Pelvetia*, but is present only on more sheltered shores at the seaward end of the Haven. At Rook's Nest Point it forms hybrids with *F. vesiculosus evesiculosus* where their zones overlap, whilst towards its upstream limit *F. spiralis* meets *F. vesiculosus* in the middle shore; occasional atypical plants in this region may be hybrids between these two or of either with *F. ceranoides*.

Ascophyllum nodosum penetrates the estuary as far as *Pelvetia*, but is slightly less tolerant of exposure than *Fucus spiralis*. Its distribution is far more local than either since it grows only on bedrock or firmly embedded boulders. Lewis (1953) found that ridges projecting into the current of the Menai Strait were bare of *Ascophyllum* even when it was abundant elsewhere on the shore; this is the situation at Cosheston Folly, where the smooth steep bedrock lacks *Ascophyllum* and is swept by strong currents on a narrow bend. *Fucus vesiculosus* and *F. serratus* are also scarce on this shore; their spread is perhaps restricted by the grazing of the abundant winkles as well as by the unfavourable physical environment. *Ascophyllum* is known to have been present on the Castle Beach transect until quite recently; its absence at the time of the survey may well be the result of an episode of oil pollution in 1960 or its subsequent cleansing with emulsifying chemicals, referred to by George (1961 and unpublished observations).

Fucus vesiculosus in its normal vesiculate form has a distribution around the mouth of the Haven closely resembling that of *F. spiralis*, ranging further into exposure than *Ascophyllum* (see Moyse and Nelson-Smith, 1963). It penetrates the furthest upstream of the marine algae studied; at Minwear Wood and in Millin Pill it mingles with *Fucus ceranoides*, probably forming hybrids. The brackish-water *F. ceranoides* has also been seen in the mouth of tributary streams at Layer's Park, Llangwm and Martin's Haven as well as in the Cresswell River at Cresswell Quay. It has been recorded on the Gann Flat, by Thomas (1953) and Jones and Williams (1966). A bladderless form of *Fucus vesiculosus*, f. *evesiculosus* Cotton (*linearis* Powell) was found at slightly above MLWN on the exposed headlands at the mouth of Milford Haven. It occurs in patches which are always well separated from the nearest normal plants occupying situations of great shelter and rarely shares the middle shore with any other large algae, although it adjoins the *F. spiralis* zone at Rook's Nest Point.

Fucus serratus penetrates as far as Landshipping and was found on all but the most exposed shores to seaward. Its upper limit is raised to around mid-tide level at its most upstream stations, where luxuriant growths of *Ascophyllum* perhaps offer protection from desiccation; around Dale it was found to extend higher up the shore in shade.

Himanthalia elongata was recorded from few shores within the Haven; around

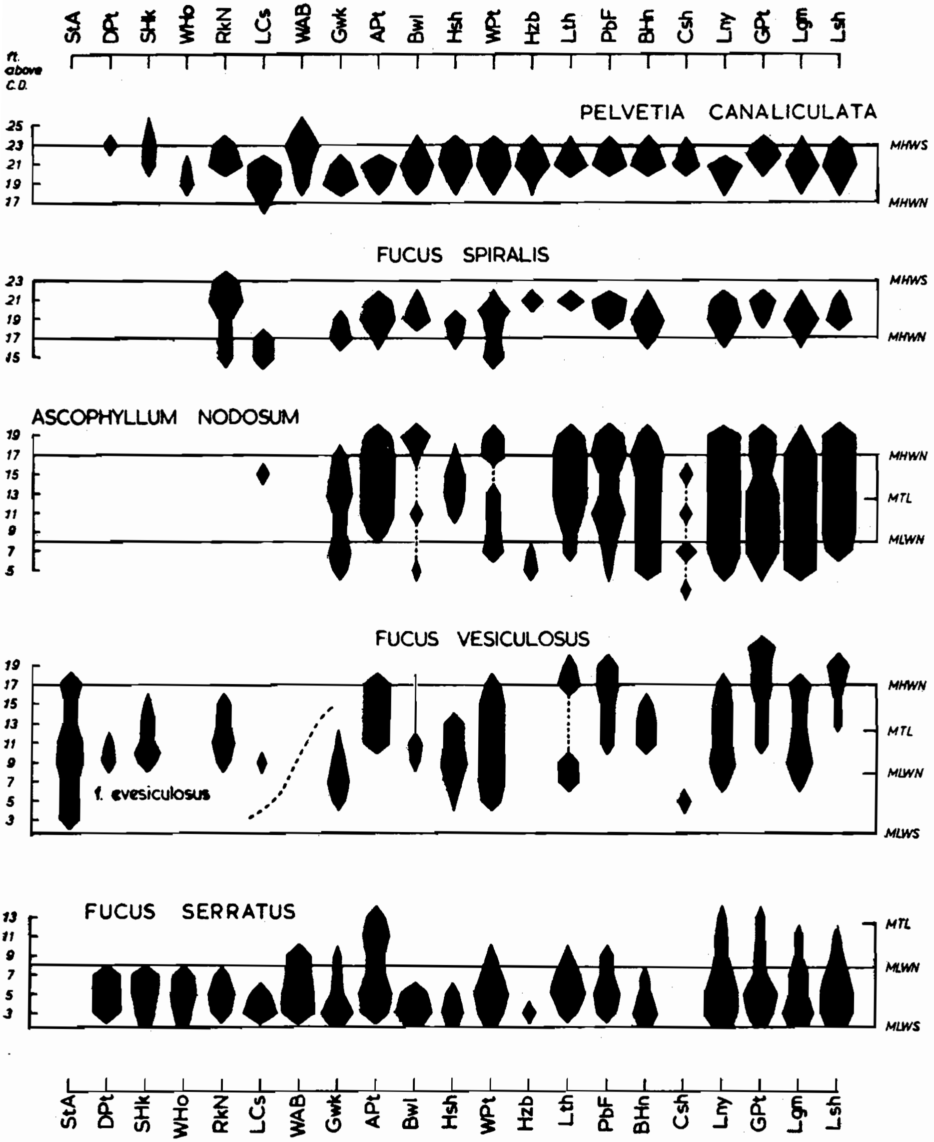

FIG. 6.

The zonation of some brown algae, shown as in Fig. 5. *Fucus vesiculosus* occurs on exposed shores around the mouth only in the bladderless form *evesiculosus*.

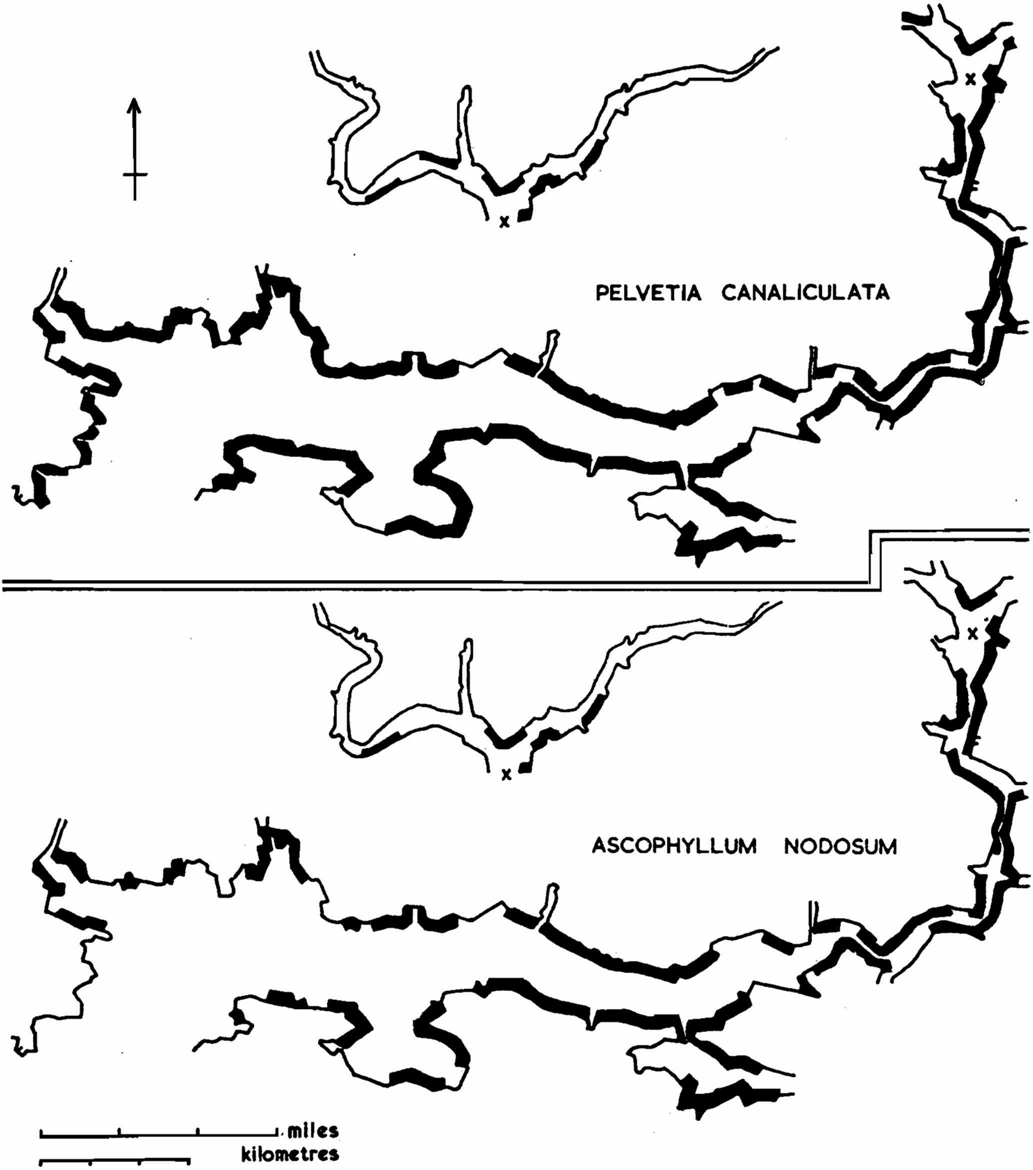

Fig. 7.
The distribution of *Pelvetia* and *Ascophyllum*.

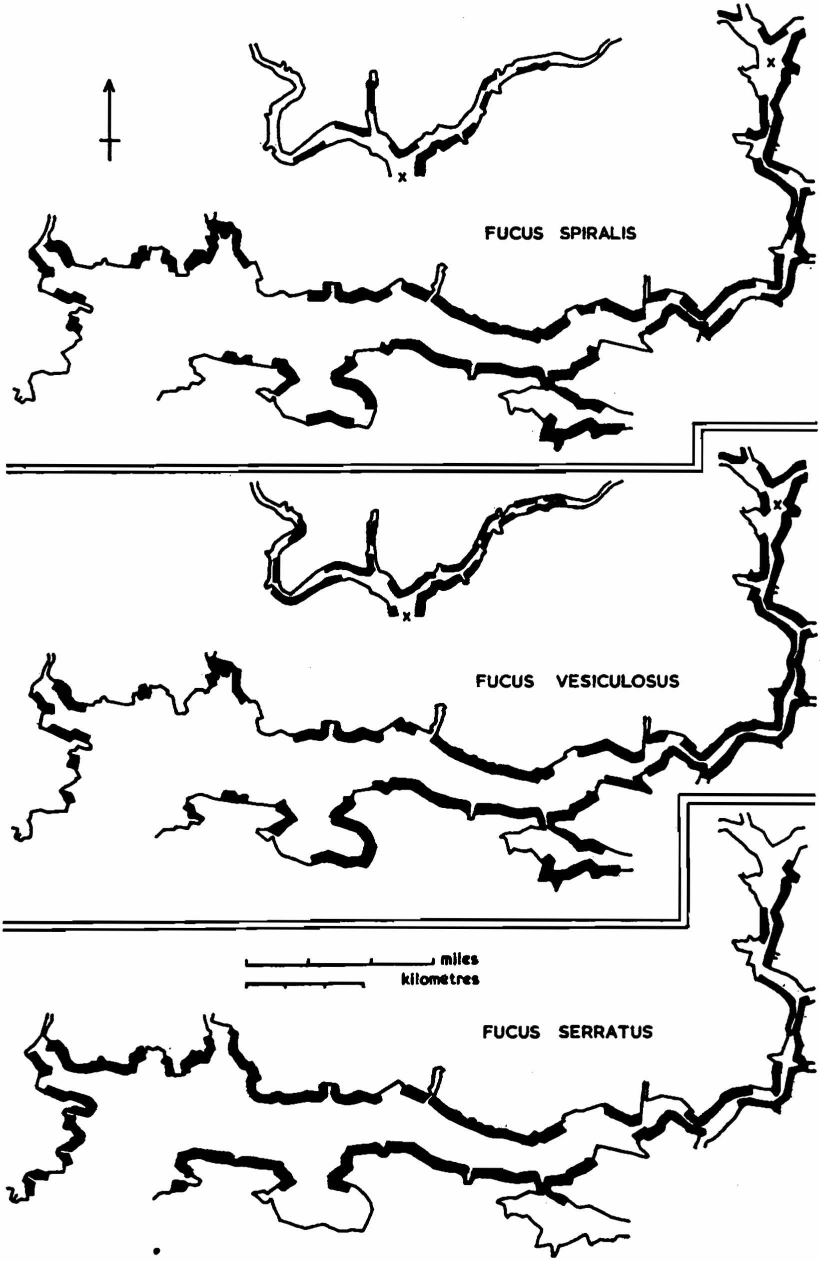

FIG. 8.
The distribution of species of *Fucus*. The bladderless, exposed-shore form *F. vesiculosus evesiculosus* is included in Fig. 9.

the Dale peninsula it is restricted to headlands on the west coast. Evans (1949), finding *Himanthalia* to be totally absent from the Tenby area, recalled that it prefers open headlands bordering deep water although Lewis (1964) has since recorded it from shallow and even brackish water where there is a strong current. Williams (1959; Jones and Williams, 1966) included Castle Beach amongst his localities for *Himanthalia* but like *Ascophyllum* it was not seen in later surveys, perhaps because of oil pollution.

Laminaria digitata was found on more shores in Milford Haven than other algae of the sublittoral fringe, perhaps because it occupies a relatively high zone (Fig. 22). *Laminaria saccharina* penetrates just as far up the estuary but around the mouth is present only on sheltered shores. Although around Dale *L. saccharina* extends further into shelter than *L. digitata*, it is less abundant and not so widespread in the upper reaches. Jorde and Klavestad (1963) recorded a similar distribution in the Hardangerfjord, where the inner portions are brackish and turbid in the early summer as they are in Milford Haven throughout the year. Presumably *L. saccharina* is more sensitive to these conditions; perhaps also *L. digitata* competes with it successfully on stones smaller than those it would be able to occupy in greater exposure.

Laminaria hyperborea and *Saccorhiza polyschides* occur between tidemarks on just a few shores around the mouth, although they are probably little more widespread sublittorally within the Haven. *Alaria esculenta* extends much less into the sublittoral (Kain, 1960; Lewis, 1953) and is found only on the most exposed shores. It completely replaces *Laminaria* at the south-western end of Skomer (Moyse and Nelson-Smith, 1963) and Grassholm (seven miles further offshore).

GREEN ALGAE (Chlorophyceae) (Fig. 22)

Enteromorpha, *Ulva* and other large green algae were recorded under this single category and were found throughout the Haven. They are commonest on the lower shore, where they are represented mainly by *Ulva*; on the more exposed shores this is often restricted to the shells of the larger limpets, perhaps as a result of their intensive grazing (see Jones and Williams, 1966). Species of *Ulva* and *Enteromorpha* are abundant at all levels where fresh water drains across the shore and on the more shaded shores in the upper reaches a band of *Enteromorpha* is prominent in the *Pelvetia* zone.

RED ALGAE (Rhodophyceae) (Figs. 5, 11)

Porphyra umbilicalis within the shelter of Milford Haven never occurs at the high levels recorded at St. Ann's Head and other headlands on the open coast (Moyse and Nelson-Smith, 1963; Evans, 1947). Its level varies from shore to shore, perhaps because of seasonal changes in abundance but also reflecting differences in suitability of the substratum. *Porphyra* does well on flat stony beaches but was found on few of the north-facing muddy shores. Around the mouth it occurs in bands at about MLWN; in the middle reaches plants are more scattered and may occupy lower levels, but show no progressive reduction in level on passing up the estuary. The general trend is seen in Fig. 22. *Porphyra* was not found beyond Burton Hawn, although it extends further into the Exe

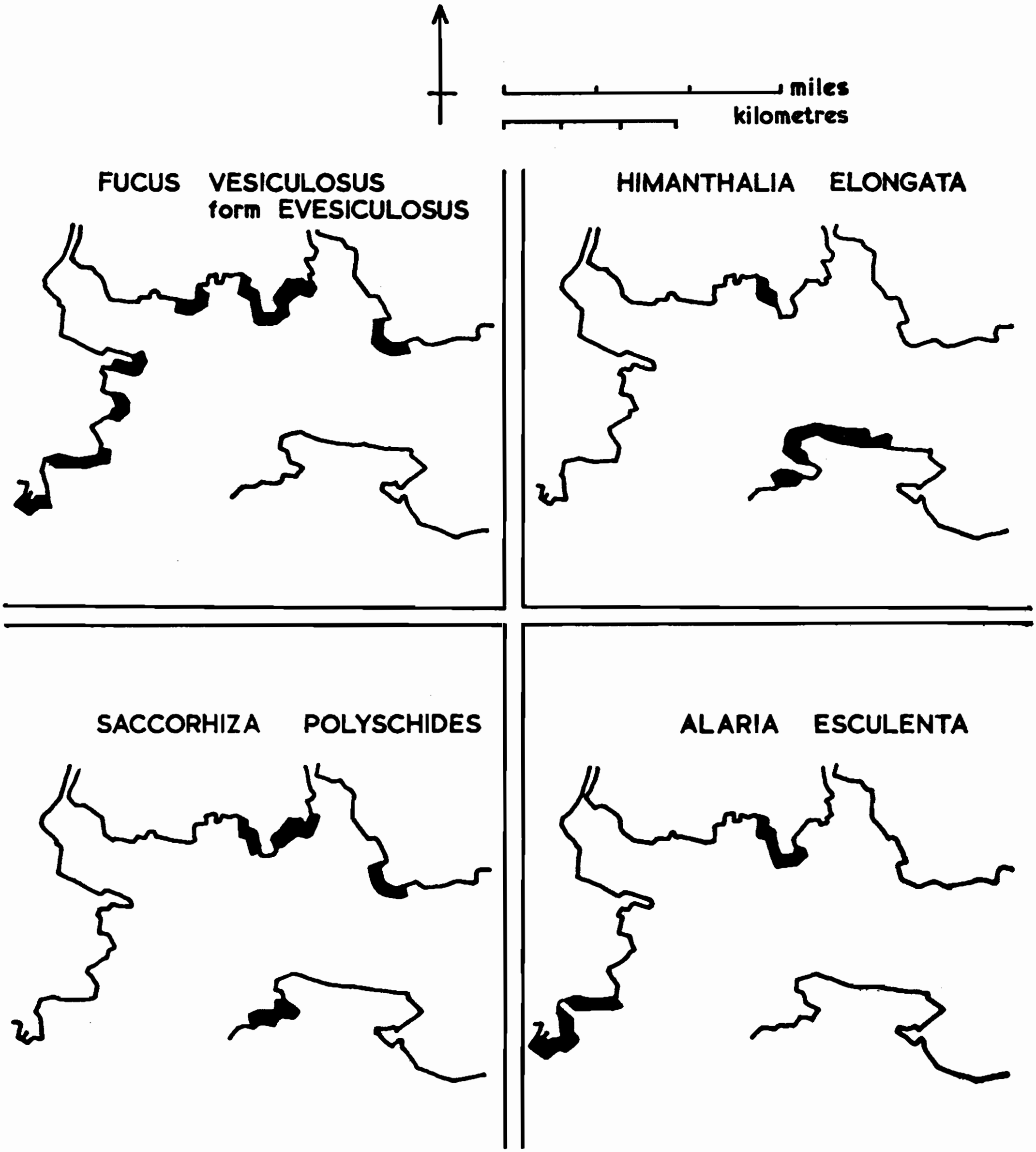

Fig. 9.
The distribution of those brown algae found only around the mouth of Milford Haven. *Laminaria hyperborea* is included in Fig. 10 and the vesiculate form of *Fucus vesiculosus* in Fig. 8.

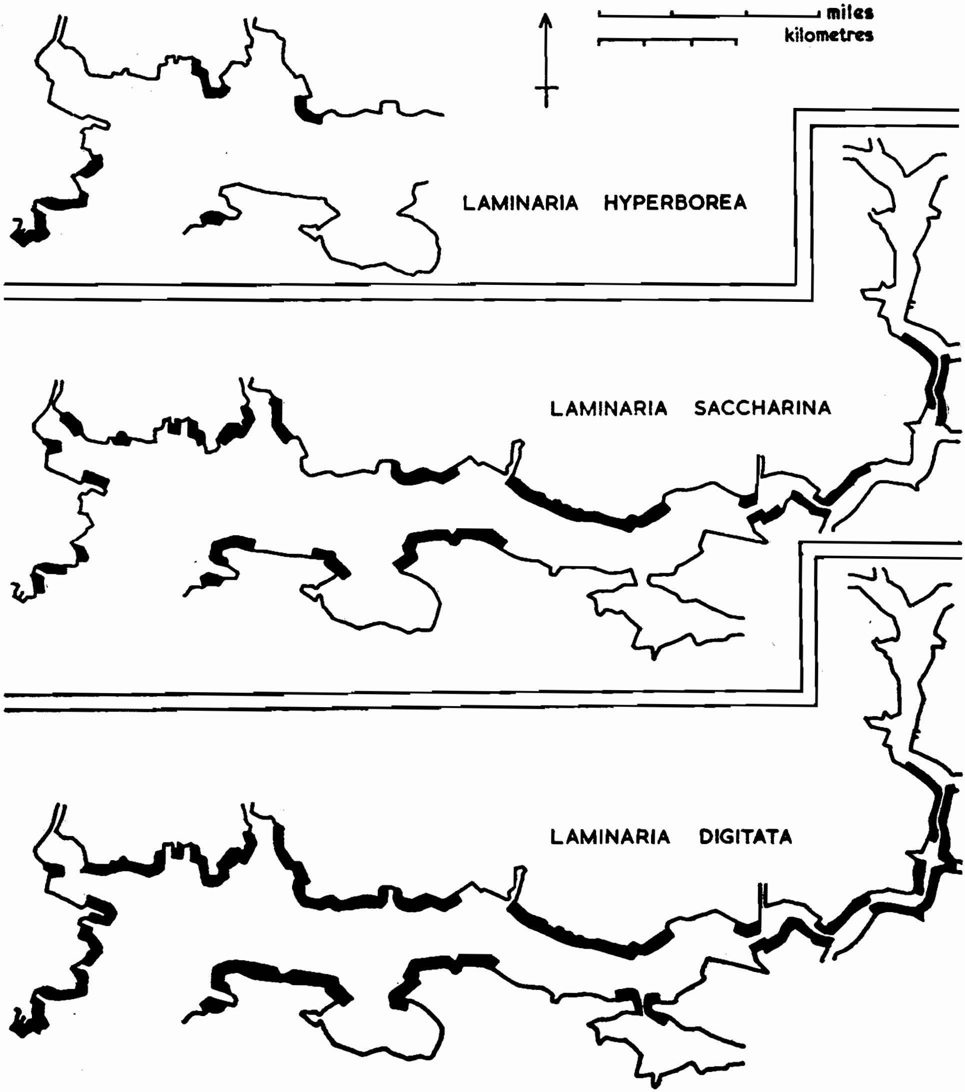

Fig. 10.
The distribution of species of *Laminaria*.

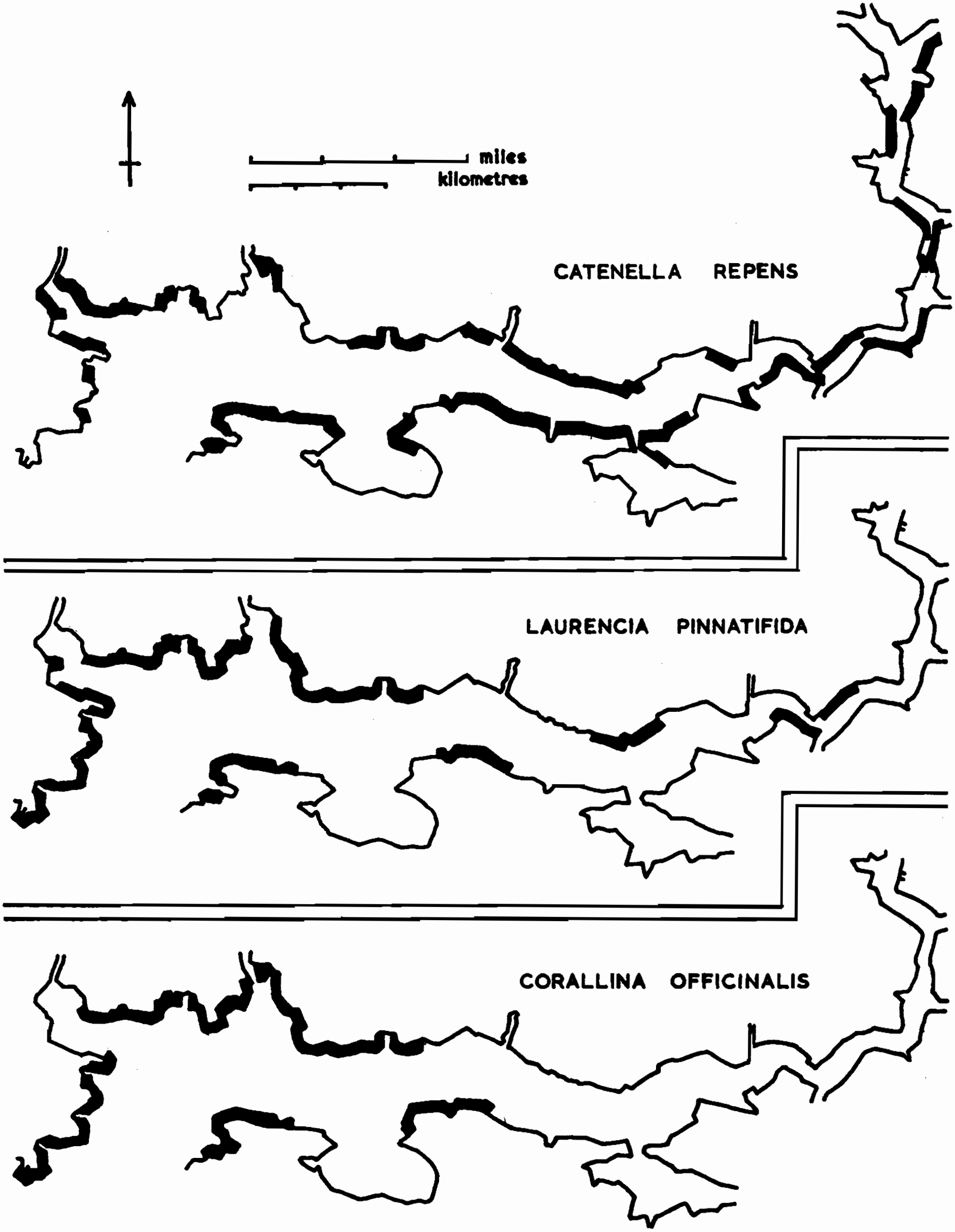

Fig. 11.
The distribution of some red algae. *Catenella* occurs around the mouth of the Haven only in sheltered situations and is replaced in exposure by *Lichina pygmaea* (see Figs. 4 and 5).

estuary than *Chondrus crispus* (Gillham, 1957) and grows best in brackish waters in the regions where it is cultivated (Chapman, 1950). *Chondrus* is widespread in the Haven and was recorded on rock ridges at Llangwm.

Catenella repens ranges far up the estuary; Gillham reported that it penetrates well into the Exe estuary together with *Rhodochorton purpureum* and although the latter alga was not included in the survey, it was observed with *Catenella* at Landshipping and has been recorded from Llangwm as *R. rothii* by Drew Baker (Burrows et al., 1957). In the mouth of the Haven, *Catenella* is favoured by shelter and shade and is thus distributed rather locally; on steep, exposed or south-facing shores it is replaced at much the same level by *Lichina pygmaea*, with which it occurs on the open rock surface at Rook's Nest Point.

Gigartina stellata grows abundantly on the shores of the lower and middle Haven, penetrating as far as Garron Point. On the sheltered shores of the upper reaches it is able to grow on quite small stones but seems to shun areas where there is heavy silting. *Rhodymenia palmata* was found as far upstream as *Gigartina*, but only on the steeper shores which are not bordered by mud or shingle banks at low water. Their zonation is shown in Fig. 22. *Laurencia pinnatifida* appears to grow well only in the lower reaches; beyond Bullwell its distribution is patchy and the upper limit of its zone is depressed.

Corallina officinalis is typical of lower levels on the exposed open coast; over the short distance to which it penetrates the middle Haven its lower limit is markedly elevated, probably by the presence of silt. All the encrusting Corallinaceae (Melobesiae) encountered were recorded under the term "lithothamnia" as for the Dale peninsula. They can spread up to MHWN in shelter where a good cover of Fucaceae prevents desiccation (Fig. 22) but they too are deterred by mud on the lower shore (Fig. 24).

BARNACLES (Cirripedia) (Figs. 12–14)

Elminius modestus has become the typical barnacle of sheltered bays and estuaries in the south of the British Isles and ranges far into Milford Haven. In the Severn Estuary (Bassindale, 1941; 1955) *Elminius* penetrates further than any barnacle except the brackish-water species *Balanus improvisus* and in the Tamar these reach the same upstream limit (Plymouth Marine Fauna, 1957). *B. improvisus* is mainly sublittoral and was not included in this survey although it was collected from Llangwm, Hook Quay and above Landshipping. *Elminius* occupies rock surfaces, stones and shells even in the immediate vicinity of soft, mobile mud and was recorded on the branches of a tree fallen across the shore at Llangwm. In the upper reaches it frequently settles on fronds of *Fucus vesiculosus* and *F. serratus*, less often on *Ascophyllum* and *Laminaria digitata*; it has been reported on *F. vesiculosus* in Finistère (Fischer-Piette and Forest, 1961) and in Galicia (Fischer-Piette and Seoane-Camba, 1962). *Elminius* also extends, rather patchily, a little into the sublittoral. Exceptionally cold weather in the early spring of 1963 (Moyse and Nelson-Smith, 1964) caused a heavy mortality, especially in the upper reaches, which was only partly compensated by a particularly good later spatfall.

Balanus balanoides occupies shores around the mouth in a wide zone. In the middle reaches its range and abundance are reduced in competition with the larger brown algae and above Cosheston Folly (where it spreads across the

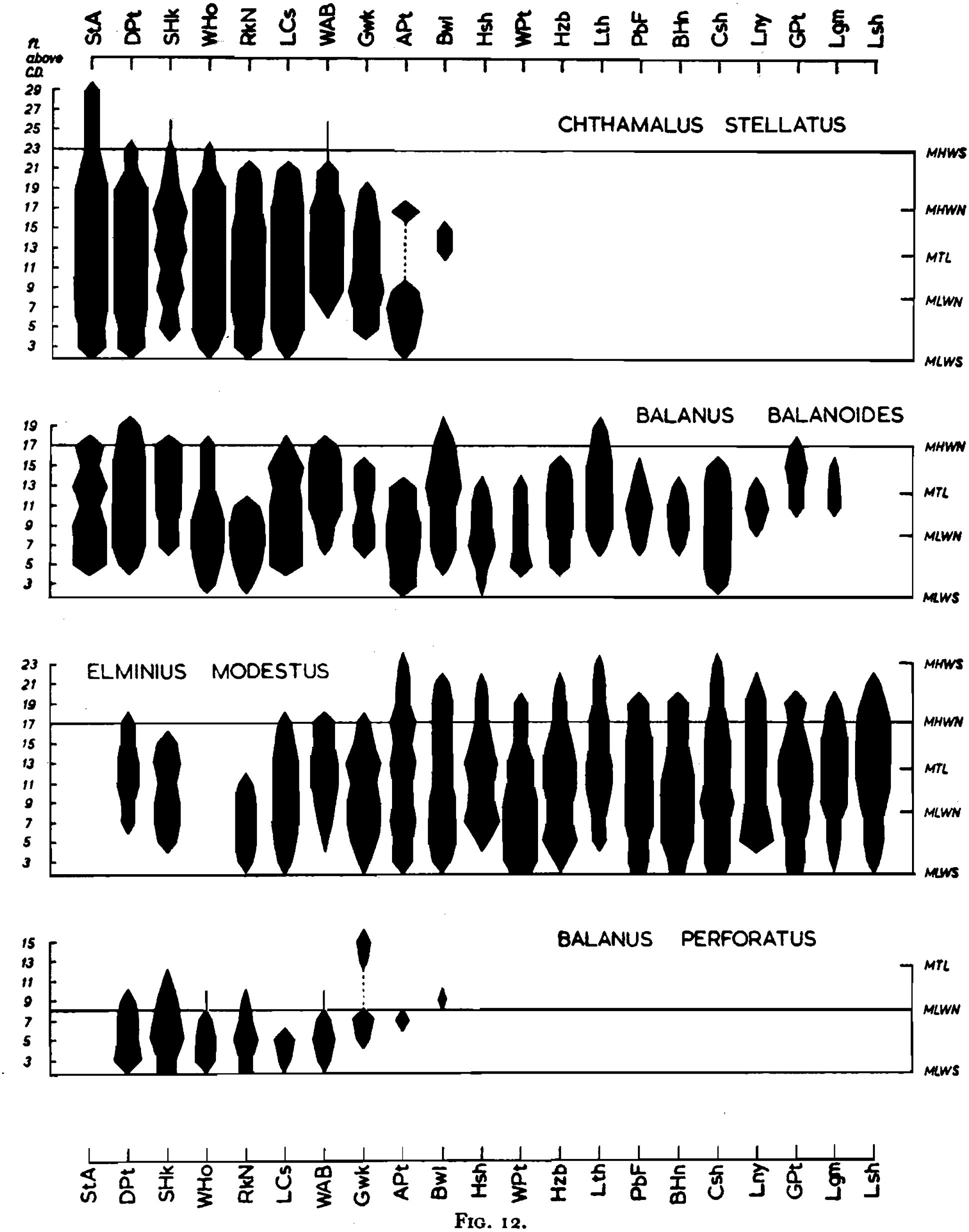

FIG. 12.

The zonation of the barnacles, shown as in Fig. 5. The top-shore "barnacle line" is formed by *Chthamalus* in exposure and *Elminius* in shelter. *Elminius* does not yet occur on the open coast to either side of Milford Haven.

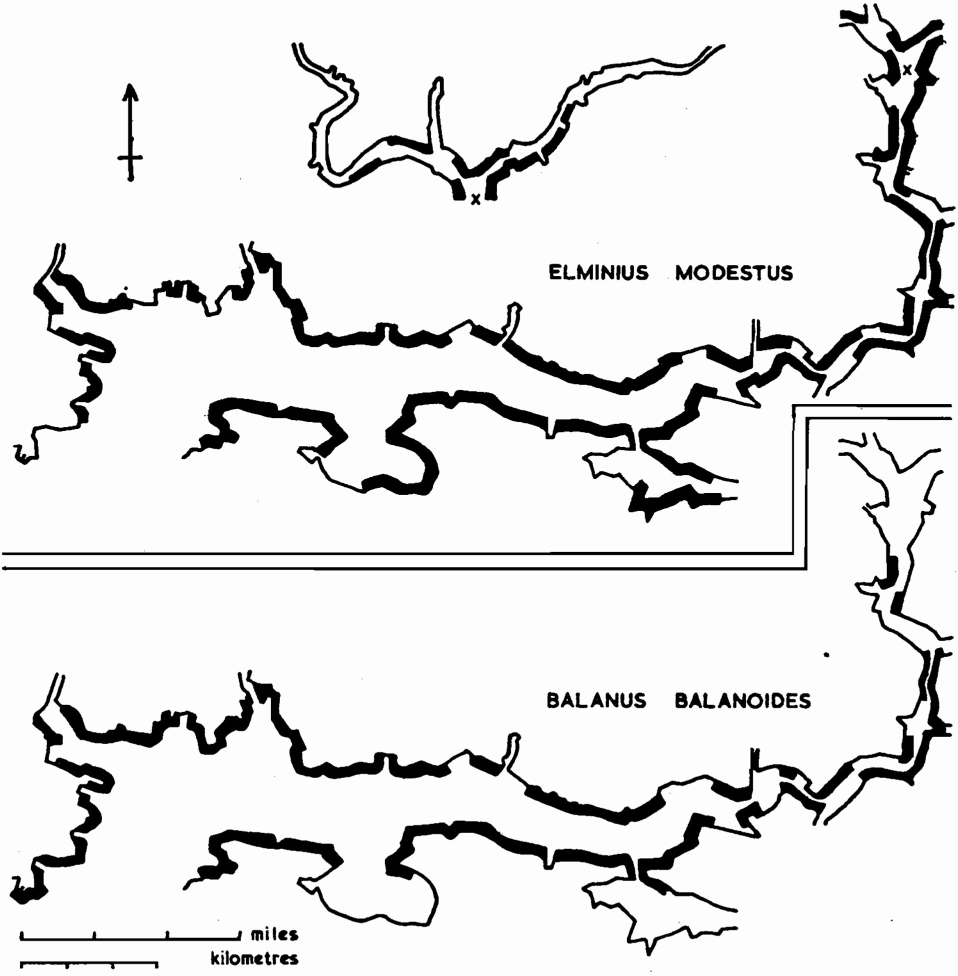

FIG. 13.
The distribution of *Elminius* and *Balanus balanoides*.

lower shore in response to deep water and strong currents) its lower limit becomes progressively elevated towards the head of the estuary. This may be correlated with increasing shelter, as reported by Evans (1947) but not clearly seen around Dale, or more directly with a combination of increased silting, reduced salinity at low water and lack of suitable rock surfaces.

Balanus crenatus is common below tidemarks throughout Milford Haven and the Daucleddau; its general distribution over the lower shore is shown in Fig. 22. *Balanus perforatus* occurs well into the middle shore, especially in local shade

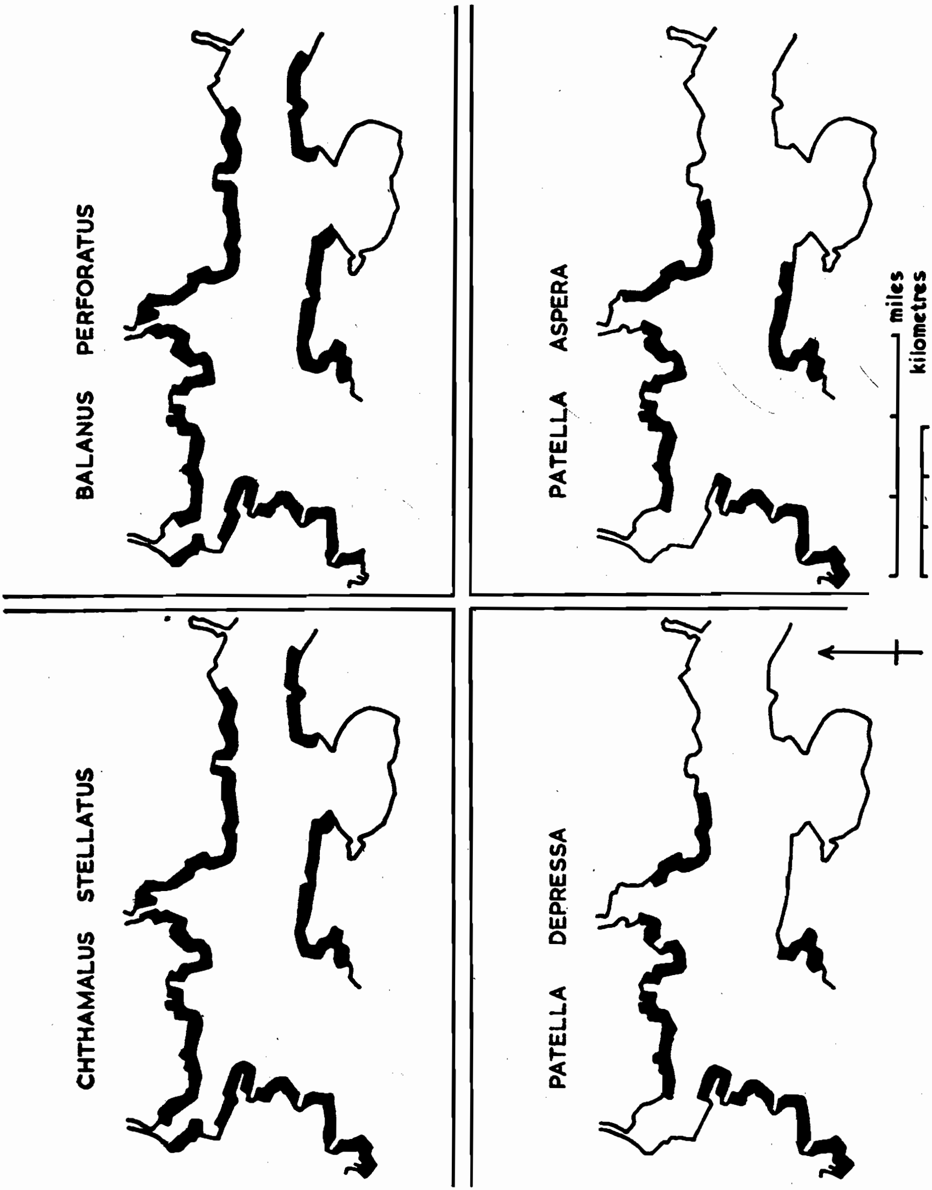

FIG. 14.
The distribution of *Chthamalus*, *Balanus perforatus* and two species of *Patella*. *Patella vulgata* occurs everywhere on rocks and stones as far as Llangwm. *B. perforatus* has also been recorded from Neyland (Norris and Crisp, 1953).

at Gelliswick, but rarely passes into the sublittoral. It is numerous at the seaward end of the Haven but only a few individuals were recorded from the middle reaches. The cold weather of early 1963 killed many of these barnacles, particularly in Sandy Haven where they occupied rocks set in the middle of a flat sandy beach, but individuals survived in all localities from which they had previously been recorded. A number of *B. perforatus* were reported by Norris and Crisp (1953) from a slipway at Neyland, but were not seen ten years later.

Chthamalus stellatus is limited to the seaward end of the Haven and occupies its full potential vertical range only on exposed shores receiving undiminished swell. Within the mouth of the Haven there is a tendency for the lower limit of *Chthamalus* to become elevated as its upper limit is depressed; this tendency is better seen on shores around the Dale peninsula. Perhaps as the narrowing of the supralittoral splash zone limits its upward spread, it is discouraged on the lower shore by the increasing unsuitability of the substratum. *Elminius*, which can successfully colonize muddy stones and grows well beneath a cover of Fucaceae, shows an extension of its vertical range on passing up the estuary, probably because *Chthamalus* is no longer found and *Balanus balanoides* becomes reduced in range and abundance.

WINKLES (Littorinidae) (Figs. 15–18)

Littorina neritoides shows within Milford Haven the same reduction in its range and abundance with greater shelter that was seen around the Dale peninsula; an unexpectedly high lower limit at Little Castle Head coincides with the presence of numerous *L. saxatilis neglecta*, suggesting that on this shore the latter winkle is particularly successful in competition for sheltering crevices. *Littorina saxatilis* was divided into the four subspecies recognized by James (1963; Fischer-Piette *et al.*, 1964). *L. saxatilis tenebrosa* occurs with *L. neritoides* above MHWN, although it is never as abundant and is even less tolerant of shelter (see Fig. 25). *L.s. neglecta* (*L.s. saxatilis* in James, 1963) is largely confined to empty barnacle shells, sharing this habitat with *L. neritoides* which it replaces below MLWN; its vertical range becomes more restricted in penetrating the Haven. *L.s. rudis* is the most widely distributed winkle in Milford Haven and in the middle reaches has the zonation shown in Fig. 22. At the Horseshoe, individuals were found ten feet (ca. 3 m) above MHWS whilst at Burton Hawn and Cosheston they extend to just below MLWS. At Llangwm and beyond the lower limit becomes elevated to about mid-tide level (Fig. 25). *L.s. jugosa* was not distinguished from *L.s. rudis* in this survey since on most rocky shores in the Haven it represents only a small fraction of the winkle population near the top of the shore; it is more abundant in the lower levels of saltmarsh at the mouths of tributary pills and in the rivers Cleddau.

Littorina obtusata (*L. littoralis*) occurs on most sheltered shores throughout the Haven on *Ascophyllum* and *Fucus*. It extends further into exposure than most of the Fucaceae and specimens may be found locally on *F. serratus* around headlands within the mouth even though not under the most exposed conditions in which this alga occurs. However, its upstream range cannot be limited by lack of the algae with which it is associated since these penetrate beyond Landshipping Ferry, the furthest station from which it has been recorded.

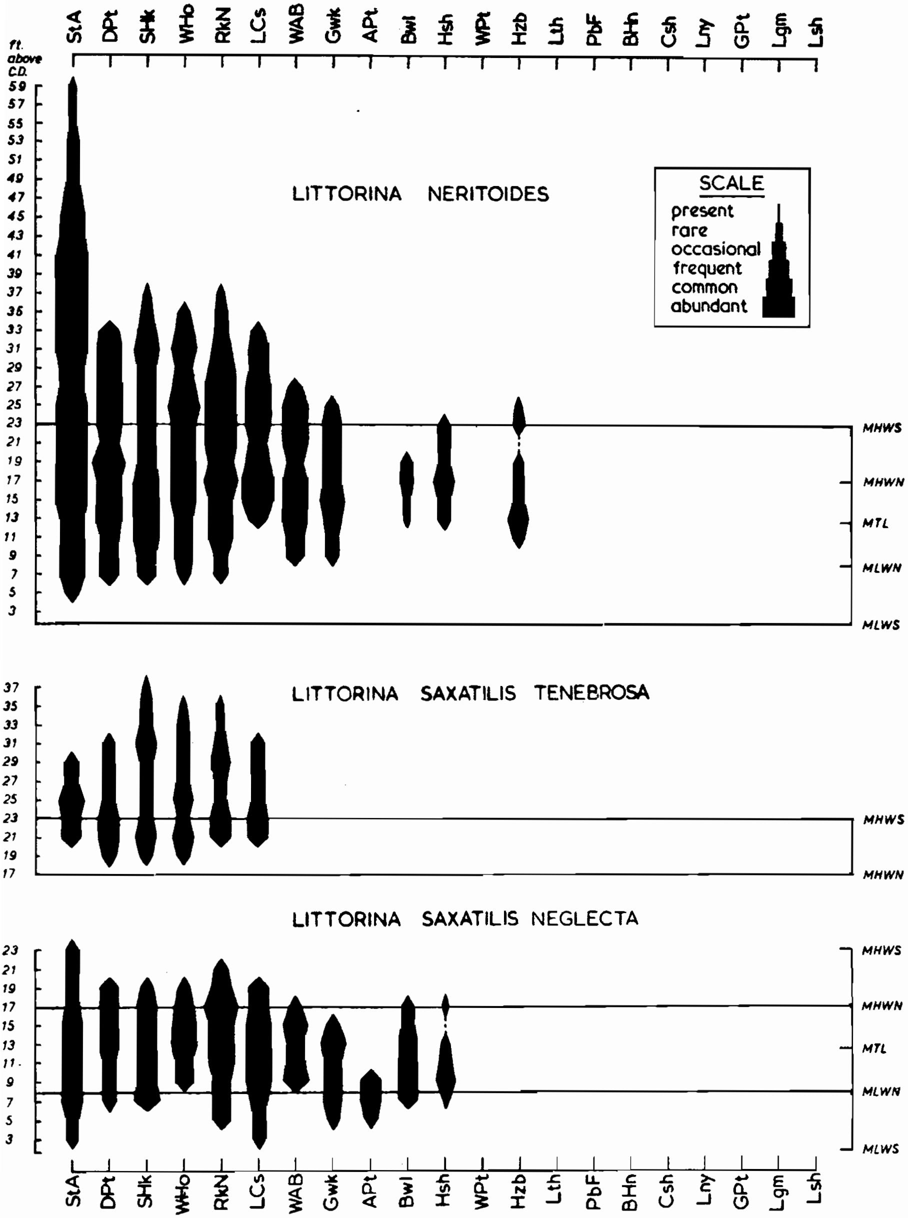

FIG. 15.

The zonation of small winkles, shown as in Fig. 5. The scale shown here applies also to Figs. 5, 6, 12 and 18; sources for the criteria of abundance are given in the text.

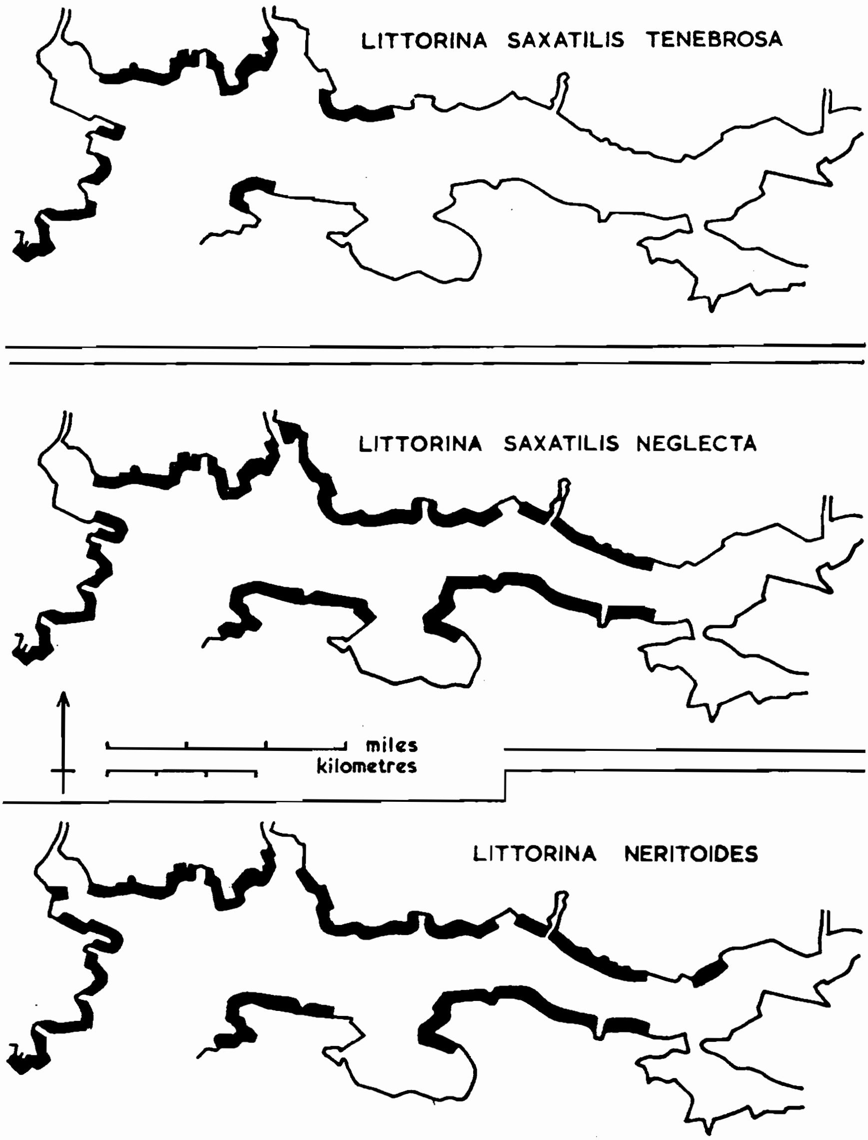

FIG. 16.

The distribution of small winkles. *L.s. neglecta* occurs mainly in empty barnacle shells and *L.s. tenebrosa* in the splash zone of exposed shores.

Littorina littorea has a range throughout the middle Haven similar to that of *L. obtusata*. In the mouth it extends less into exposure, as was observed by Lewis (1953) in Anglesey. Its upstream limit also falls short of *L. obtusata*; they were found to penetrate to the same extent in the Tamar (Percival, 1929) and La Rance (Fischer-Piette, 1931). In the Hardangerfjord *L. littorea* is more widespread than *L. obtusata* towards their inner limit, probably because some of its free-swimming larvae are able to avoid the surface layers of low-salinity water which, in that region of small tides and slack water-currents, must prevent or disturb the hatching and proper development of the attached eggs and non-swimming larvae of *L. obtusata* (Brattegard, 1966). In Milford Haven many pelagic larvae must be carried away in the strong surface currents whose net movement in the estuarine circulation is downstream, as are the herring larvae hatched in the Daucleddau (Nelson-Smith, 1964; 1965). *L. littorea* is said to need wetting by every tide (Moore, 1940) but it occurs several feet above MHWN in shade at Pembroke Ferry House and Cosheston Folly. It is abundant on the latter shore in the virtual absence of *L. obtusata* and Fucaceae. The abundance and large size of edible winkles at Martin's Haven have been commented upon by Cole (1955) and earlier fisheries investigators (see Crothers, 1966) and were noted during the present survey. On the similar neighbouring shore at Bullwell these winkles are, by contrast, few and local although *L. obtusata* and *L. saxatilis rudis* are widespread and quite numerous amongst scattered fucoids. At Lawrenny Ferry Point, which has a denser covering of large algae, *L.s. rudis* is almost as scarce as *L. littorea* while *L. obtusata* is common over much of its range.

TOPSHELLS (Trochidae) (Figs. 18, 19)

Gibbula umbilicalis is never as numerous up the Haven as on the shores of Dale Bay, reaching its optimal abundance and range between West Angle Bay and Angle Point, where it occurs as high as MHWN. Moore (1940) reported a general upper limit at MLWN. Towards the head of the estuary, as at the mouth, its upper limit becomes progressively depressed (Fig. 25). *Gibbula cineraria* is essentially a sublittoral form. On the lower shore it appears to require greater shelter than *G. umbilicalis*, occurring more patchily in the mouth and extending further up the Haven. Fischer-Piette (1931) found the reverse order of penetration in La Rance. The sublittoral *G. magus* and *Calliostoma zizyphinum* have been recorded at MLWS as far upstream as Pembroke Dockyard.

Monodonta lineata occupies a much more restricted range than the two common species of *Gibbula*. Around Dale it occurs almost entirely in Dale Bay; it was found on surveyed shores only between Angle Point and Hazelbeach Point, although it was also recorded from Sandy Haven, Neyland and Burton Quay. On the lower shore *Monodonta* may be found amongst quite mobile stones, occupying at higher levels the moist gullies or shallow pools between bedrock ridges. It shows a marked seasonal migration from the upper shore in winter (Williams, 1965) and, perhaps because it is near the northern limits of its range in Milford Haven, the exceptionally cold conditions of early 1963 caused a high mortality there, leaving *Littorina littorea* and *L. saxatilis rudis* largely unaffected.

LIMPETS (Patellidae) (Figs. 14, 22)

Patella vulgata is abundant on all shores from the mouth of the Haven to above Lawrenny; a few scattered specimens were found around Llangwm and the furthest upstream was recorded from the west shore opposite Landship-

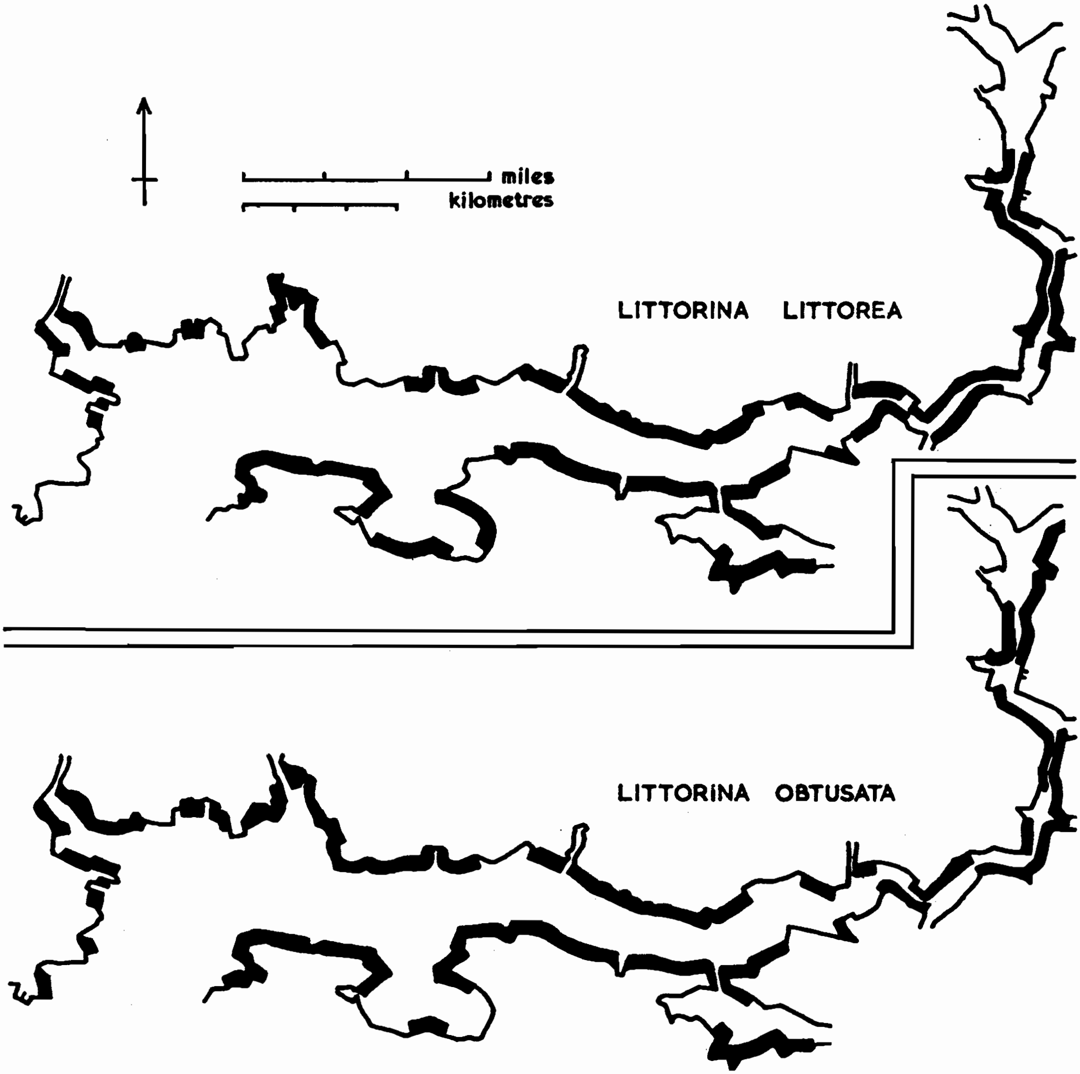

FIG. 17.
The distribution of the larger winkles. *L. obtusata*=*L. littoralis*. *L. saxatilis rudis* occurs almost everywhere (see Fig. 25).

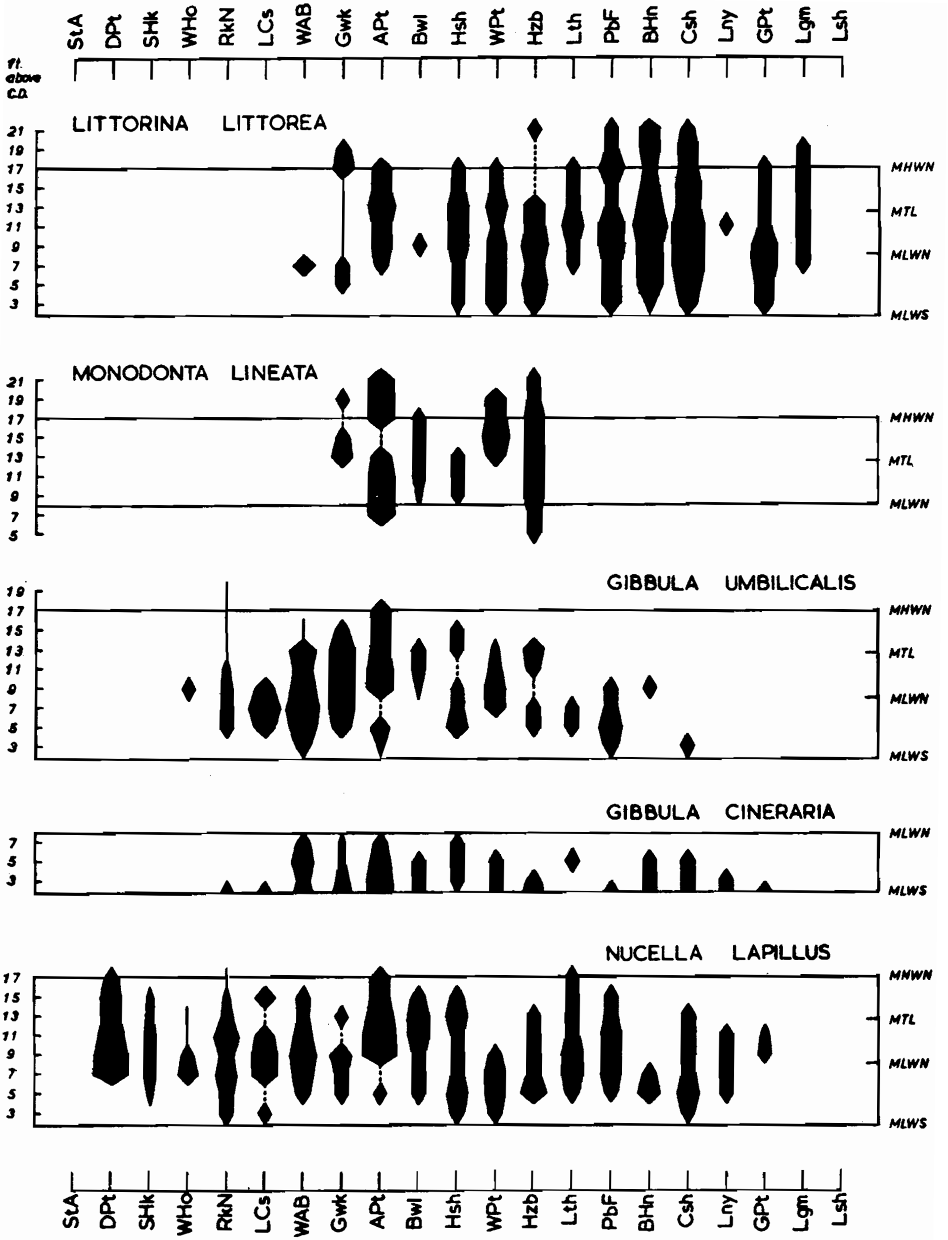

FIG. 18.
The zonation of *L. littorea*, *Nucella* and some topshells, shown as in Fig. 5. Although not present on some shores in the mouth, all occur in shelter around Dale.

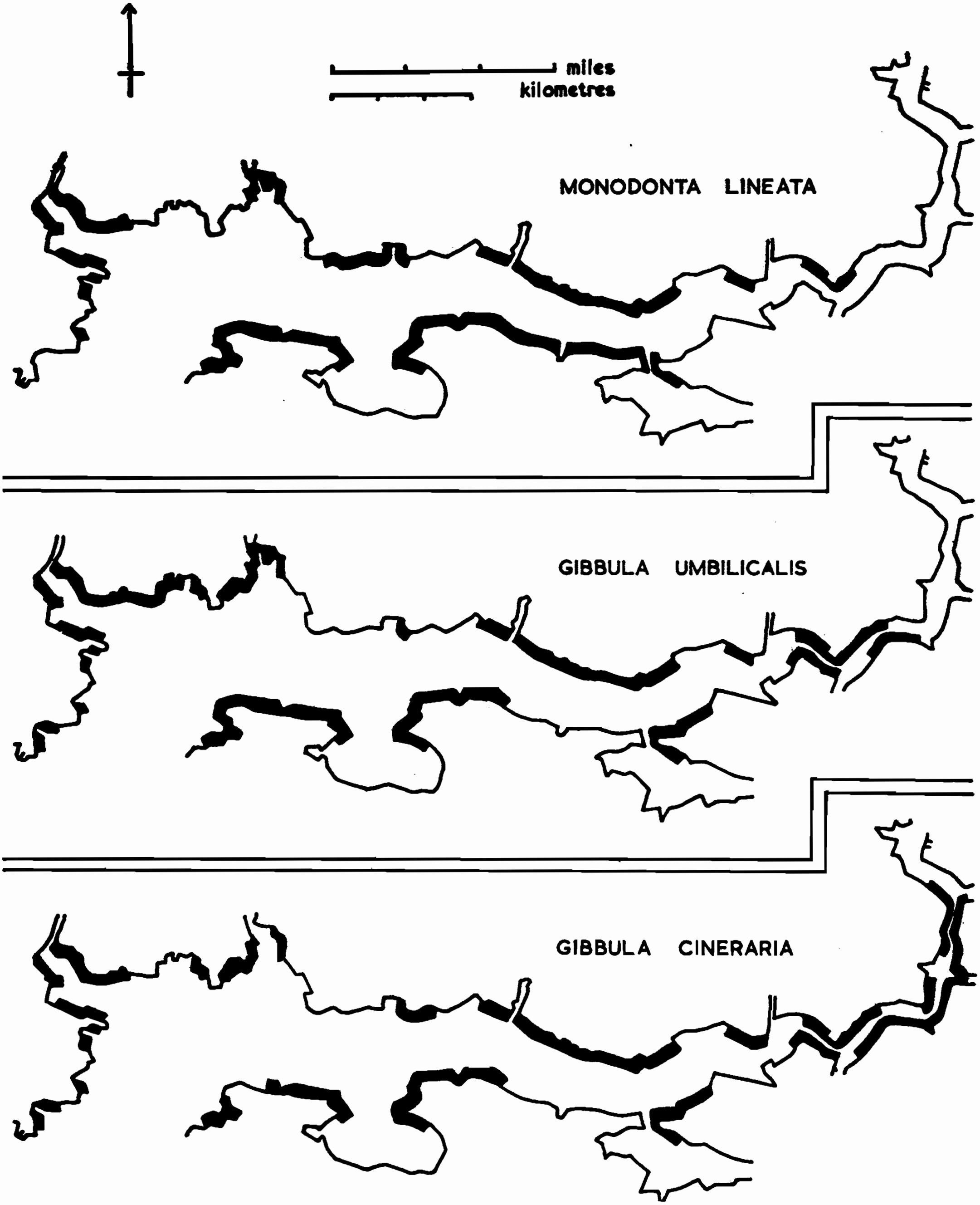

FIG. 19.
The distribution of some topshells.

ping Quay. Although limpets even at their most numerous are less abundant upstream, their biomass is greater there than on exposed shores. Measurements made near Lawrenny show that the total volume of limpets in unit area is nearly twice as great as on comparable surfaces at Dale Point. Limpets from the higher tidal levels of exposed shores often grow shells with high apices and narrow apertures; Orton (1933) suggested that this is due to the prolonged contraction of shell muscles while the animal is clamped tightly to the rock avoiding desiccation. Those from the shaded and weed-covered rocks at Garron Point proved to have shells with equally high apices, presumably because limpets there spend much of their time avoiding water of an unsuitably low salinity (see below, p. 475).

Patella depressa (*P. intermedia*) is restricted to exposed shores within the mouth of the Haven. Although near the northern limit of its geographical distribution, this limpet suffered little in south-west Wales during the cold spell of 1963, perhaps because it favours steep surfaces receiving full sunlight; a heavy mortality was recorded among *P. vulgata* occupying horizontal surfaces at higher levels on the shore. *Patella aspera* was also found only in the mouth, where it is the dominant limpet of the lower shore.

OTHER MOLLUSCA

The dog-whelk *Nucella lapillus* (Figs. 18, 20) extends throughout the Haven, although on the most exposed shores it is present only in local shelter. Its upper limit on the shore usually coincides with that of *Balanus balanoides*, since barnacles form its major food. *B. balanoides* is scarce above Lawrenny, but its distribution cannot be the main factor determining that of *Nucella* as alternative prey is available above the upper limit of *Balanus* (*Chthamalus* in exposure and *Elminius* in shelter) and beyond Llangwm (*Elminius* and the mussel *Mytilus*). *Nucella* is probably unable to stand desiccation as well as shore barnacles do. It does not appear to be much deterred by silt but its upper limit becomes progressively depressed upstream even in shade. Another whelk, *Ocenebra erinacea*, has been recorded from the lower shore in the middle reaches and occurs sublittorally to above Lawrenny. Although the slipper limpet *Crepidula* is abundant, the American oyster drill *Urosalpinx cinerea* has not yet been reported in the area.

Mytilus edulis was recorded on all rocky shores to the head of the estuary and also covers large areas of muddy shingle on the flats near Pembroke and within the tributary rivers. Its zonation depends much on local features of substratum and aspect but is in general as in Fig. 22. *M. galloprovincialis* was not considered (see Crothers, 1966).

SERPULIDAE (Figs. 20–22)

Nelson-Smith and Gee (1966) have recently described the distribution around Dale of this family of tubicolous polychaetes. Only certain of the littoral species are considered in detail here.

Spirorbis pagenstecheri is the most widespread, occurring on small flat stones as well as rock ridges, in pools and on *Laminaria*. Sublittoral specimens may show a reduction in the ridging of the tube; *S. spirillum*, with which such specimens might otherwise be confused, has not been recorded from the inner parts of

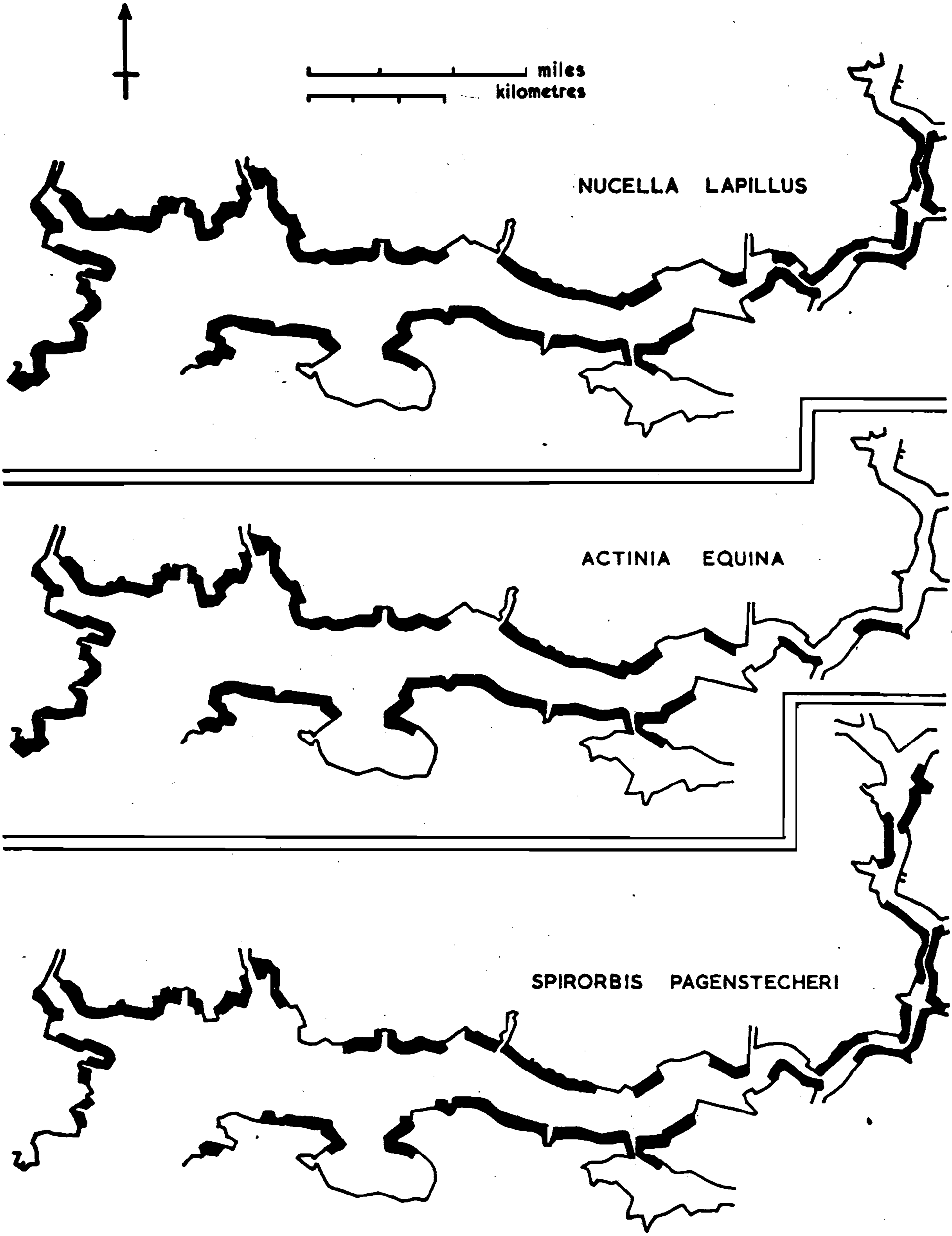

FIG. 20.
The distribution of *Nucella*, *Actinia* and *Spirorbis pagenstecheri*.

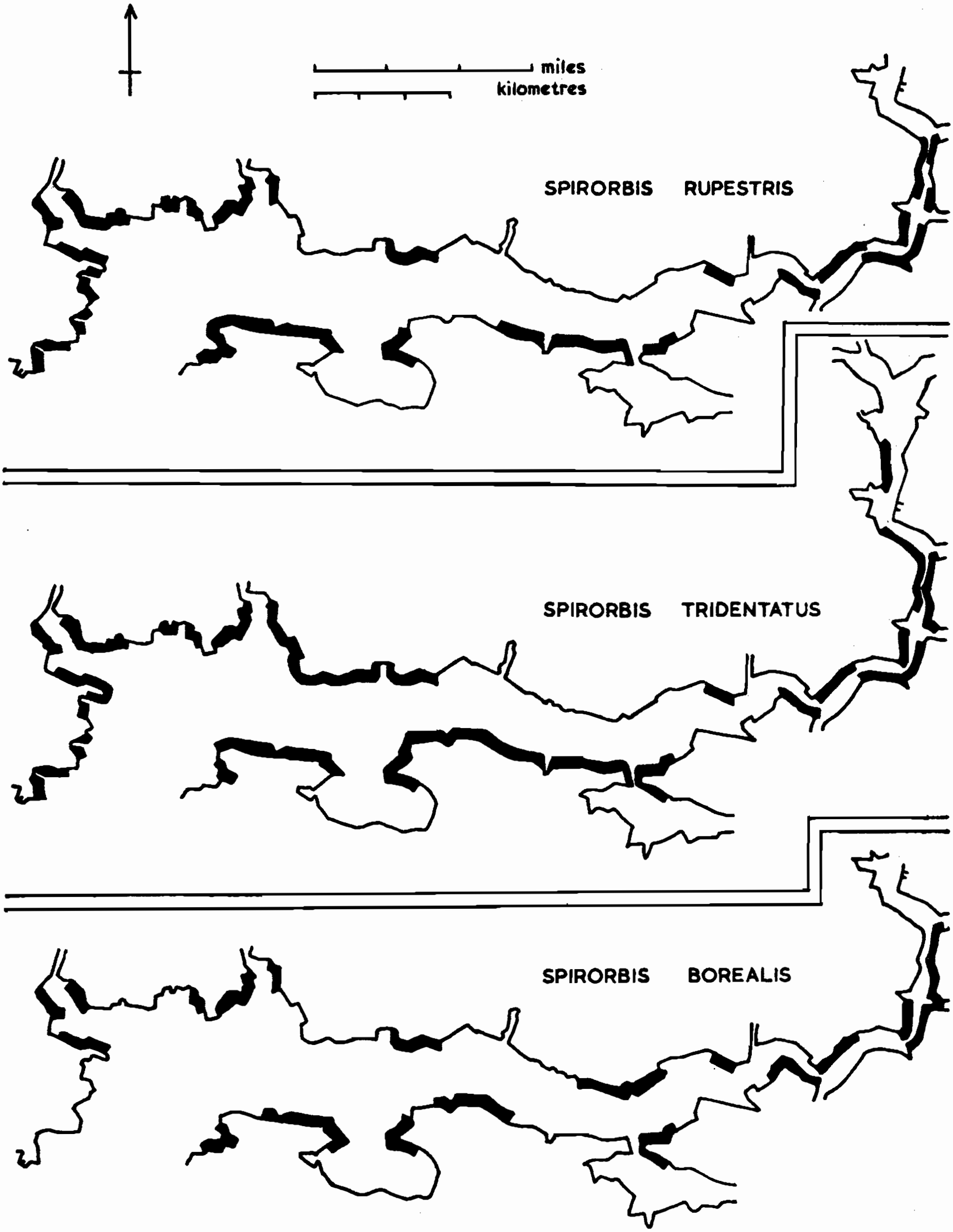

Fig. 21.
The distribution of some species of *Spirorbis*; *S. pagenstecheri* is included in Fig. 20.

Milford Haven. *Spirorbis rupestris* Gee and Knight-Jones (1962) tolerates greater exposure than *S. pagenstecheri* but penetrates less far up the estuary. It is found in association with lithothamnia and is thus restricted to bedrock or large cobbles; lithothamnia as a group extend beyond the upstream limit of this worm but may not include the associated species, tentatively identified by Gee (1965) as *Lithothamnion polymorphum*. Amongst the numerous species of lithothamnia recorded throughout the Hardangerfjord, *L. polymorphum* is common only in the middle and outer regions (Jorde and Klavestad, 1963).

Spirorbis tridentatus is not associated with algae but again seems restricted to bedrock and large stones. Below Llangwm it is particularly abundant but hard to distinguish from *S. rupestris* in the field because of a marked reduction in the characteristic ridging of the tube. *Spirorbis borealis* grows on *Fucus serratus* and occasionally on other lower-shore algae such as *Himanthalia*, *Gigartina* and *Chondrus*; it does not, however, occupy the full range of these algae. The closely related *S. inornatus* L'Hardy and Quiévreux (1964) occurs typically on *Laminaria* but at a few stations in the middle reaches of Milford Haven it has recently been found on *Fucus serratus*; it is thus easily mistaken in the field for *S. borealis*, although where one species is abundant the other is usually rare.

Spirorbis corallinae de Silva and Knight-Jones (1962) has been recorded around the mouth of the Haven but not on shores beyond Gelliswick, where the *Corallina* on which it grows is scarce and local. *Pomatoceros triqueter*, a larger worm than these Spirorbinae, occurs on bedrock, stones and shells throughout the Haven and extends well into the sublittoral.

SPONGES (Porifera) (Fig. 22)

Sponges occur throughout the Haven and were recorded on all surveyed shores other than the very exposed St. Ann's Head and at the Horseshoe and Llanreath, where there is mobile silt on the lower shore. The greatest variety was to be found at the seaward end of the Haven. *Halichondria panicea* and *H. bowerbanki* are very abundant in the middle and upper reaches, especially below tide-marks; *Hymeniacidon perleve* was also prominent and extends further up the shore. *Grantia compressa* and *Dysidea fragilis* were found on the lower shore as far as Pembroke Ferry.

COELENTERATA (Figs. 20, 22)

Actinia equina is the only sea-anemone included in detailed shore surveys here or around Dale. Many specimens occur in pools, although others may be found in open situations quite free of algal cover. Nevertheless, *Actinia* tends to occupy lower tidal levels towards its upstream limit and therefore seems to be restricted by reduced salinities rather than by the presence of mud.

The patterns of distributions in the estuary

The common marine plants and animals included in this survey seem to reach the limits of their penetration, or to suffer abrupt changes in their vertical zonation, largely within one of three distinct boundary regions. These occur at about 3, 11 and 15 miles above Thorn Island. They are also characterized by fairly sharp changes in the physical environment (Fig. 23; see also Nelson-Smith, 1965).

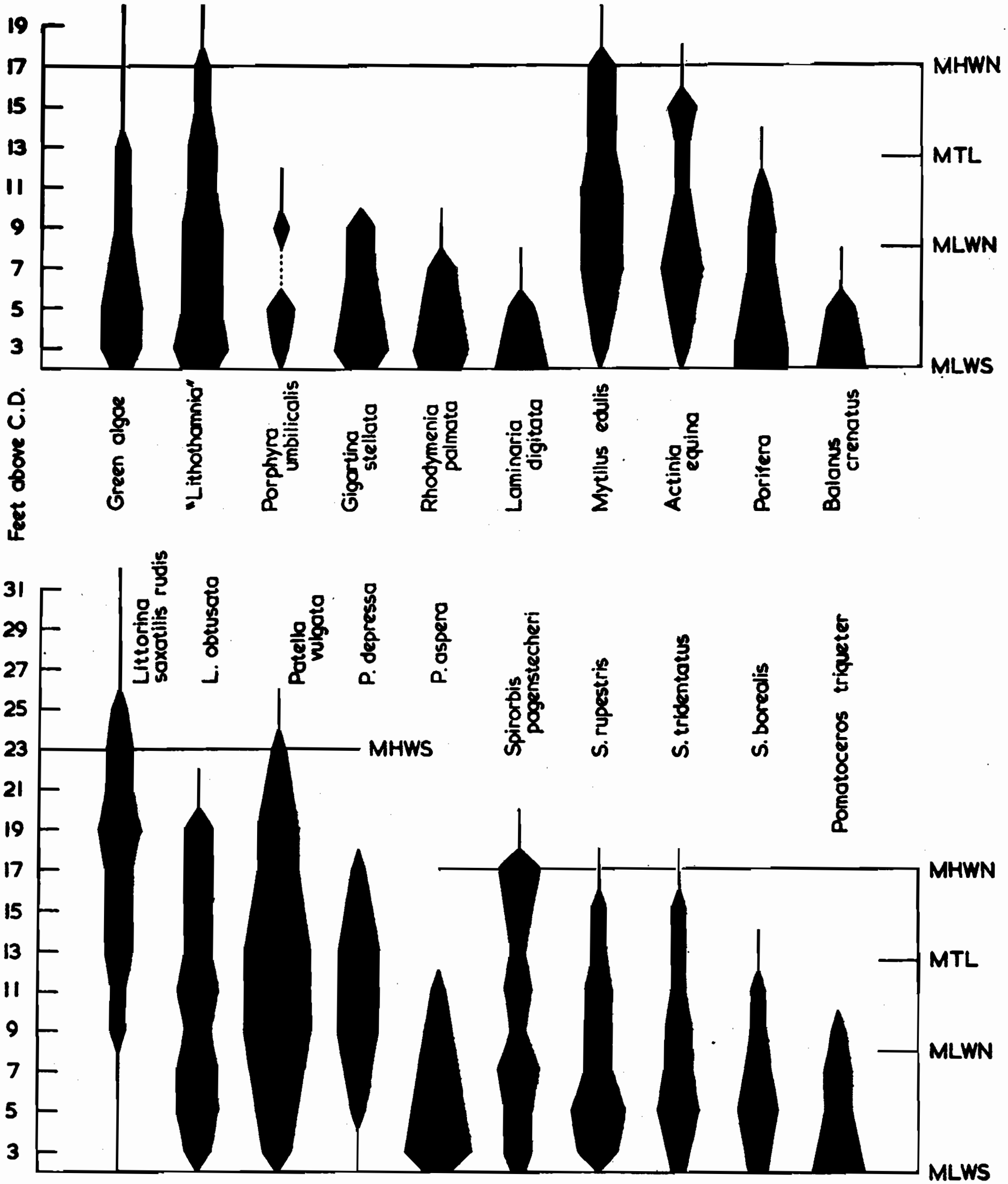

FIG. 22.

Zonations which are typical of some species throughout most of their range in Milford Haven. Green algae, lithothamnia and Porifera were not separated into their species (but see text). The scale of abundance is graded as in Fig. 15, the widest part of the histogram for *Patella vulgata* representing "abundant".

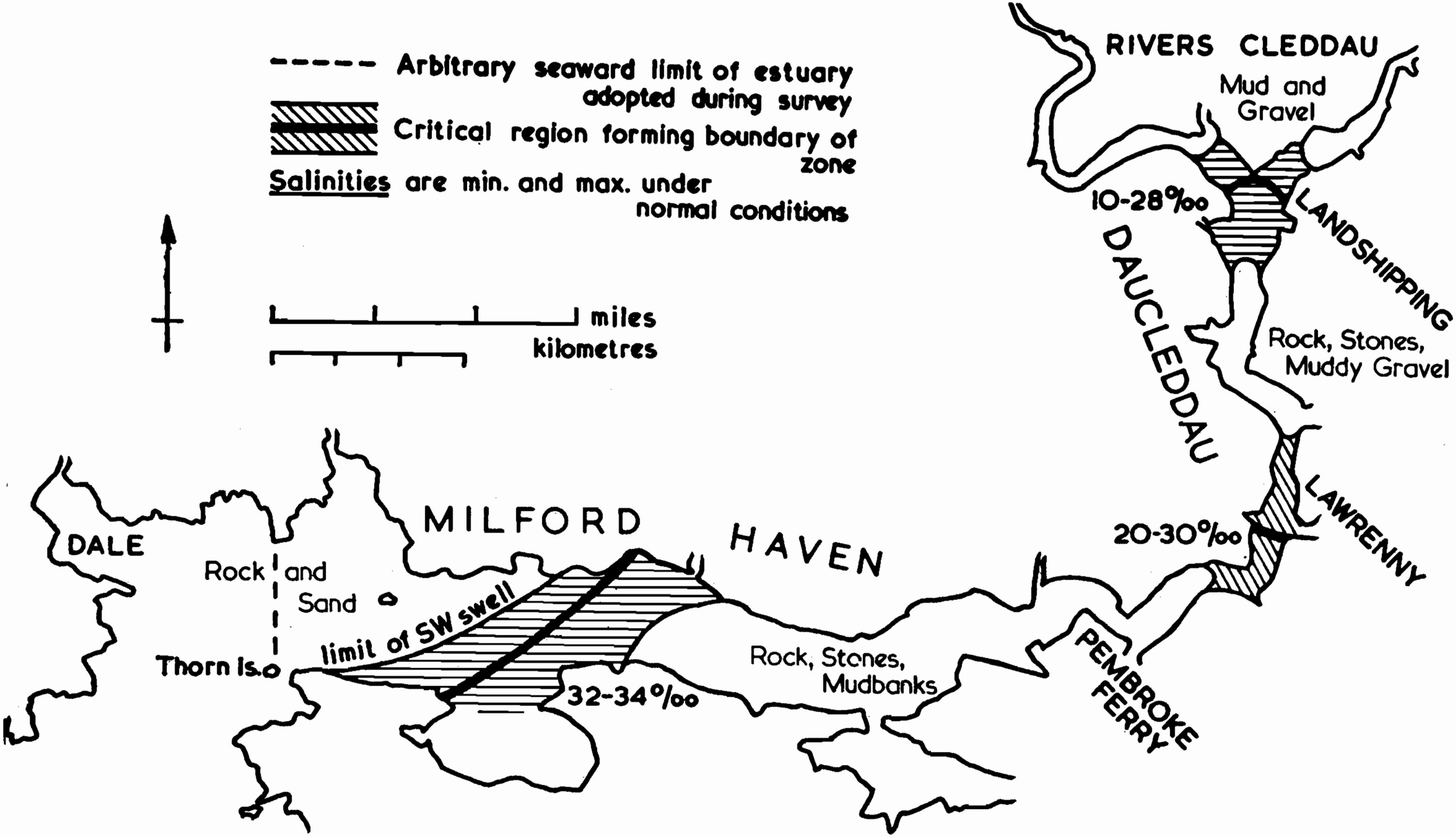

FIG. 23.
Ecological zones in Milford Haven (modified from Nelson-Smith, 1965).

The first region represents the natural seaward limit of the estuary; in it the salinity is always high, the shores and bottom are of clean sand or rocks and much of the coastline is exposed to ocean swell. Because the prevailing winds are from the south west, this limit intrudes obliquely into the Haven in such a way that Angle Point lies beyond it while Gelliswick Bay, further upstream but on the opposite shore, is within it. Amongst the species which penetrate no further than this first boundary *Lichina pygmaea*, *Fucus vesiculosus evesiculosus*, *Laminaria hyperborea* and *Alaria esculenta* are diagnostic of exposed shores. *Chthamalus stellatus*, *Littorina saxatilis tenebrosa* and *L. neritoides* seem to be dependent on wave-swash (*L. neritoides* penetrates as far as Hazelbeach Point but is very restricted beyond Gelliswick Bay) whilst *Himanthalia elongata*, *Saccorhiza polyschides* and *Patella aspera* are typical of clean oceanic shores. In Figs. 24 and 25 outlines of the distribution of some of these have been plotted along an axis of distance up the estuary.

Many species more common on sea-shores than in estuaries penetrate well beyond this boundary where, because the tidal volume is much greater than river flow, salinities are still high. Some, for example *Spirorbis borealis*, *Gibbula umbilicalis* and *Monodonta lineata*, require shelter from powerful wave-action and therefore pass little to seaward of the boundary, although they may be found there in such sheltered situations as Dale Bay. *Monodonta* also fails to penetrate far upstream of this boundary; its inner limit lies about six miles up the estuary, corresponding with the absolute upstream limit of the small winkles *Littorina neritoides* and *L. saxatilis neglecta* and the reduction of a continuous zone of *Lichina confinis* to scattered patches. These changes may be related to the sharp bend at Pembroke Dock. The Haven below this is wide and tidal currents are relatively weak so that extensive mudbanks occur in shelter. Because the upper reaches and the Daucleddau are narrow, currents are stronger and mud is deposited only at bends in the channel. However, the next major boundary region is found further upstream in the vicinity of Lawrenny where the salinity gradient becomes critical. *Laminaria saccharina*, *Spirorbis borealis* and *Littorina littorea* are diagnostic of shelter, as is *Monodonta*, but they penetrate little if at all beyond this second region. *S. borealis* is very abundant at Lawrenny Ferry Point but seems to suffer occasional heavy mortalities amongst younger individuals there, perhaps because they are less able to withstand the extremes of estuarine conditions. This region also forms an upstream boundary to *Laminaria digitata*, *Gigartina stellata*, *Rhodymenia palmata* and *Gibbula umbilicalis*; *Laurencia pinnatifida* fails to penetrate as far while *Balanus balanoides* and *Gibbula cineraria*, like *L. littorea*, extend a little further upstream. The lithothamnia, *B. balanoides*, *L. littorea* and *L. saxatilis rudis* all show a marked restriction in their vertical spread at about this region.

One half of the animals and plants included in this survey do not pass the second boundary region; more than three-quarters fall short of a third boundary lying across the junction of the rivers Cleddau above Landshipping Quay. Here the salinity gradient is steepest; this part of the estuary experiences the greatest range of salinities during a tidal cycle and the water may be very fresh for longer periods during spate. Soft substrata with a few patches of stones or gravel replace the rocky or stony shores of the Daucleddau, limiting the penetration of such species as *Fucus serratus*, *Patella vulgata*, *Spirorbis tridentatus*

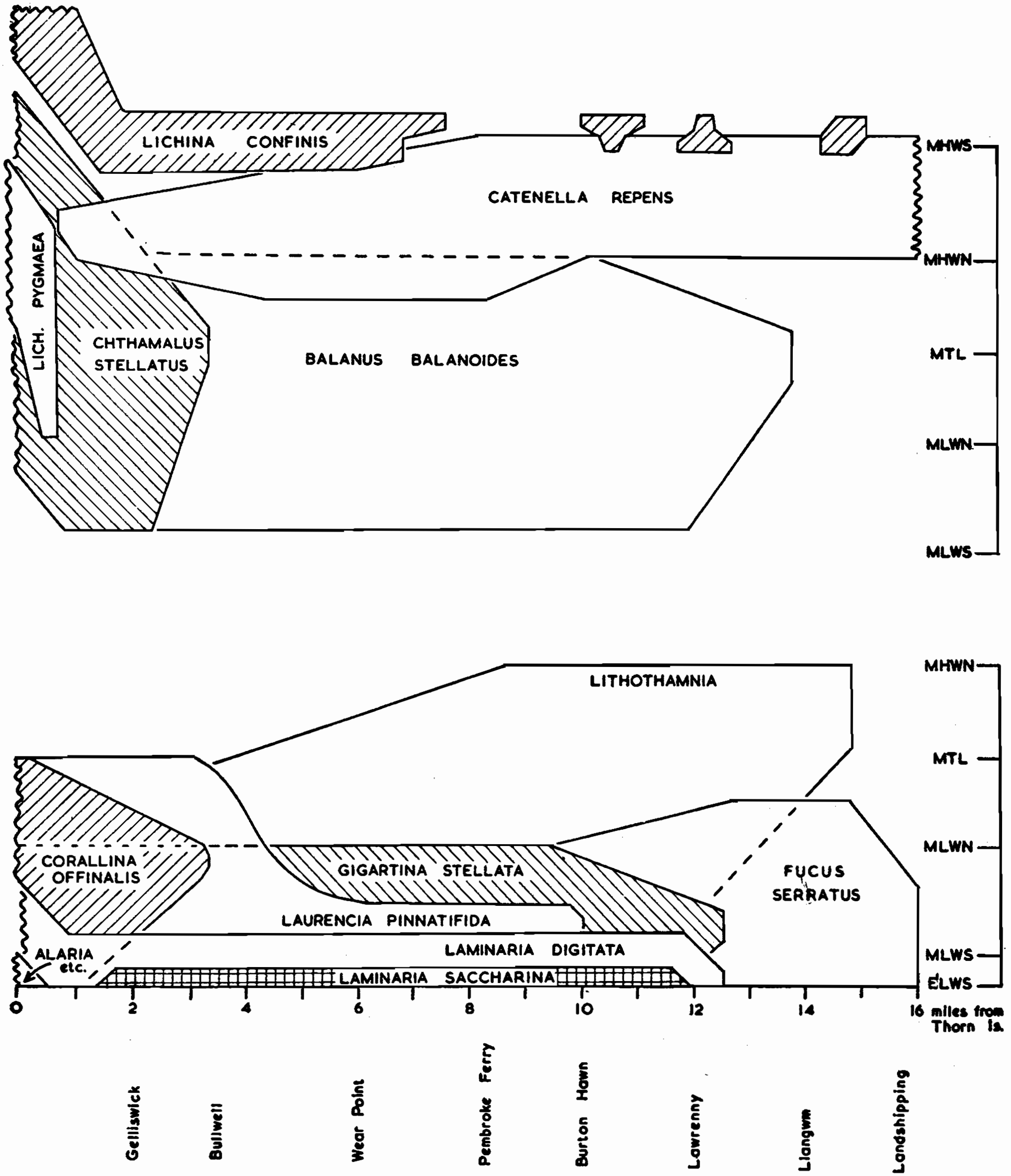

FIG. 24.

An outline of the horizontal and vertical distribution of some barnacles, lichens and algae throughout Milford Haven. A line passing through Thorn Island is taken to be the seaward limit of the estuary, lying to the left of the diagram (see Fig. 23).

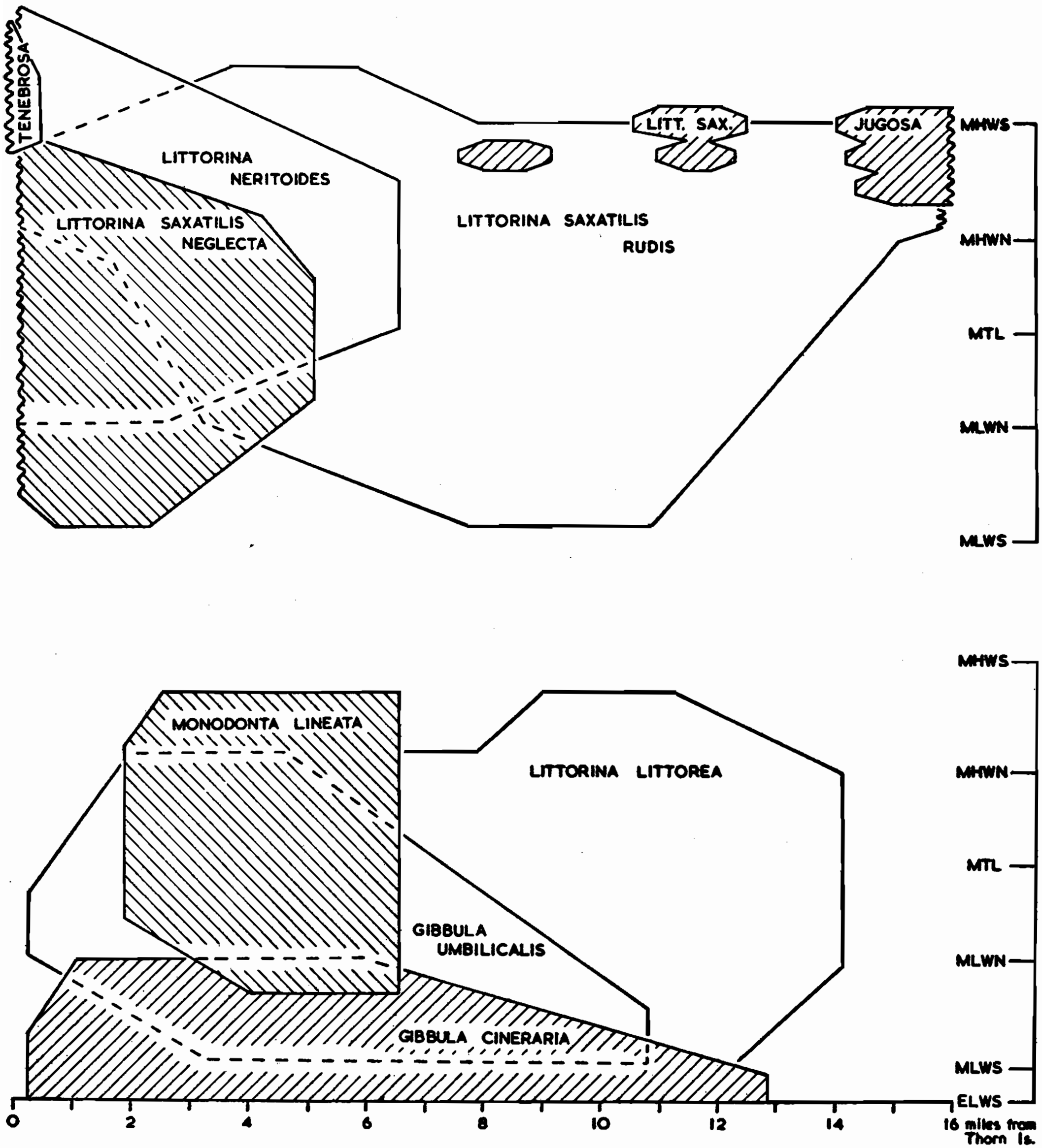

FIG. 25.
An outline of the horizontal and vertical distribution of some gastropod molluscs in Milford Haven, drawn as in Fig. 24.

and *S. pagenstecheri* which are widespread on rocky shores throughout the estuary. *Catenella repens*, *Littorina obtusata* and *L. saxatilis rudis* are to be found on small stones for a short distance beyond this boundary, while *Ascophyllum nodosum*, *Fucus vesiculosus*, *F. spiralis* and *Elminius modestus* extend well into the tidal reaches of the rivers. This boundary region similarly forms a downstream limit to the occurrence in any large numbers of the few common species which are more or less limited to brackish waters, such as *Fucus ceranoides*, *Balanus improvisus* and *Littorina saxatilis jugosa*. However, very few fresh-water species are encountered below the limits of tidal influence, even where the tide is merely a movement of fresh water up and down stream.

Milne (1940) compared distributions in the Aberdeenshire Dee with the Tay, Tees, Tamar and La Rance; Fischer-Piette and Seoane-Camba (1963) extended these comparisons to include three rias in north-west Spain, taking six species for their comparison of eight Spanish, French and British inlets. The Hardangerfjord, whose shore ecology has recently been investigated in detail by Jorde and Klavestad (1963) and Brattegard (1966) has, during the summer, gradients of salinity and turbidity similar to those in an estuary, although in the winter it is marine throughout its length. The list of Fischer-Piette and Seoane-Camba was modified to include this Norwegian fjord and Milford Haven (Table 4). The order in which animals were found to penetrate each of these inlets was compared in turn with that in Milford Haven by calculating a rank correlation coefficient (in which perfect correlation is indicated by a coefficient of 1·0). The pattern of distribution of these common species in the Haven seems to be significantly similar not only to that of the deeper inlets, regardless of latitude, but also of the more northerly river-estuaries.

Table 4. *Order of penetration of some common animals into various brackish inlets*

	Ria de Vigo	Ria de Camariñas	Ria del Barquero	La Rance	Milford Haven	R. Tamar	R. Tees	R. Tay	R. Dee	Hardangerfjord
Mytilus edulis	1=	3	3	2=	1	2=	2	2=	2=	1
Littorina littorea	1=	1	1	4=	2	3=	3=	2=	2=	2
Patella vulgata	3	4	2	3	3=	4	3=	3=	3	4
Balanus balanoides	4	2	A	1	3=	2=	1	1	1	3=
Pomatoceros triqueter	2	5	4	4=	4	1	3	4	5	3=
Actinia equina	5	6	5	2=	5	3=	4	3=	4	5
Rank correlation coeff. (ρ)	0·828	0·786	0·700	0·485	—	0·514	0·772	0·786	0·800	0·943

1 indicates furthest and larger numbers proportionally less penetration upstream. A means absent. The rank correlation coefficient of each inlet with Milford Haven is also listed. Data from Fischer-Piette & Seoane-Camba, 1963 and Brattegard, 1966.

Correlation with the shallower estuaries is less close. The "average" order in which these inlets are penetrated is with *Mytilus* furthest and *B. balanoides*, *L. littorea*, *Patella*, *Pomatoceros* and *Actinia* passing progressively less far upstream. The penetration of Milford Haven is very nearly in this order, although the significance of this is doubtful; the agreement would be even closer if *Elminius* were substituted for *B. balanoides*. *Elminius* is still absent from some of the inlets listed and others were surveyed before it invaded Europe; it is abundant and widespread in the Haven. There is much greater agreement in the order of penetration amongst Fucaceae (Table 5) and here the most frequent order is

Table 5. *Order of penetration of some Fucaceae into various brackish inlets*

	Ria de Vigo	Ria de Camariñas	Ria del Barquero	La Rance	Milford Haven	Severn Estuary	R. Exe	R. Tees	R. Tay	R. Dee	Hardangerfjord
Fucus vesiculosus	2	4	4	1	1	1	1	1	1	1=	1
Fucus spiralis	1	1	3	3	2	2=	4	N	N	1=	5
Pelvetia canaliculata	4	2	1	2	3=	2=	2	N	2	2=	4
Ascophyllum nodosum	3	3	2	4	3=	2=	3	2	3	2=	2
Fucus serratus	N	N	N	5	4	3	5	N	N	A	3

As Table 4; N means insufficient data. Data from Fischer-Piette, 1931; Milne, 1940; Bassindale, 1943; Gillham, 1957; Fischer-Piette & Seoane-Camba, 1963 and Jorde & Klavestad, 1963.

that found in Milford Haven. Data are insufficient for correlation calculations here. The brackish-water species *Fucus ceranoides* penetrates further than any of these into Milford Haven and most other estuaries, but not in the Tees or Tay (see Milne, 1940).

The factors responsible for changes in vertical zonation are as varied as those limiting horizontal distribution. Amongst the forms diagnostic of exposed shores a marked narrowing of the vertical range on passing into the Haven (as in *Corallina* or *Chthamalus*—see Fig. 24) or a depression of the entire zone (as in *Lichina confinis*) must be due to the increase in shelter (see e.g. Moyse and Nelson-Smith, 1963) since these changes take place outside the estuary proper. A similar lowering of the upper limit of the small winkles is also adequately explained by reduction in their upward spread once inside the limit of swell even though they do well in shelter at Dale. It has been pointed out earlier (Nelson-Smith, 1965) that vertical stratification in the estuary, with fresher water flowing downstream on the surface during the ebb and saltier water entering along the bottom with the flood, exaggerates tidal changes in salinity so that the inhabitants of the lower shore are subjected to a greater range of salinities as well as lower values. Between Lawrenny and Llangwm the salinity at the surface may be as much as 8‰ less than on the bottom; towards the limit of tidal influence in the rivers Cleddau stratification is extreme, with water at 18–20‰ flooding in beneath an almost fresh surface layer. However, sublittoral regions throughout most of the estuary experience a smaller range of salinities during one tidal cycle and salinity values may always be higher than intertidally. Some marine species, unable to survive these conditions on the lower shore, may either occupy successively higher levels towards their upper limit (as do *Balanus balanoides*, *Littorina saxatilis rudis* and the lithothamnia) or pass into the sublittoral (as does *Ocenebra erinacea*). Marine animals which cannot extend their vertical range upwards may still penetrate far into the estuary at their normal levels if they can close up or protect themselves in some other way when conditions become unfavourable. *Gibbula umbilicalis* and *Actinia equina* may perhaps do this. *Littorina obtusata* and *Elminius* also show a vertical distribution which remains substantially unchanged throughout their range in the Haven and are clearly able to close up tightly. Limpets on the lower shore at Garron Point clamp their shells down well before the tide uncovers them, as was demonstrated by sampling at various tidal levels the water trapped in the mantle cavity as they closed. The external salinity at high water was not measured on the day of sampling (during a poor spring tide) but is known to be about 28‰. Limpets at MHWN contained water at 24.0–26.5‰ and thus did not close until the tide left them, whereas those at MLWN contained water at 23.7–25.0‰ although at low tide the water had a surface salinity of only 11.8‰. Control observations at Dale Point showed limpets to contain water at 34.2‰, which approximates to the salinity of the sea there at all states of tide. Mobile shore animals probably avoid extreme conditions by making seasonal migrations either down the estuary or into the sublittoral during the winter (see Naylor, 1962). Some fish may remain within the same favourable conditions by moving up and down with the tide, although spawning herring do not (Nelson-Smith, 1964) and other species recorded from the upper reaches are known to be indifferent to salinity changes.

In the estuary of the Dee, which has smaller tides and a proportionally much greater freshwater inflow, Milne (1940) found that the horizontal and vertical "order of resistance" was the same, i.e. those species occupying higher levels on the shore (and therefore subjected to lower salinities in that estuary) also penetrated further upstream. This is not quite true for Milford Haven, where the regime of salinity changes is probably far more complex. Table 6 lists orders of resistance for four animals common to the Dee and Milford Haven. Horizontal and vertical orders of resistance are certainly not the same among the larger species of brown algae, which Milne did not separate.

Table 6. *Horizontal and vertical "Order of Resistance"*

R. DEE	MILFORD HAVEN			
Horizontal and vertical order	Horizontal order (miles above Thorn Is.)		Vertical order (ft. above CD at Lawrenny)	
B. balanoides	*Mytilus*	18	*Patella*	21
L. littorea	*L. littorea*	15	*L. littorea*	19
Mytilus	*Patella*	14	*Mytilus*	17
Patella	*B. balanoides*	14	*B. balanoides*	15

The organism at the head of each list is either found highest on the shore or penetrates furthest up the estuary. For the river Dee (Milne, 1940) the order is the same in each case.

Ballantine (1961) suggested that exposed shores enjoy a slightly more temperate climate than sheltered shores in the same locality and observed a latitudinal trend on European coasts, where some exposed shore species seem to occupy increasingly sheltered shores towards the southern end of their range. The majority of the common sedentary species penetrating well upstream in Milford Haven have either a northern or a cosmopolitan distribution; most of the southern forms occur only in the lower reaches or around the mouth. It is interesting to speculate on the possible changes in distribution which may follow the inevitable if slight heating effect of cooling-water effluent from the Pembroke Power Station.

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