THE MEDITERRANEAN CREVICE HABITAT

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INTRODUCTION

For a number of years the Mediterranean coast, in the region of Banyuls-sur-Mer, has been a centre for marine ecological studies. General faunistic investigations have been undertaken by PRUVOT (1895, 1897) and DELAMARE DEBOUTTEVILLE (1954). Most ecological studies have been concerned with invertebrate groups, or with individual species (TOPSENT, 1892; PRUVOT and RACOVITZA, 1895; HARANT, 1927; RABAUD, 1939; CHARNIAUX LEGRAND, 1951; PICARD, 1951; HARTMANN, 1953; BRÉMOND, 1958; MONNIOT, 1961; to name only a few).

Recently several papers have appeared on the faunas of specialised habitats, such as the mesopsammon (ANGELIER, 1950; DRAGESCO, 1953*a*, 1953*b*; DELAMARE DEBOUTTEVILLE, 1953), coralligènes (LAUBIER, 1958, 1959, 1961), « des herbiers de Posidonies » (KERNEÏS, 1960), and the trottoir (DELAMARE DEBOUTTEVILLE and BOUGIS, 1951; SCHUSTER, 1956, 1962). Another previously neglected environment, with a characteristic microfauna, is the littoral rock crevice habitat.

The crevice habitat has been described briefly by STELFOX (1916) for northeast Ireland, BARNES (1924) for southwest England, and BAUDOIN (1939, 1946) for Brittany in northwest France. Many other writers have observed the habitat or noted members of its fauna (MONIEZ, 1889; IMMS, 1905; KEW, 1911; MORTON, 1960; SCARRATT, 1961; GABBUTT, 1962; LEWIS, 1962; KENSLER, 1964*a*). The first major investigation of the habitat was published by GLYNNE-

TABLE 1. *Classification of the coastal geology for the area delineated in Figure 1.*

	METAMORPHIC
A :	Schistes de Laroque noirs bleuâtres souvent sériciteux, à petits nodules siliceux, rappelant les schistes à nodules de l'horizon de Trémadoc dans la Montagne-Noire (Laroque, Cerbère).
B :	Cambrien. — Dans la chaîne des Albères et le massif du Roc-de-France, on observe une épaisse masse de schistes plus ou moins grossiers, alternant avec des lits quartziteux verdâtres. Cette série est affectée le plus souvent par un métamorphisme plus ou moins complet allant des schistes sériciteux aux gneiss granitoïdes.
AB :	Combination of formations A and B.
	SEDIMENTARY
C :	Terrasses quaternaires caillouteuses de 30 à 35 mètres, en général très démantelées et à l'état de lambeaux.
D :	Alluvions modernes fines et sablo-limoneuses en surface, caillouteuses en profondeur des basses vallées du Réart, du Tech et du Llobregat.

WILLIAMS and HOBART (1952), on crevices in North Wales. Their paper gives field and laboratory observations on the feeding habits of some selected species, as well as notes on the physical conditions operating within crevices. Shortly thereafter, MORTON (1954) examined similar crevices at Plymouth, in the southwest of England, and discussed the ecological factors of importance within the habitat. More recently, KENSLER (1964*b*) compared the fauna and physical conditions in the crevice habitat of western Norway, with those of North Wales (GLYNNE-WILLIAMS and HOBART, 1952) and southwest England (MORTON, 1954).

During the latter months of 1963, I investigated the crevice habitat in southwestern Europe and North Africa, studying suitable areas in France, Spain, Gibraltar, Portugal and Morocco. This paper is the result of a month's stay at Laboratoire Arago, Université de Paris, and deals in detail with the type of crevice habitat and its fauna found in the Banyuls-sur-Mer area (Pyrénées-Orientales). Figure 1 shows the locality studied, extending approximately 25 kilometres from Collioure, France, in the north, to Punta Cañones, Spain, in the south — along the Côte Vermeille of the Mediterranean Sea.

The *Plymouth Marine Fauna* (1957) has been followed, wherever possible, in regard to scientific nomenclature and authorities.

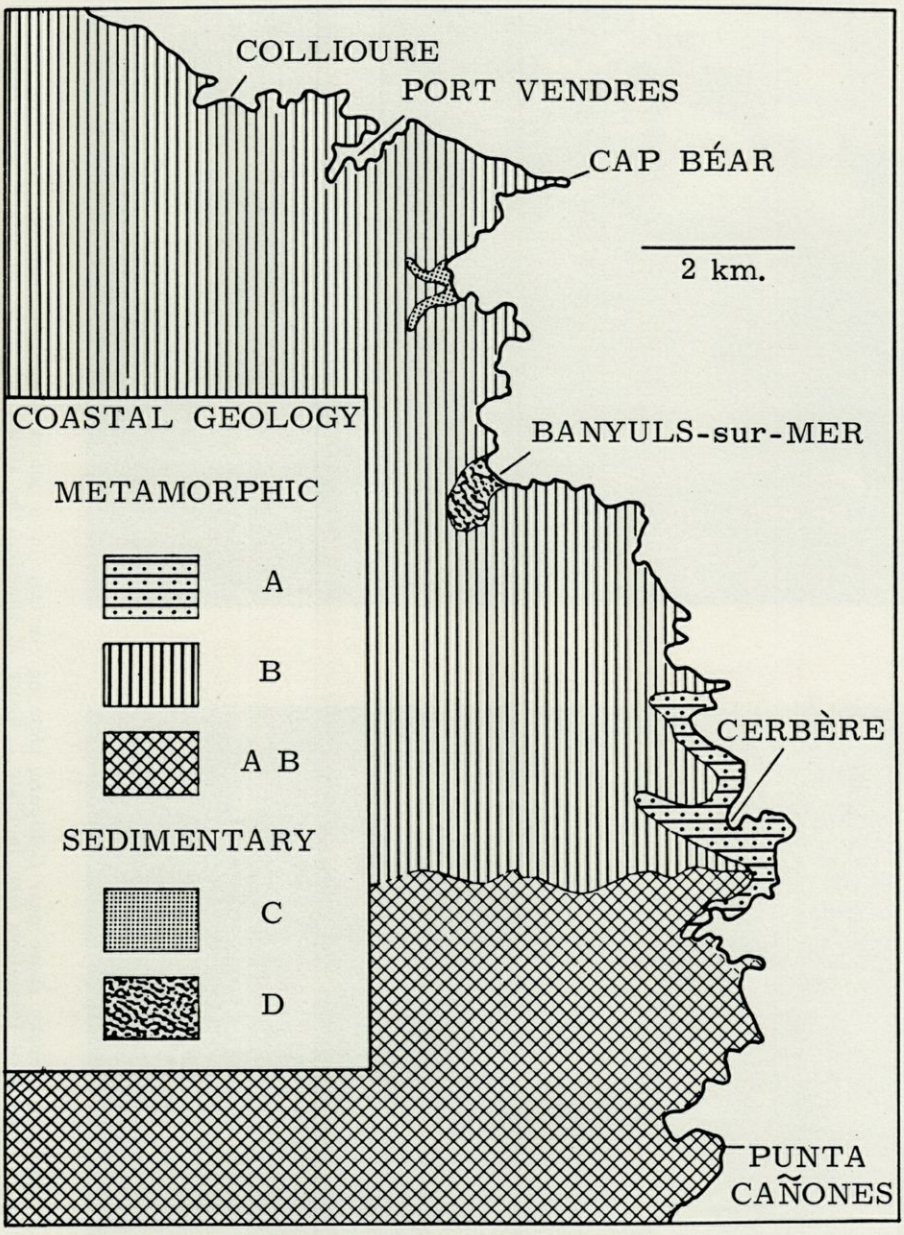
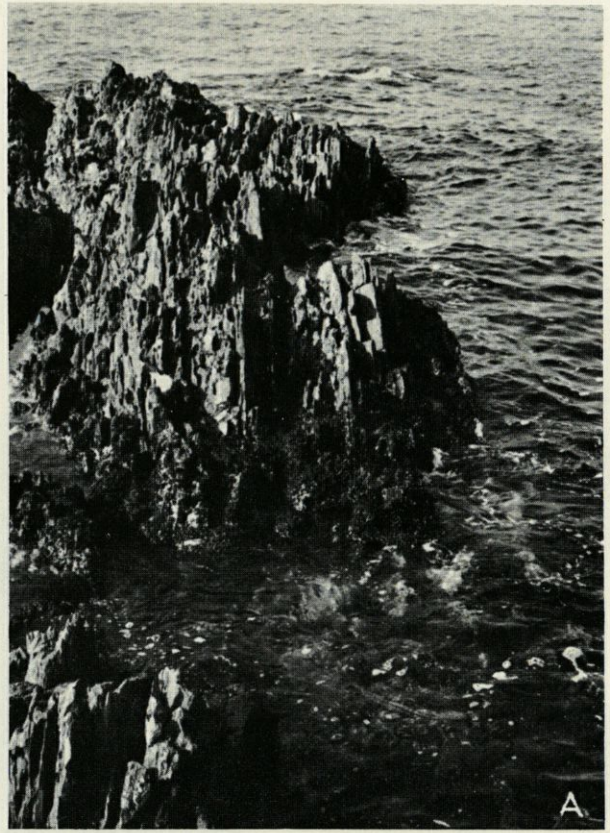


Fig. 1. — Map of the area investigated in the western Mediterranean, in the vicinity of Banyuls-sur-Mer, France. The coastal geological formations are shown in stipple, and are defined in Table 1.



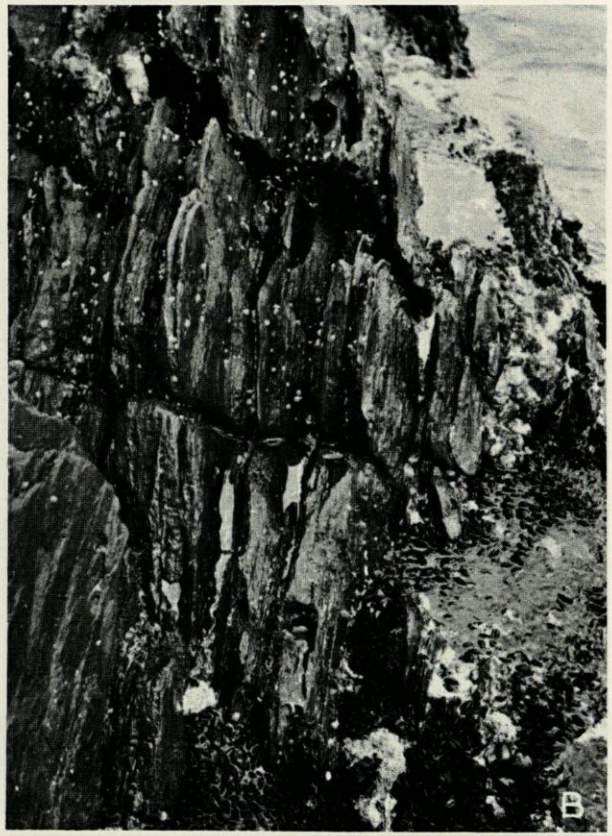


PLATE 1. — A, a rocky shore near Collioure, showing crevices in a schist formation, suitable for examination. B, crevices in the schist formation seen in Plate I, figure A, showing the ability of schist to cleave upon action of weather and water. The crevice openings portrayed are 2 to 10 mm wide.

DESCRIPTION OF SHORE AND HABITAT

The shoreline of the region studied (fig. 1) is a series of exposed rocky headlands separated by sheltered sandy coves. From figure 1 and table 1 it is seen that the majority of the coastal region is composed of schists, with two small pockets of sedimentary rock occuring at Banyuls-sur-Mer, and again four kilometres to the north. Most of the coastline was unfit for this study as few suitable crevices were available for investigation. However, the shore between Collioure and Port-Vendres contained an abundance of suitable crevices, and the majority of field work was therefore accomplished in this region. Plate 1, figure A, shows a shore near Collioure possessing many crevices appropriate for the study. A limited number of crevices were also examined in the immediate vicinity of Punta Cañones, Cerbère, and Banyuls-sur-Mer.

The crevices examined in this study were narrow fissures, up to 10 mm. wide at the opening, with a narrow inward extension of up to 30 cm. The ability of schist to cleave into deep narrow crevices by the action of weather and water has been discussed by KENSLER (1964*b*), and is shown in detail in plate 1, figure B.

The sediments within the Banyuls crevices varied greatly from one site to another, depending on tidal level and exposure to water and wind. Generally, little sediment was present in comparison with crevices examined in Wales, Norway, Portugal, or the Atlantic coast of Morocco, where much of the sediment was composed of broken shells, and pieces of algae. Sand and silt were the main sediments in crevices in the Banyuls region, with only a small amount of broken shell and algae being present.

The shore in general, and the crevice habitats in particular, of the Banyuls region can be contrasted in other respects with those investigated by GLYNNE-WILLIAMS and HOBART (1952) and KENSLER (1964*b*). The predicted tidal range at Banyuls varied from only 0.12 metres at Spring Tides to 0.06 metres at Neap Tides, with an average of 0.09 metres (THE ADMIRALTY TIDE TABLES, 1962). On the west coast of Anglesey, in North Wales, the predicted average tidal range was 3.2 metres (KENSLER, 1964*b*), whilst in western Norway the average was 0.9 metres (KENSLER, 1964*b*). The Banyuls region experiences maximum and minimum surface water temperatures of 23.1 °C and 9.5 °C (unpublished records from Laboratoire Arago, 1958), as compared to values of 15.0 °C and 6.9 °C for waters off Anglesey, North Wales (BOWDEN, 1955), and 16.2 °C and 2.5 °C for western Norway (KENSLER, 1964*b*). Surface salinity

values, for the three localities, also show appreciable differences. As would be expected, the Banyuls area generally experiences high salinities, the maximum and minimum figures being 38.29 $^0/_{00}$ and 34.21 $^0/_{00}$ (unpublished records from Laboratoire Arago, 1958). In comparison, the salinity of the Irish Sea, off North Wales, generally lies between 34.24 $^0/_{00}$ and 34.05 $^0/_{00}$ (BOWDEN, 1955), and lower values would be expected inshore. Waters in the fjords of western Norway, where the investigation was made (KENSLER, 1964*b*), have maximum and minimum salinities of 34.31 $^0/_{00}$ and 24.31 $^0/_{00}$.

METHODS AND MATERIALS

This study was primarily descriptive and quantitative methods (see MORTON, 1954, pg. 191-192) were not used. The fauna was sampled in a number of suitable crevices at various tidal levels, and at sites subjected to different degrees of wave and wind exposure. A greater variety of crevice species was encountered by this procedure than would have been found had a smaller number of crevices been examined quantitatively.

Two methods can be used to force open a suitable crevice for examination. I have found that a long (40-50 cm) crowbar is the best tool for the purpose, as a great amount of leverage is obtainable with it. A hammer and cold chisel can also be used, but the pounding necessary to force in the chisel tends to break the rock or slate laminae into small pieces which are more difficult to examine for the fauna. On opening a crevice it is always advisable to secure the quickly moving specimens first, and then to search for the more sedentary forms. Useful instruments for collecting the fauna are tweezers, probes, various sized spatulae, and camel hair brushes (which are essential for the collection of arachnida and insecta specimens). The collected specimens and samples of the sediments were brought to the laboratory, in plastic vials and containers, for identification and examination.

THE FAUNA

During the study 105 species were listed from crevices. This list is probably by no means complete, but indicates the commoner species and groups within the habitat. As remarked by MORTON (1954), « ... This part of the tidal zone forms an interesting meeting place of two faunal elements, those intertidal animals of terrestrial

origin and those which are truly marine... ». The terrestrial element is defined as those species which have been derived from groups that are regarded as terrestrial, for example, the arachnida, myriapoda, insecta and pulmonate gastropods. Many of these species are still dependent on atmospheric oxygen for their respiration even though they live in a predominately marine environment. Similarly, the marine element is defined as those forms derived from typically marine groups, such as the nemertini, polychaeta, prosobranchia and lamellibranchia. Some of these species have developed means of using atmospheric oxygen, such as species of *Littorina* and *Chthamalus,* where the gill surface is enclosed in a chamber communicating with the air outside by means of a small aperture.

The fauna was extremely varied, some forms being permanent crevice species, whilst other forms were temporarily present because the crevice formed a temporary refuge. Some species were present only when juvenile and spend their adult life outside the crevice. Others, not obligatory crevice forms, are also found under stones (hypobiotic), whilst some species were accidental to the crevice and were more common outside the habitat. Therefore, the faunal communities within the habitat were classified into five ecological groups with decreasing affinity for the habitat. These groups are listed below.

**** Permanent crevice species ... spend their whole life in the crevice.

*** Temporary crevice species ... use the crevice as a refuge throughout life.

** Juvenile crevice species ... use the crevice as a habitat when young, but must emerge to complete their growth.

* Hypobiotic species ... common in crevices and also under stones and similar restricted habitats.

Those species without astericks (*) are accidental crevice species ... found in some crevices but more common outside.

The following 105 species were recorded from the crevice habitat during the study.

The marine forms :

COELENTERATA

Anthozoa

** *Actinia equina* L., ** *Anemonia sulcata* (Pennant).

PLATYHELMINTHES

Turbellaria

* *Leptoplana alcinoi* Schmidt, * *Thysanozoon brocchii* Grube.

NEMERTINI

Anopla

* *Lineus gesserensis* (O.F. Müller).

Enopla

* *Emplectonema gracile* (Johnston), * *Eunemertes peronea* Quatrefages, * *Prosorhochmus claparedi* Keferstein, * *Amphiporus lactifloreus* (Johnston), * *Tetrastemma melanocephalum* (Johnston).

ANNELIDA

Polychaeta (sedentary)

* *Terebella lapidaria* (L.), *Sabella pavonina* Savigny, *Dasychone bombyx* (Dalyell), *Serpula vermicularis* L., * *Spirorbis (Dexiospira) pagenstecheri* Quatrefages, * *Spirorbis (Leodora) laevis* Quatrefages, * *Spirorbis (Laeospira) borealis* (Daudin), * *Spirorbis (Laeospira) cornu-arietis* Philippi, * *Pomatoceros triqueter* Philippi.

Polychaeta (errant)

* *Harmothoë imbricata* (L.), * *Lagisca extenuata* (Grube), * *Lepidonotus clava* (Montagu), * *Eulalia viridis* (O.F. Müller), * *Syllis gracilis* Grube, * *Syllis amica* Quatrefages, * *Syllis (Typosyllis) armillaris* (Müller), * *Syllis (Typosyllis) prolifera* (Krohn), * *Syllis (Typosyllis) vittata* Grube, * *Trypanosyllis zebra* (Grube), * *Nereis diversicolor* O.F. Müller, * *Perinereis cultrifera* (Grube), * *Perinereis macropus* (Claparède), * *Perinereis marionii* (Audouin et Milne Edwards).

SIPUNCULOIDEA

* *Physcosoma granulatum* (Leuckart), * *Aspidosiphon clavatus* (Blainville).

ARTHROPODA

Cirripedia

* *Verruca stroemia* (O.F. Müller), *Chthamalus stellatus* (Poli), * *Chthamalus depressus* (Poli), *Balanus perforatus* (Bruguière).

Tanaidacea

* *Tanais cavolini* Milne Edwards.

Isopoda

Anthura nigropunctata Luc., * *Gnathia maxillaris* (Montagu), * *Sphaeroma serratum* (Fabricius), * *Dynamene bidentata* (Adams), *Idothea hectica* Pallas, * *Jaera albifrons* Leach.

Amphipoda

Lysianassa longicornis Luc., * *Gammarus locusta* (L.), * *Orchestia gammarella* (Pallas), * *Hyale nilssoni* (Rathke), * *Amphithoë rubricata* (Montagu), *Caprella aequilibra* Say.

Decapoda

** *Eriphia spinifrons* Herbst, * *Porcellana platycheles* (Pennant), ** *Pachygrapsus marmoratus* Fabricius, ** *Carcinus maenas* (L.), * *Pilumnus hirtellus* (L.), *Acanthonyx lunulatus* Risso.

Pycnogonida

* *Ammothea echinata* Hodge.

MOLLUSCA

Polyplacophora

** *Chiton olivaceus* Spengler, *Lepidochitona cinereus* (L.), ** *Acanthochitona crinita* (Pennant).

Gastropoda

*** *Diodora apertura* (*Montagu*), *** *Patella vulgata* L., *** *Patella intermedia* Jeffreys, *** *Patella caerulea* L., *** *Patella aspera* Lamarck, *** *Patella lusitanica* Gmelin, *** *Patella tarentina* von Salis, *** *Acmaea unicolor* Forbes, *** *Cantharidus striatus* (L.), *** *Calliostoma zizyphinum* (L.), *** *Monodonta turbinata* Born, * *Gibbula umbilicalis* (da Costa), *** *Gibbula rarilineata* Michaud, * *Littorina neritoides* (L.), *** *Clanculus cruciatis* L., * *Hydrobia ulvae* Pennant, * *Cerithiopsis tubercularis* Montagu, *** *Triphora perversa* (L.), *Pisania striata* Gmelin, *** *Fossarus ambiguus* L.

Lamellibranchia

Arca tetragona Poli, * *Arca lactea* L., * *Arca pulchella* Reeve, * *Cardita calyculata* L., * *Chama gryphoides* L., ** *Mytilus galloprovincialis* Lamarck, ** *Mytilus minimus* Poli, * *Lasaea rubra* (Montagu), * *Hiatella arctica* (L.), * *Hiatella striata* (Fleuriau), * *Gastrochaena dubia* (Pennant).

ECHINODERMATA

Asteroidea

** *Asterina gibbosa* (Pennant).

Ophiuroidea

** *Ophiothrix fragilis* (Abildgaard), * *Amphiura filiformis* (O.F. Müller).

Echinoidea

** *Paracentrotus lividus* (Lamarck).

VERTEBRATA

Pisces

** *Blennius montagui* Fleming.

The terrestrial forms :

ARTHROPODA

Isopoda

* *Ligia italica* Fabricius.

Acarina

*** *Hydrogamasus salinus* (Laboulb.), *** *Halotydeus hydrodromus* Halbert., *** *Bdella* sp.

Pseudoscorpionidea

**** *Garypus littoralis* L. Koch.

Chilopoda

**** *Henia bicarinata* Meiner.

Apterygota

* *Anurida maritima* Laboulbéne.

SPATIAL DISTRIBUTION WITHIN THE HABITAT

The crevice may be divided into outer zones, closer to the opening, and the inner zones penetrating more deeply toward the interior. Usually the terrestrial species are found in the inner zones, whilst the majority of the truly marine species occupy the outer zones.

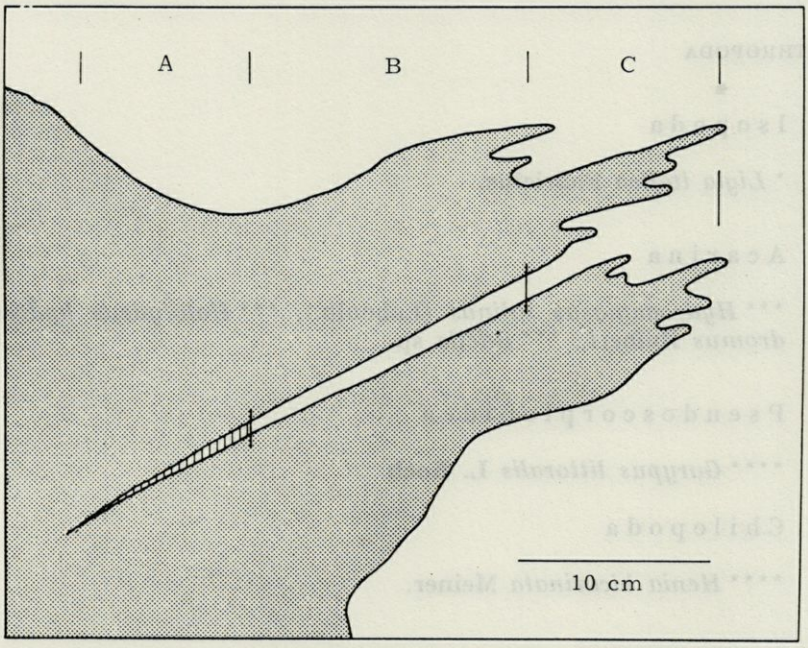


Fig. 2. — Drawing of a « typical » crevice examined during the study, showing the zones A, B, and C within the habitat, which are discussed in the text.

A diagrammatic section of a typical crevice in the Banyuls region is shown in figure 2. Three zones have been recognised within the crevice, A the innermost, B the intermediate, and C the outer zone. Figure 3 shows distribution and density diagrams of twelve selected species within a typical crevice. In this figure, A, B and C refer to the same three zones illustrated in figure 2. As the abundance of each species varied from one crevice to another the quantities shown in figure 3 are averages calculated from the examination of twenty suitable crevices, and refer to the average number of specimens per crevice.

The inner region (A) of the crevice is always the least inhabited. This narrow section is partially filled with detritus, sand, and clay deposits, with some air filled interstices between the

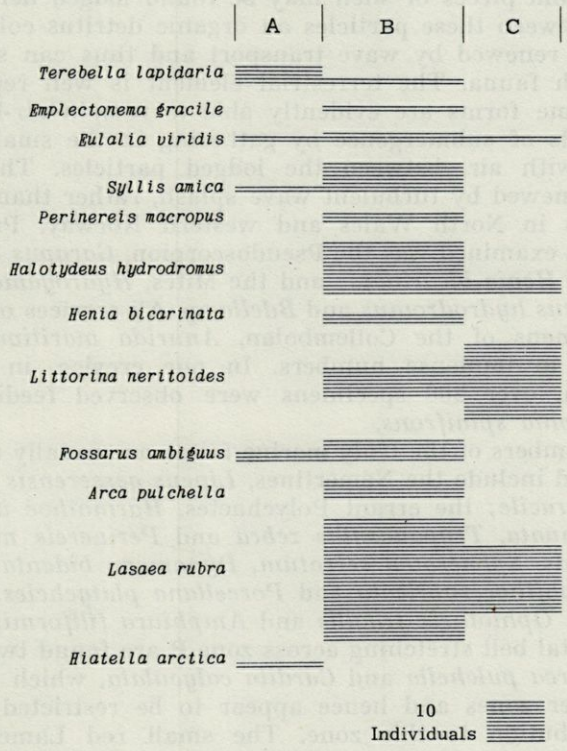


Fig. 3. — Histograms showing abundance and spatial distribution, of 12 selected species, within crevices in the Banyuls region. The letters A, B, and C refer to the zones portrayed in Fig. 2. Each horizontal line regardless of length, represents one individual.

material. In such clean spaces are found some specimens of the Chilopod *Henia bicarinata,* and the small Collembolan *Anurida maritima,* both of which are more common to zone B. The burrowing Lamellibranches, *Hiatella arctica* and *Gastrochaena dubia;* the Nemertines, *Eunemertes peronea* and *Tetrastemma melanocephalum,* are also found in this area, as is the Sipunculoid, *Physcosoma granulatum.* Several errant Polychaetes likewise penetrate into this narrow sedimented zone A. *Syllis amica* and *Eulalia viridis* are the most common, though both occur more frequently in zone B.

The region of greatest abundance and variety of species is found in the second zone (B) of the crevice, as can be seen from figure 3. At this depth the crevice is kept relatively free of permanent deposits by the action of wave splash, but small stones, coarse sand and pieces of shell may be found lodged here. In the interstices between these particles an organic detritus collects and is frequently renewed by wave transport and thus can support a relatively rich fauna. The terrestrial element is well represented here, and some forms are evidently able to remain air-breathing during periods of submergence by gathering in the small spaces, interlocked with air, between the lodged particles. This air is frequently renewed by turbulent wave splash, rather than by tidal oscillation as in North Wales and western Norway. Present in some crevices examined was the Pseudoscorpion, *Garypus littoralis;* the Chilopod, *Henia bicarinata;* and the Mites, *Hydrogamasus salinus, Halotydeus hydrodromus* and *Bdella* sp. All crevices opened revealed specimens of the Collembolan, *Anurida maritima,* which was present in immense numbers. In one crevice, in an area 11 cm $\times$ 4 cm, over 200 specimens were observed feeding on a decaying *Eriphia spinifrons.*

Some members of the truly marine fauna are usually restricted to zone B, and include the Nemertines, *Lineus gesserensis* and *Emplectonema gracile;* the errant Polychaetes, *Harmothoë imbricata, Lagisca extenuata, Trypanosyllis zebra* and *Perinereis macropus;* the Arthropods, *Sphaeroma serratum, Dynamene bidentata, Hyale nilssoni, Amphithoë rubricata* and *Porcellana platycheles,* and the Echinoderms, *Ophiothrix fragilis* and *Amphiura filiformis.* In this same horizontal belt stretching across zone B are found two Lamellibranches, *Arca pulchella* and *Cardita calyculata,* which were not noted in other zones and hence appear to be restricted in their spatial distribution to this zone. The small red Lamellibranch *Lasaea rubra* was found to be one of the most abundant animals of the Mediterranean crevices examined during this study, as in the southwest of England, where it is the most abundant animal on the upper shore (MORTON, 1954). *Lasaea* penetrates inward to the junction of zones B and C, where it sometimes forms a dense horizontal belt stretching across zone B. At this depth *Lasaea* reaches its maximum size, 3 mm in length, and is pale in colour or transparent. In the outer region (zone C) *Lasaea* grows to a smaller size and becomes more deeply pigmented. In some low water crevices an interesting hypobiotic variety of *Chthamalus depressus* was found in zone B, extending up to the junction of zones B and C. The taxonomic status, and some ecological features, of this form (referred to as var. b, and thus distinguished from the splash zone form var. a) are discussed by KENSLER, BHATNAGAR and CRISP (1965).

Zone C, the outermost region, is characterised by an abundance of larger animals which may shelter in the crevice opening, or move freely in and out whilst feeding. As this region receives a maximum of wave exposure, the crevice lip is populated by the barnacle *Chthamalus stellatus,* which quickly thins out before reaching zone B. Other sessile suspension feeders at this horizontal level are the sedentary Polychaetes, *Spirorbis pagenstecheri, Spirorbis borealis,* and *Pomatoceros triqueter.*

Small specimens of the colourful sea-Anemones, *Actina equina* and *Anemonia sulcata* are sometimes noted around the crevice opening, or actually attached to the sides of the inner lip. Tiny specimens of *Actina,* 3 to 10 mm in diameter, were found as deep as the junction of zones B and C. A number of other species occur up to the junction of zones B and C, such as the flatworms, *Leptoplana alcinoi* and *Thysanozoon brocchii;* the Isopod, *Idothea hectica;* and Amphipod, *Caprella aequilibra;* small specimens of three Decapods, *Eriphia spinifrons, Pachygrapsus marmoratus,* and *Carcinus maenas;* young *Mytilus galloprovincialis* and *Mytilus minimus,* pale brown in colour, attached to the substrate by their byssus; and the Echinoderms, *Asterina gibbosa* and *Paracentrotus lividus.* Many of the Gastropods given in the fauna list exhibited a « wandering behaviour », being commonly found foraging on the rock surfaces outside the crevice, as well as around the crevice lip, and penetrating inward to the junction of zones B and C. Although they are not, properly speaking, crevice-dwelling animals the young stages regularly enter the habitat and are encountered in a quarter of the crevices examined. Among such « wanderers », *Diodora apertura, Patella caerulea, Patella tarentina, Acmaea unicolor* and *Gibbula umbilicalis* are the most frequently noticed.

Immense numbers of *Littorina neritoides,* the small lusitanian periwinkle, were found in crevices higher on the shore in the splash zone. This species is highly adapted to withstand desiccation and is able to live for weeks without wetting. Its favourite haunt is inside empty barnacle shells along the inner crevice lip, where it is always plentiful in association with *Lasaea rubra* and the minute, bluish-black, Collembolan, *Anurida maritima.* To a lesser extent *Littorina* penetrates into zone B, where small specimens can be found in clusters. Occasionally a small specimen of the Teleost, *Blennius montagui* was noted lodged in air-filled crevices lower on the shore. *Ligia italica,* the terrestrial Isopod, is also to be found in this region in large numbers. It is an active scavenger, and probably emerges from the crevice at night to feed, as does the boreal species *Ligia oceanica* (Linnaeus) (Nicholls, 1931*a*, 1931*b*).

It is interesting to note that only two species, *Anurida maritima* and *Eulalia viridis,* were common to all three zones of the habitat,

and were also observed occasionally outside the crevice wandering over the rock surface. Specimens of *Anurida maritima* shelter in the empty shells of *Chthamalus stellatus* on the lower shore in the company of the minute red and black Mite, *Halotydeus hydrodromus*. Higher on the shore *Anurida*, and the large red Acarian *Bdella*, inhabit the vacant shells of *Chthamalus depressus*, which also contain *Littorina neritoides* in plenty. Solitary specimens of *Eulalia viridis*, the dark green errant Annelid, were encountered outside the crevice wandering over the *Chthamalus* belt. Although no specimens were noted to be feeding on barnacles, it is almost certain that further observations will reveal *Eulalia* to be a predator of *Chthamalus*. On numerous occasions, whilst investigating crevices in North Wales and northwest Scotland, I have observed *Eulalia* feeding on *Balanus balanoides* (L.), by inserting its proboscis into the slightly gaping valves and absorbing the soft parts.

SOME COMPARISONS OF MEDITERRANEAN CREVICE FAUNA WITH THAT OF NORTH WALES AND WESTERN NORWAY

KENSLER (1964*b*) has compared the more northern fauna of west Norwegian crevices with that of North Wales and southwest England. As a number of systematic differences were revealed, it seemed worthwhile to extend this comparison to crevices examined in the Mediterranean, to the south.

Twenty species were common to crevices examined in Norway, Wales, and the Banyuls region. Figure 4 shows the abundance, and spatial distribution within the crevice, of six selected species common to all three localities. The distributions within crevices examined in southwest England by MORTON (1954) are not given as they correspond closely to those of North Wales. Figure 4 illustrates the similarities in distribution in the crevices, whenever they are found, and the variations in abundance of the same species from one geographical area to another. From figure 4 it can be seen that *Lineus gesserensis, Emplectonema gracile* and *Carcinus maenas* are progressively less plentiful in southern waters. On the other hand, *Eulalia viridis* and *Anurida maritima* are cool temperate species, being found in greatest numbers in temperate waters, and soutwest England, and slightly less common in western Norway and the Mediterranean. The periwinkle, *Littorina neritoides*, has a more southern distribution, being extremely abundant in the Mediterranean but scarce in southwestern Norway (LEWIS & TAMBS-

LYCHE, 1962; KENSLER, 1964*b*). Another warm water species found in all three localities, but omitted from figure 4, is *Lasaea rubra*. Although the species was a regular element in the crevice fauna community of western Norway (KENSLER, 1964*b*), it was found in much greater abundance in the Banyuls region.

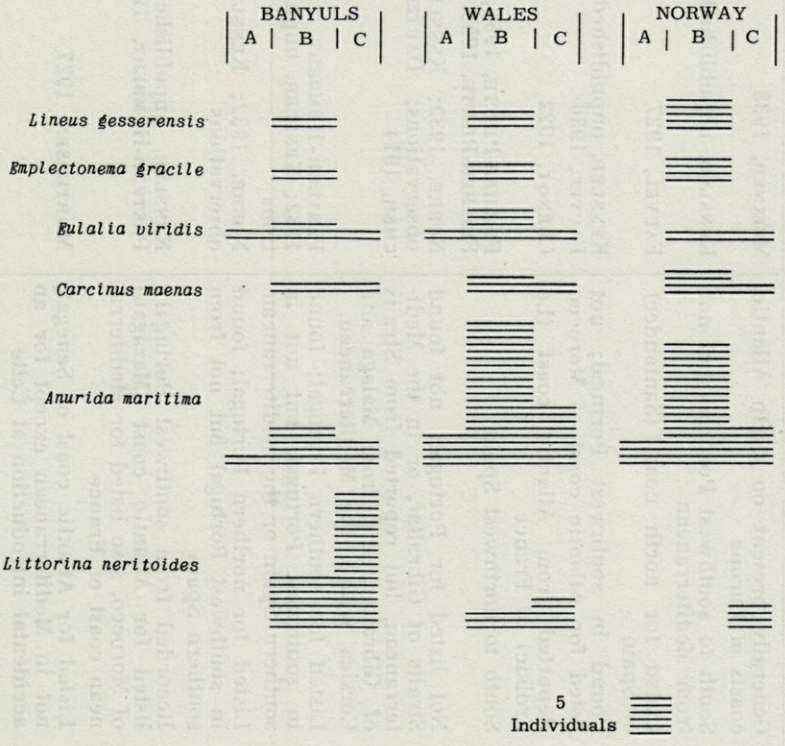


Fig. 4. — Comparative histograms of abundance and spatial distribution of six species common to crevices in the Banyuls region, North Wales and western Norway. The letters A, B, and C refer to the zones portrayed in Fig. 2. Each horizontal line, regardless of length, represents one individual.

In addition to the six species shown in figure 4, a number of other forms were also common to crevices examined in western Norway, North Wales, and Banyuls. The species were as follows, *Amphiporus lactifloreus, Spirorbis (Laeospira) borealis, Pomatoceros triqueter, Harmothoë imbricata, Syllis (Typosyllis) prolifera, Nereis diversicolor, Tanais cavolinii, Jaera albifrons, Gammarus locusta, Orchestia gammarella, Hyale nilssoni, Lepidochitona cinereus, Acanthochitona crinita,* and *Lasaea rubra.*

TABLE 2. *Species commonly noted in crevices in western Norway and North Wales but not at Banyuls. Information is also given on the southern distribution of each species.*

Species	Information on southern limits of distribution	Reference
Procerodes ulvae (Oersted)	Generally present on north Atlantic coasts of Europe	MEIXNER, 1938
Lineus longissimus (Gunnerus)	South to southwest Portugal, but not from Mediterranean	KENSLER, unpublished observations
Scolecolepis girardi (Quatrefages)	Listed for north coast (Santander) of Spain	FAUVEL, 1927
Cirratulus cirratus (O.F. Müller)	Found in southwest Portugal; not listed for Atlantic coast of Morocco	KENSLER, unpublished observations; FAUVEL, 1936
Golfingia minuta (Keferstein)	Reported from Atlantic coast (Le Croisic) of France	CUÉNOT, 1922
Balanus balanoides (L.)	South to northwest Spain	FISCHER-PIETTE, 1955; CRISP & FISCHER-PIETTE, 1959
Littorina littoralis (L.)	Not listed for Portugal; not found Straits of Gibraltar, or in the Mediterranean, but reported from Straits of Gibraltar, and from Malaga and Corsica within the Mediterranean.	NOBRE, 1932; KENSLER, unpublished observations; DAUTZENBERG & FISCHER, 1914
Littorina littorea (L.)	Listed for southern Portugal; found in southwest Portugal, but not in southern Spain or the mediterranean.	PASTEUR-HUMBERT, 1926*a*; NOBRE, 1932; KENSLER, unpublished observations
Littorina saxatilis (Olivi)	Listed for northern Portugal; found in southwest Portugal but not from southern Spain	NOBRE, 1932; KENSLER, unpublished observations
Nucella lapillus (L.)	Recorded from southwest Portugal : listed for Atlantic coast (Mazagan) of Morocco, also listed for Mediterranean coast of France	KENSLER, unpublished observations : PASTEUR-HUMBERT, 1962*a*
Asterias rubens L.	Listed for Atlantic coast of Senegal; not in Mediterranean except for an accidental introduction at Cette	MORTENSEN, 1927
Scolioplanes maritimus (Leach)	Listed for southwest England; found along north coast of France	PLYMOUTH MARINE FAUNA, 1957; BRÖLEMANN, 1930
Petrobius maritimus (Leach)	Listed for southwest England	PLYMOUTH MARINE FAUNA, 1957

TABLE 3. *Species commonly noted in crevices on the coast of North Wales but not at Banyuls. Information is also given on the southern distribution of each species.*

Species	Information on southern limits of distribution	Reference
Audouinia tentaculata (Montagu)	Listed for English Channel, and Atlantic; not listed for Banyuls	FAUVEL, 1927; LAUBIER & PARIS, 1962
Elminius modestus Darwin	Northwest Portugal, but still spreading	FISCHER-PIETTE & PRENANT, 1957
Tanais chevreuxi Dollfus	Found at Casablanca, Morocco; found along Atlantic coast (Cap Blanc) of Morocco, but not in Mediterranean	MONOD, 1925; KENSLER, unpublished observations
Campecopea hirsuta (Montagu)	Generally present on Atlantic and Mediterranean coasts of southern Spain	KENSLER, unpublished observations
Cingula (Onoba) semicostata (Montagu)	Reported from Mediterranean	FRETTER & GRAHAM, 1962
Blennius pholis L.	Found in western waters of the Mediterranean	JENKINS, 1925
Neobisium maritimum (Leach)	Present along northern and western coasts of France	KEW, 1911
Aëpophilus bonnairei Signoret	Reported from northwest France	BAUDOIN, 1939, 1946
Aëpopsis robinii (Laboulbène)	Listed for the Isle of Man; listed for southwest England; reported from Roscoff in northwest France	MARINE FAUNA OF THE ISLE OF MAN, 1963; PLYMOUTH MARINE FAUNA, 1957; LE MASNE, 1938, BAUDOIN, 1946
Cyrthydrolaelaps hirtus Berlese	Listed for southwest England	PLYMOUTH MARINE FAUNA, 1957
Leucophytia bidentata (Montagu)	Reported from Mediterranean, and Madeira	JEFFREYS, 1869
Ovatella myosotis (Draparnaud)	Reported from Mediterranean, and Madeira	JEFFREYS, 1869
Otina ovata (Brown)	Listed for southwest Portugal; found along south Atlantic coast of Spain, but not found in the Mediterranean	NOBRE, 1932; KENSLER, unpublished observations

Comparisons of the three faunas also revealed significant absences from one locality to another. Table 2 lists some boreal species commonly noted in crevices in western Norway and at Anglesey in North Wales, but not encountered in the habitat at Banyuls. Brief information on the southern distribution for each species is also given. Some species were commonly noted in crevices in North Wales but were not found in the Banyuls region. Such species, and information on their southern distribution, are given in table 3.

The majority of the above species, listed in tables 2 and 3, are boreal forms. Therefore temperature may well be the most important factor apparently limiting these species to regions outside the Mediterranean. However, species such as *Cirratulus cirratus, Audouinia tentaculata, Cingula (Onoba) semicostata, Leucophytia bidentata* and *Ovatella myosotis* are usually restricted to crevices containing considerable deposits of finer grades of silt and mud. The absence of such species from Mediterranean crevices might be attributed to the scarcity of organic suspended matter in the unusually clear waters of this sea. In all the stations I have studied, *Tanais chevreuxi* and *Otina ovata* are found only in crevices on exposed shores. The absence of heavy surf may account for the species not being found in the crevices at Banyuls. Both species were noted at exposed sights in southern Spain at the Atlantic entrance to the Gibraltar Straits (Unpublished Observations), but were not recorded from any localities within the Mediterranean, all of which however were relatively sheltered. So far as the needs of *Tanais chevreuxi* are concerned, the crevices at Banyuls also lacked 1) suitable coarse deposits of broken shell and gravel, used in the construction of the « galleries » inhabited by the species, and 2) organic detritus on which the species feed.

Table 4 lists some southern species that were frequently noted in crevices at Banyuls but their biogeographical limits apparently did not extend to North Wales or western Norway. Table 5 lists four additional southern species commonly found at Banyuls and in North Wales but not noted in western Norway. For tables 4 and 5 some information on the northern distribution of each species is also given. It indicates that in most instances the southerly distribution of these members of the crevice fauna is attributable to the operation of biogeographical factors, of which temperature is probably the most important.

The amount and type of material present in a crevice depends primarily upon the transport of water-borne material from locally formed deposits. These in turn depend upon the degree of exposure to wave action (Crisp & Southward, 1958). Consequently, a crevice subjected to a high degree of exposure will contain sediments of

large coarse particles such as gravel, broken shell, and pieces of algae. Finer sediments of sand, mud, and silt do not accumulate in the vicinity of such exposed shores because of the severity of the wave action which wash them away before they can form deposits. Crevices experiencing a medium degree of wave action usually contain deposits of sand, mixed with small amounts of shell, silt and algae. Larger particles such as stones, gravel and broken shell cannot be transported by more gentle wave action and are therefore not usually present. Fine grades of mud and silt also are not present if the exposure is too great to permit their accumulation. Exposure of a low degree, as in confined landlocked harbours and narrow channels, results in great accumulations of mud and silt being formed, sometimes with smaller amounts of sand. Larger particles cannot be readily transported, but mud and silt is present in the water as a result of small waves and tidal currents. Hence, in regions where the degree of exposure is low, the crevices are quickly filled with deposits of mud and silt.

Furthermore, the amount of organic matter in the water will influence the biomass that the crevice can support. In regions of high productivity, with rich quantities of suspended organic matter, the material accumulating in crevices will in turn have a high organic content and will support more organisms. Conversely, in clear oligotrophic waters, as in many parts of the Mediterranean, the crevice will be poorly endowed with organic detritus.

A comparison of crevices from western Norway, North Wales, and Banyuls bore out these general principles. It revealed that the quantity of organic matter (both living and dead) and the amount of inorganic deposit were quite obviously greatest in crevices in North Wales, where both exposure and water opacity due to suspended particles were high, and least in crevices at Banyuls where the exposure was less but the water very clear. From a number of observations along various European and North African coasts (which will be published later) it appears that the abundance of animal life in crevices increases with the amount of deposited sediment, provided that this is coarse enough to remain aerobic. The results are therefore as might be expected in a relatively dark and confined habitat where the animals depend mainly on allochthonous nutrients.

The results of various investigations on the crevice faunas of western Norway (KENSLER, 1964*b*), North Wales (GLYNNE-WILLIAMS & HOBART, 1952; KENSLER, unpublished observations), southwest England (MORTON, 1954) and Banyuls are tabulated in table 6, and reveal several additional points. Firstly, the total number of species recorded for each locality varied greatly. From table 6 it would appear that North Wales had the richest fauna, and western

TABLE 4. *Species commonly noted in crevices at Banyuls but not in North Wales or western Norway. Information is also given on the northern distribution of each species.*

Species	Information on northern limits of distribution	Reference
Leptoplana alcinoi	Listed for Mediterranean; not listed for southwest England	LANG, 1884; PLYMOUTH MARINE FAUNA, 1957
Eunemertes peronea	Found in southern Portugal; not listed for southwest England	KENSLER, unpublished observations; PLYMOUTH MARINE FAUNA, 1957
Terebella lapidaria	Listed for southwest England; not listed for the Isle of Man	PLYMOUTH MARINE FAUNA, 1957; MARINE FAUNA OF THE ISLE OF MAN, 1963
Perinereis macropus	Found in the Mediterranean (Naples, Monaco); not listed for southwest England	FAUVEL, 1923; PLYMOUTH MARINE FAUNA, 1957
Perinereis marionii	Listed for southwest England; not listed for the Isle of Man	PLYMOUTH MARINE FAUNA, 1957; MARINE FAUNA OF THE ISLE OF MAN, 1963
Chthamalus depressus	Mediterranean, and adjacent south Atlantic coast of Spain	KENSLER, BHATNAGAR & CRISP, 1965
Eriphia spinifrons	Southwest Brittany (Concarneau), France	CRISP & FISCHER-PIETTE, 1959
Pachygrapsus marmoratus	Southwest Brittany (Concarneau), France	CRISP & FISCHER-PIETTE, 1959
Fossarus ambiguus	Common in western Mediterranean to Straits of Gibraltar; not listed for Portugal; not listed for southwest England	KENSLER, unpublished observations; NOBRE, 1932; PLYMOUTH MARINE FAUNA, 1957

Arca pulchella	Common in Mediterranean; not listed for Portugal	Pasteur-Humbert, 1962*b*; Nobre, 1932
Cardita calyculata	Listed for south and west Portugal; not listed for southwest England	Nobre, 1932; Plymouth Marine Fauna, 1957
Blennius montagui	Listed for southwest England; not listed for the Isle of Man	Plymouth Marine Fauna, 1957; Marine Fauna of the Isle of Man, 1963
Mytilus minimus	Present along Atlantic coasts of Portugal and France; not found north of Arcachon, France; not listed for southwest England.	Pasteur-Humbert, 1962*b*; Crisp & Fischer-Piette, 1959; Plymouth Marine Fauna, 1957
Paracentrotus lividus	Found on west coast of Ireland; not listed for the Isle of Man	Southward & Crisp, 1954; Marine Fauna of the Isle of Man, 1963
Ligia italica	Not listed for southwest England	Plymouth Marine Fauna, 1957
Hydrogamasus salinus	Listed for southwest England; not listed for the Isle of Man	Plymouth Marine Fauna, 1957; Marine Fauna of the Isle of Man, 1963
Garypus littoralis	Littoral Mediterranean; not listed for southwest England	Perrier, 1954; Plymouth Marine Fauna, 1957
Henia bicarinata	Found on Mediterranean shores; not listed for southwest England	Brölemann, 1930; Plymouth Marine Fauna, 1957

TABLE 5. *Species commonly noted in crevices at Banyuls and in North Wales but not in western Norway. Information is also given on the northern distribution of each species.*

Species	Information on northern limits of distribution	Reference
Dynamene bidentata	Listed for the Isle of Man; found in northwest Scotland; not listed for Norway	MARINE FAUNA OF THE ISLE OF MAN, 1963; KENSLER, unpublished observations; SARS, 1896-9; KENSLER, 1964*b*
Gibbula umbilicalis	Listed for the Isle of Man; northern limit northwest coast of Scotland	MARINE FAUNA OF THE ISLE OF MAN, 1963; LEWIS, 1957; CRISP & FISCHER-PIETTE, 1959
Asterina gibbosa	Listed for the Isle of Man; found on west coast of Scotland	MARINE FAUNA OF THE ISLE OF MAN, 1963; MORTENSEN, 1927
Halotydeus hydrodromus	Found in Anglesey, North Wales, but not in northwest Scotland; not listed for the Isle of Man; listed for western Ireland	KENSLER, unpublished observations; MARINE FAUNA OF THE ISLE OF MAN, 1963; HALBERT, 1915, 1920

Norway the poorest. The figure of 53 species recorded for the habitat in southwest England (MORTON, 1954) is probably misleadingly low. MORTON did not purport to give an exhaustive list, but was primarily interested in particular aspects of the habitat, such as the classification of microhabitats, the vertical and horizontal distribution of animals in crevices, and the ecological factors and ,successions operating within the crevice. Probably the crevice fauna of southwest England agrees closely in richness of species with that of North Wales.

Table 6 also shows that the number of marine species is always greater than the number of terrestrial species. It is also seen that very few species are permanent and exclusively crevice forms. Western Norway had only one such species, the Chilopod, *Scolicoplanes maritimus*. North Wales and southwest England had several exclusively crevice species in common, the Tanaidacean, *Tanais chevreuxi;* the Hemiptern, *Aëpophilus bonnairei;* the Coleopteran, *Aëpopsis robinii; Scolicoplanes maritimus;* the Pseudoscorpion, *Neobisium maritimum;* and the Pulmonates, *Leucophytia bidentata* and *Otina ovata*. The Banyuls region had only three exclusively crevice species, the Gastropod, *Fossarus ambiguus;* the Pseudoscorpion, *Garypus littoralis;* and the Chilopod, *Henia bicarinata*.

A large percentage of hypobiotic species was recorded from each locality, and such forms are usually not readily dsitinguished from permanent crevice species. A comparison of the percentage of 'specialised crevice forms' (permanent + hypobiotic) with the percentage of relatively 'non specialised crevice forms' (temporary + juvenile + accidental) shows the following : western Norway, 78 % specialised and 22 % non specialised; North Wales, 87 % specialised and 13 % non specialised; southwest England, 89 % specialised and 11 % non specialised; and Banyuls, 59 % specialised and 41 % non specialised. Thus, Banyuls recorded the lowest percentage of 'specialised crevice forms' and the highest percentage of 'non specialised forms'. Several factors may account for such findings. As mentioned earlier in this paper, the crevices at Banyuls contained little deposited material. Therefore, as the crevices were relatively clean they were not highly specialised as a habitat. Thus fewer highly 'specialised crevice forms' were present and a greater space was available for 'non specialised crevice forms' to enter into the habitat.

TABLE 6. *Ecological divisions of the crevice fauna for various geographical regions.*

	WESTERN NORWAY	NORTH WALES	*SOUTHWEST ENGLAND	BANYULS
Total number of species recorded	46	127	53	105
Number of marine species	41 (89.1 %)	121 (95.3 %)	36 (67.8 %)	98 (93.3 %)
Number of terrestrial species	5 (10.9 %)	16 (4.7 %)	17 (32.2 %)	7 (6.7 %)
Number of permanent species	1 (2.2 %)	8 (6.3 %)	8 (15.1 %)	3 (2.8 %)
Number of temporary species	5 (10.8 %)	4 (3.1 %)	1 (1.9 %)	17 (16.2 %)
Number of juvenile species	3 (6.5 %)	9 (7.1 %)	4 (7.5 %)	13 (12.4 %)
Number of hypobiotic species	35 (76.1 %)	102 (80.4 %)	39 (73.6 %)	59 (56.2 %)
Number of accidental species	2 (4.4 %)	4 (3.1 %)	1 (1.9 %)	13 (12.4 %)

The figures in brackets refer to the percent of the population per each locality.
* The information is taken from the work of MORTON (1954), and is based on the assumption that species behave in southwest England as in North Wales.

SUMMARY

Rock crevice habitats were studied in the vicinity of Laboratoire Arago, Banyuls-sur-Mer, France —— extending from Collioure, France, in the north, to Punta Cañones, Spain, in the south. The action of water and weather cleave narrow crevices into the schist formations to depths of as much as 30 cm, and with openings of up to 10 mm wide.

One hundred and five species were recorded from the habitat during the study. The groups comprising the crevice community were of two origins, terrestrial, and truly marine. Furthermore, the fauna was classified into five ecological groups, with decreasing dependence on the habitat : 1) permanent crevice species, 2) temporary crevice species, 3) juvenile crevice species, 4) hypobiotic species, and 5) accidental crevice species. Twelve regularly occurring species were shown to be limited to certain regions in the crevice, some showing preference for the innermost regions, and some for the outermost regions.

Crevices at Banyuls were compared with those of two localities at higher latitudes. Twenty species found at Banyuls were common to crevices examined in western Norway and North Wales. In six species, whose abundance was measured objectively, the abundance varied with latitude but the distribution within the crevice was similar. Differences in the cervice fauna of Banyuls from those of localities at higher latitudes are attributed largely to differences in seasonal temperature and the amount and type of deposit present within the crevice. The biomass supported by the crevice is believed to be closely determined by the amount of organic matter that enters the crevice from the water.

A comparison of the faunas from crevices in western Norway, North Wales, southwest England, and Banyuls revealed the following general points. Firstly, the number of marine species is always greater than the number of terrestrial species. Also, very few permanent and exclusively crevice forms are recorded, whereas a large percentage of hypoboitic species (i.e. species common both to crevices and similar protected habitats) was recorded from each locality. The crevices examined in the Banyuls region were found to contain relatively little deposited material and therefore did not provide as specialised a habitat as did crevices in western Norway, North Wales, and southwest England, where much greater deposited material was present. Thus fewer ' specialised crevice forms '

(i.e. permanent + hypobiotic) were present and a greater number of relatively 'non specialised crevice forms' (ie. temporary + juvenile + accidental) were found in the habitat.

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