THE BIOLOGY OF *PURPURA LAPILLUS*. PART III. LIFE HISTORY AND RELATION TO ENVIRONMENTAL FACTORS

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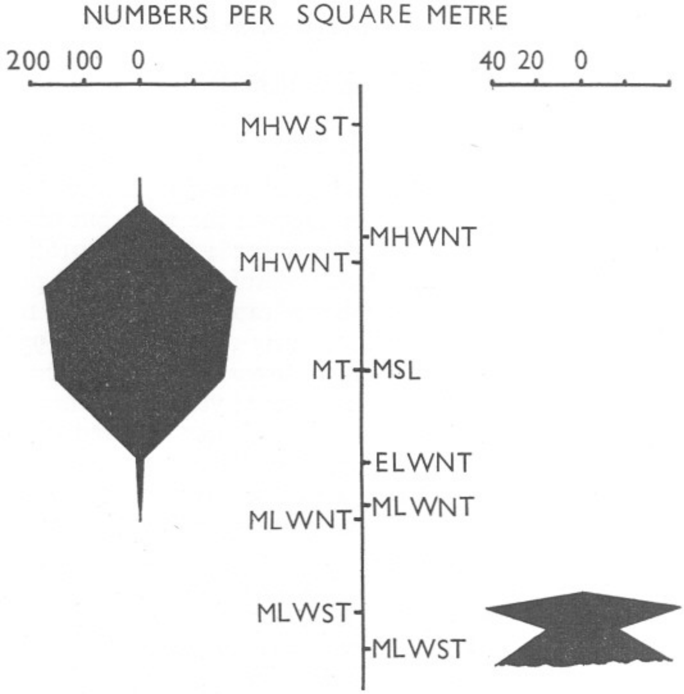
(Text-fig. 1 and Plate I)

Life History

The eggs of *Purpura* are laid in vase-shaped capsules, attached in clusters to the rocks. Spawning takes place throughout the year, but chiefly in the winter and spring (Pelseneer, 1935; Moore, 1938; Colton, 1916). It is said to take more than an hour to produce one capsule, and 24 hr to produce ten (Pelseneer, 1935, p. 508), and the number of capsules laid at one time is said to average fifteen, and to range from six to thirty-one (Pelseneer, 1935, p. 490). Cooke (1895, p. 124) states that a single *Purpura* produces as many as 245 capsules. The capsules contain a large number of yolky eggs, the estimates of the numbers of these per capsule varying from three hundred to a thousand (Colton, 1916; Pelseneer, 1935, p. 527). Most of these ova are unfertilized and serve as food for the few embryos which develop: five to forty according to Pelseneer (1935, p. 481), ten to twelve according to Colton (1916). The time of development is about 4 months (Pelseneer 1935, p. 527). The capsules are laid in crevices in the rocks, or sometimes under stones, but at the same tidal level as that inhabited by the adults. The young, when hatched, are generally supposed to retreat into cracks in the rocks, presumably at the same level, and Colton states that they feed there on small *Mytilus*. I myself have examined many such crevices close to hatching groups of *Purpura* eggs, but have rarely found young shells less than 5 mm. high in them. On the other hand I have frequently found numbers of young *Purpura* down to 2 mm. in height living among the tubicolous polychaete *Spirorbis borealis* on the underside of stones at a much lower tidal level than that inhabited by the adults, and have come to the conclusion that this is their normal habitat for the first few months. And, since the distance would be great for such small shells to walk, it seems probable that they are washed down there by wave action, from the capsules from which they have hatched. In experiments in a tidal tank (Moore, 1938), it was found that the newly hatched *Purpura* would not eat even very small barnacles, but lived well on a diet of *Spirorbis*. It was noticed further, that at a height of about 8–10 mm., they showed a tendency to climb out of the tank as if conditions there did not suit them, and that this tendency was stopped if they were provided with some stones covered with barnacles. It is probable therefore that at about this size they normally change their diet and begin to move up the shore on to the barnacle-covered rocks, and it is at about this size that they are first found there in any numbers. Probably even then they at first spend a good deal more of their time sheltering in crevices than do the larger individuals, a possibility which has already been suggested on the ground of shell coloration (Moore, 1936, p. 82). The difference in tidal level of the young and adult habitats is clearly brought out in Text-fig. 1.



Text-fig. 1. Vertical distribution of adult *Purpura* (> 10 mm.) at Òb Allt an Daraich, on barnacle-covered rocks (left), and of young (< 10 mm.) under *Spirorbis*-covered stones at Wembury (right). Note that, owing to tidal differences in the two localities, the relative tidal levels do not exactly coincide.

The diet which the adult *Purpura* seems to prefer is barnacles, either *Balanus balanoides* or *Chthamalus stellatus*. They do not bore the shells of the barnacles, but force the valves apart and then eat out the soft parts. Dubois (1909), in discussing the extremely toxic nature of purpurin, suggests that the animal may use it to kill and relax its prey so that it can force the valves apart and attack the exposed body. It is quite possible that this may happen with barnacles, although nothing can be seen of the process, since the greater part of the barnacle is covered by the foot of the *Purpura* attacking it. Various gastropods are attacked by *Purpura* including *Patella vulgata*, *Gibbula cinerarea* and *G. umbilicalis*, *Littorina littorea*, *L. obtusata* and even sometimes *Purpura* itself, although in the last-named I have never seen a shell which was bored right through. The hole has been shown to be bored entirely by the radula, unaided by any acid secretion (Pelseneer, 1935). The mollusc which is most subject to attack, and in some places comprises the entire diet of the *Purpura*, is the mussel *Mytilus edulis*. Fischer-Piette (1935) has given an extremely interesting account of the changes which took place on a piece of shore which was at first inhabited mainly by barnacles and by *Purpura* which fed on them. Over this shore there was an invasion of *Mytilus*, and gradually the *Purpura* ate all the available barnacles and found themselves forced to eat the mussels. Apparently they did this at first only when forced to, taking by preference their accustomed diet of barnacles. Their efforts to penetrate the mussels, which had never before been included in their diet, were at first clumsy. Some wasted time by boring holes in empty shells, and some even settled inside empty shells and bored a hole outwards. After a time these mistakes became less frequent and finally ceased, and later still the *Purpura* learned to force apart the valves of the smaller shells without having to bore them at all. Finally the *Purpura* killed so many mussels that the barnacles, which had been displaced from the rocks, were able to recolonize them, and eventually the *Purpura* returned to their original barnacle diet. This slowness of the *Purpura* in learning to utilize mussels when these first colonize a normally barnacle-covered rock has been noted elsewhere also, and may account for the fact that in some places where the barnacle-covered rocks have small patches of mussels growing on them, the latter are left completely untouched by the *Purpura* which are feeding all round them on the barnacles, while in other apparently similar situations the bulk of the *Purpura* are feeding on the mussels, and a few only are on the barnacles. Fischer-Piette noted that when the barnacles recolonized the rocks the *Purpura* did not attack them until they were some six months old and had attained a fair size.

The mortality which they cause is very great: as described by Fischer-Piette it was sufficient to change the whole balance of life on a piece of shore. An estimate for the mortality rate of *Balanus balanoides* made at Port Erin (Moore, 1934, p. 860) was 35 and 21 % per annum at the two lower stations worked, this being probably almost entirely due to *Purpura* although these particular rocks were frequently cleared of all *Purpura*, as they were wanted for experiments on the growth of the barnacles. The rate would no doubt be much greater on rocks habitually crowded with *Purpura* like those shown in Plate I, fig. 1.

The *Purpura* do not feed continuously, and are frequently found clustered in large numbers in crevices, either for shelter or for the purpose of breeding. According to Fischer-Piette (1935) they are driven to shelter by extreme cold or by the risk of drying up, and they then pass into a state of aestivation. Probably this also is liable to happen after a large meal, and he notes that those which are living among clusters of mussels are frequently trapped at such times by the mussels' byssus threads, which become attached to their shells and anchor them so firmly that they are unable to escape and so die.

Relation to Environmental Factors

There are very few observations available on the tolerance of this species to variation in the environment, although certain notes on limiting values have been made. With regard to tidal level, Colman (1933) says that *Purpura* occurs at Wembury from one foot above mean sea level to half way between mean and equinoctial low water of spring tides, that is from 55 to 10 % emersion. Fischer-Piette (1936) gives its upper limit as high water of neap tides. It certainly does not extend above the upper limit of barnacles, and this is usually about high water of neap tides, unless elevated by splash. Usually, however, *Purpura* becomes less abundant some way below the top of the barnacle zone. Its lower limit is less well defined and varies greatly from one place to another. It can certainly live in the sublittoral zone in some places, and even down to a depth of 10 fathoms (Moore, 1936, p. 84), but this is unusual; extreme low water of spring tides is probably its normal lower limit, and its occurrence even as low as this will depend on the presence of barnacles or other suitable food at that level. In sheltered waters barnacles may not go below half-tide level, and unless there are *Mytilus* present the *Purpura* also will stop at that level. The above statement applies only to the larger sizes, above about 10 mm. in height. The young, as has already been shown, live in the *Spirorbis* zone which frequently takes the place of the *Balanus* zone towards low water, and all those places where we have found very small *Purpura* in abundance have been about low water of spring tides. It is usually difficult to find sufficiently large unbroken surfaces on which to make comparative counts of the density of population of the larger *Purpura* at the different levels, but Text-fig. 1 shows the result of such a count made at Òb Allt an Daraich, in Skye, one of the levels being also shown in Pl. I, fig. 1. The distribution of small *Purpura*, at a stage when they are still feeding on *Spirorbis*, made in a stony gully at Wembury, Devon, is also shown in Text-fig. 1, for comparison with the zonation of the adults.

Gowanloch (1927) gives the upper lethal temperature for *Purpura* as 35–35·5° C.; and the proximity of its northern limit of distribution to the 0° C. winter isotherm (Moore, 1936) suggests the presence of ice as the limiting factor there. Colton (1916) also comments on its absence from places where ice accumulates, whilst Gislén (1930) states that in the Gullmar Fjord it descends below low water for the winter, presumably to avoid the ice. Caullery (1929) has noted it as one of the species which suffered from the coincidence of a very cold spell during the winter on the Boulogne coast with the occurrence of low water of spring tides, and Orton & Lewis (1931) record the effect of the unusually cold weather in January–February 1929 in greatly reducing the proportion of *Purpura* to *Urosalpinx* on the oyster beds of the Blackwater estuary. On the latter occasion, however, it is not possible to say whether the result was directly due to the low temperature or perhaps to a reduction of tolerance to low salinity produced by the lowering of the temperature, comparable with that recorded by Broekhuysen (1936) for *Carcinus maenas*.

Its tolerance to low salinity is probably low, despite Pelseneer's statement (1935, p. 323) that it can survive 9·5 days in fresh water. Fischer (1928) records it in the estuary of La Rance between the salinities of 35·0 and 22·8 ‰; Alexander, Southgate & Bassindale (1935) also state that it is confined to the extreme mouth of the Tees estuary (which, however, is strongly polluted), and it certainly does not penetrate beyond the extreme mouths of the Tamar and Yealm estuaries at Plymouth. Ökland also (1933) has shown that round the island of Tromö, *Purpura* does not occur where the summer salinities fall below 20–25 ‰, even where *Mytilus* and *Balanus balanoides* offer abundant food for it. Fischer (1928) states that the eggs are tolerant of the same salinity range as the adults, but he found (1931), during a winter drop in salinity in La Rance estuary, that the eggs were killed although the adults survived.

With regard to limiting values of other factors there are practically no data available. Fischer (1927) gives its upper limit of *p*H in pools as 9·3, and later (1931) gives its *p*H range in pools as 9·3 to 7·45. He also gives its oxygen range in pools as 26 to 5·8 mg. per l. These figures however mean little without a knowledge of how long such conditions can be endured. *Purpura* occurs occasionally, though not commonly, in muddy surroundings, where it has the appearance of having been introduced accidentally and not having bred there. At Blue Anchor Bay, near Minehead, just beyond the extreme eastern limit of penetration of *Chthamalus stellatus* up the south side of the Bristol Channel, no *Purpura* were found, although *Balanus balanoides* was present in small numbers. The limiting factor here was probably the muddiness of the shore.

Enemies

There are no data available at present as to the mortality rate or normal duration of life of *Purpura*. Several marked individuals lived on the shore at Port Erin for $2\frac{1}{4}$ years, and were probably $1\frac{1}{2}$–$2\frac{1}{2}$ years old when first marked, but they can probably live much longer than this. If the rings found on the shells of *Purpura* by Colton were really annual, then the oldest specimens recorded by him were 7 years old, but these must have been much slower in maturing than is normal in England, since at maturity they would stop growing and form no more annual rings, that is if cessation of growth occurs at all in his communities.

Various animals are recorded as occasionally eating *Purpura*, although most of them probably do not take sufficient numbers to have any appreciable effect on the community as a whole. Colton (1916) suggests that they may be taken by *Gadus virens* at Mount Desert Island, and probably wrasse sometimes take them in English waters. Bauer (1913) has found that shells of *Nassa* inhabited by hermit crabs frequently show a fracture of the last whorl which suggests that they have been broken open by the crab and the animal eaten out of them. He further suggests that the thickening of the lip found in some species of *Nassa* is a protection against the attacks of hermit crabs. Since empty shells of *Purpura* also are frequently found inhabited by hermit crabs the same suggestions would presumably apply to them, but my own impression is that they occupy only shells which are already empty, and that the fractured shells found are the work of birds.

Probably the most serious enemies of *Purpura* are birds, and these in certain localities only. Dewar (1910) has given a detailed account of how *Purpura* shells are broken open by oyster-catchers (*Haematopus ostralegus*). The *Purpura* are removed from the rock and carried either to a crevice or to a patch of firm sand where they can be held steady. They are then turned with the opening up, the lower part of the bill inserted between the operculum and the outer lip, and a piece of this lip broken away either by pressure or by hammering. The shell is then turned slightly and a second chip broken away in a similar manner, by which time the animal is sufficiently exposed for the soft parts to be picked out of the shell. A good many shells resist the attacks of the birds. In a later paper (1913) Dewar records that out of 294 *Purpura* attacked by oyster-catchers, 1 % had only one chip removed, 21 % were completely opened (two chips), while 78 % remained undamaged. He states also (1910) that *Purpura* is an uneconomical food for the oyster-catcher as compared with mussels. In 20 min. a single bird attacked seven shells and opened three of them, whereas many more mussels could have been opened in the time, and he says further that they only eat the *Purpura* sporadically, having a habit of feeding on them for a few days and then leaving them again completely. Colton (1916) says that herring gulls (*Larus argentatus*) eat them, swallowing the smaller shells whole, but carrying the larger shells into the air and dropping them until they break. He says too that on certain islands where the gulls are particularly numerous, the *Purpura* are practically exterminated. In the British Isles gulls certainly take *Purpura* at times as shown in Plate I, fig. 2, which is a photograph of part of the contents of a herring gull's nest containing numerous *Purpura* shells; but an examination of numbers of heaps of shells regurgitated by herring gulls on different parts of the coast shows that, while they may at times be feeding almost entirely on molluscs, *Purpura* forms only a very small proportion of their food.

The *Nassa* shells with a chip out of the lip, attributed by Bauer to the action of hermit crabs, seem to be very similar to those chipped open by oyster-catchers, and similarly chipped shells of *Purpura* have been found by us on grounds where oyster-catchers were common. Quite frequently the animal escapes, although with a damaged shell, and the proportion of shells showing a repaired fracture is high in some populations. Probably a similar cause accounts for the populations in which many of the animals have a damaged operculum or none at all. Cooke (1917) records one such population in which, out of 121 animals examined, fifty-six had damaged opercula, and eleven had none. Other birds also may attack *Purpura* on occasions, and there is even a record by Venables (1936) of a song-thrush which was seen hammering a *Purpura* on a stone during a spell of very cold weather, with a heap of dead *Purpura* shells alongside.

The shells may be attacked by boring algae such as *Gomontia* and *Plectonema* (Moore, 1936), and even very seriously pitted by their action, and the shell may also be damaged by the boring sponge *Cliona cellata* and the polychaete *Polydora*; but it is unlikely that any of these ever kill the animal, since it is able to repair a damaged shell. Various trematode parasites infect the soft parts and may destroy the reproductive organs, but probably these also rarely kill the animal.

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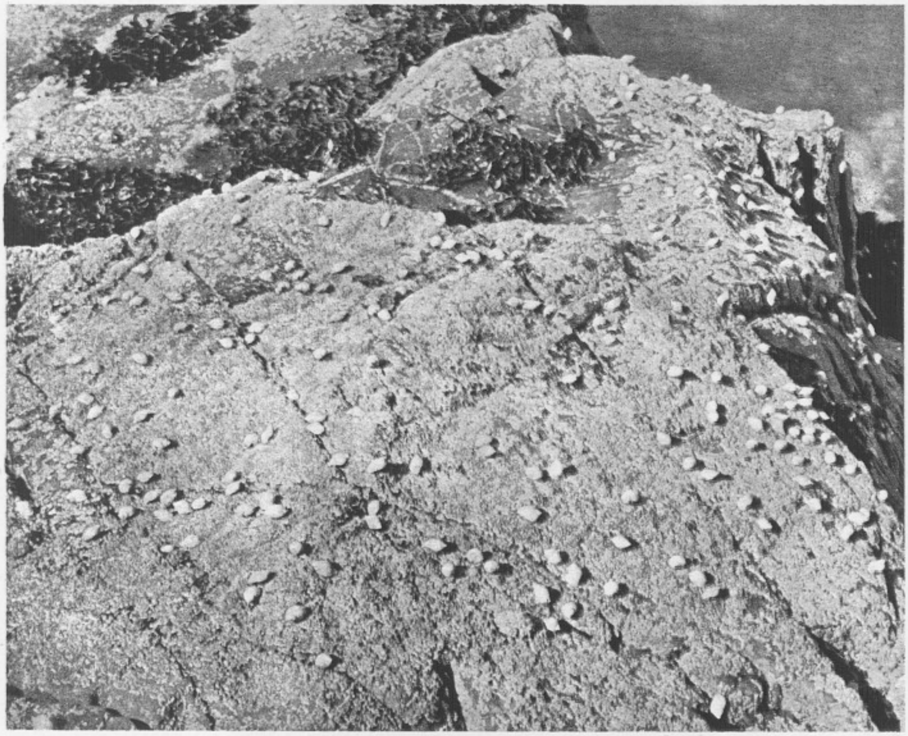
EXPLANATION OF PLATE I

Fig. 1. *Purpura* feeding on *Balanus balanoides* at Òb Allt an Daraich, Skye. 12. vi. 36.

Fig. 2. Part of the contents of a herring gull's nest, Geodha Chobhair, Sutherland, 24. vi. 36, showing fragments of *Purpura lapillus*, *Patella vulgata*, *Balanus balanoides*, *Cancer pagurus*, *Portunus puber* and egg shells. ×0·81.



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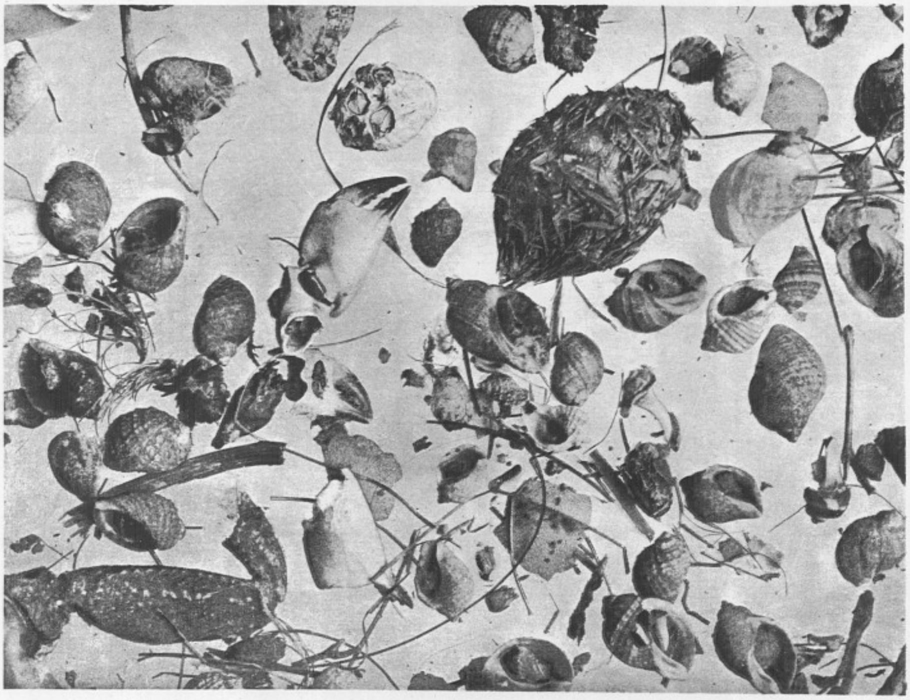

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