THE HABITATS OF FRESH-WATER MOLLUSCA IN BRITAIN[1]

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Ask now the beasts, and they shall teach thee. Job xii. 7

(*With* 63 *Figures in the Text*)

CONTENTS

1. Introduction

We have 62 fresh-water species, 26 bivalves and 36 gastropods, 10 of which are operculates and breathe by gills while the rest are pulmonates which normally breathe air. There are also 4 operculates (*Assiminea grayana, Paludestrina stagnalis* (*ulvae*), *P. ventrosa, Amnicola confusa*) and 2 pulmonates (*Ovatella bidentata, Phytia myosotis*) which affect the junction between fresh and salt water, but I know little about their habitats and shall not consider them further.

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Fresh-water differ from terrestrial habitats in two important particulars. (*a*) The environment is much more uniform from place to place than on land and less variable in any one place from time to time. Hence there is less difference between the inhabitants of various loci: no two watery habitats which are at all favourable to Mollusca will have such diverse contents as, for example, an old acid woodland and a chalk down. It follows too that transplantations, natural or deliberate, should be more likely to succeed than with land Mollusca, and that experimentation under controlled conditions is relatively easy, though it needs far more exploration than it has received from those who like keeping aquaria. (*b*) The habitats are mostly divided into discrete units and are definitely limited in size: some of them are presumably infinitely large from the molluscs' point of view, but others are so small and circumscribed that it seems likely that questions of roominess must arise, almost or quite unknown on land.

For descriptive purposes we may distinguish several groups of habitats classified by common human usage, though these do not of course necessarily correspond with the essential categories of molluscan ecology: they naturally grade into one another and it would be waste of time to try to define them too closely:

Rivers.

Streams.

Springs and the streamlets and trickles which come from them.

Canals.

Ditches.

Lakes, i.e. bodies of water large enough for the wind to raise significant waves and generally too deep in the middle parts for phanerogamic vegetation.

Ponds, of $\frac{1}{2}$ acre downwards and mostly of the order of 400 sq. yd. ($\frac{1}{12}$ acre) or less.

Marshes.

Ponds and, less often, lakes and marshes have to be further distinguished into (1) those through which a stream of water runs either perennially or in the winter and which are thus in communication with the river systems ("running"), and (2) those without any direct connection with another watery habitat ("closed"). We also have to note whether any of the smaller habitats always contain water or whether they dry up in the average summer ("drying") or in exceptional droughts. Ditches include permanent draining ditches connected with marshes, often of considerable size, and ditches made to keep land dry in wet weather which contain no water for most of the year.

The nomenclature is confused in a variety of ways. Thus what would be called a pond in lowland country may be dignified as a tarn, loch, lough or llyn in the hills. A "lake" in many parts of England may be a stream; a "pool" may be a pond, a good-sized lake or a slow-flowing piece of a river; a "ditch" in Ireland sometimes means a fence or bank

(259); and you may either fall into a "dyke" or climb over it; "spring" may mean a wood, and the dialect dictionary would no doubt reveal many other possibilities of perplexity, most of which would, as I hope to show, be solved by a knowledge of the Mollusca present.

It is evident that man has had a good deal to do with many of these habitats, and his influence on our water Mollusca is perhaps hardly less than on the land species. Canals, ditches, marl pits and brick diggings are entirely human and so are most ponds: they provide habitats of which there are few or no natural replicas. Man's interest has always been to get rid of marshes, drain river valleys and generally to make as clear a distinction as he can between dry land and water. In the result most of the places in which we collect, especially in the southern two-thirds of England, are more or less unnatural.

2. General biology

(a) *Food*

The bivalves feed at random by sucking in water and entangling any particles it may contain in their intestinal mucus "with catholic impartiality" (256), though Allen (192) thinks that the labial palps can exercise a certain amount of discrimination. They are therefore dependent on the Algae, etc., which happen to be present, which they filter out quickly and very efficiently, as Dodgson (20) has shown in his work on the cleansing of *Mytilus* from bacterial contamination. Allen found that a 200-gm. *Lampsilus* passed through 35 litres (10 gallons) a day; Dodgson got 53 litres (15 gallons) for *Mytilus* 3 in. long. Algologists would find the intestines of mussels worth study: Latter (1, p. 174) gives a list of the things found in *Anodonta*, and Prof. E. J. Salisbury got some rare Algae in some we caught in the Elstree reservoir. Except *Dreissena*, the bivalves live mostly on the bottom, though *Sphaerium corneum*, *S. lacustre* and some *Pisidium* often climb up plants, and sand or mud in some form seems to be a necessity: *Sphaerium* and *Pisidium* do no good in aquaria without it. But whether this substratum is needed to grow their microscopic food or to give them something to burrow in, I do not know: it may be useful in both ways.

The gastropods are more mobile, can fix themselves anywhere with their adhesive feet, and have the same type of rasping apparatus as the land Mollusca, so that selection is possible. They feed on the decayed remains of water plants and especially on Algae which they scrape off the leaves of the plants, the mud, stones and other surfaces (e.g. floating logs), as may be well seen as they crawl over the glass of an aquarium. In some loci (e.g. mountain lakes, or cement tanks), where there is little or no obvious vegetation it seems quite clear that the normal food of the *Limnaea peregra* and *Ancylus fluviatilis*, which may be abundant, is the algal slime on the stones. As with land Mollusca, it is most exceptional to see any evidence in the field that they eat land Mollusca and beech trees. Similarly, a good many Mollusca will generally be found (in England) with water-lilies or with *Potamogeton crispus*, because these plants usually grow in places which are on other grounds favourable for them, and incidentally the large flat lily leaves provide a convenient and profuse growth of Algae. But the snails can get on quite well without the plants and there is no essential biological connection between them.

(*b*) *Life histories*

Reproduction. The larger mussels (*Anodonta, Unio*) are generally described as unisexual and there is commonly a considerable excess of females: Bloomer (**10**), however, finds a good many hermaphrodites in *Anodonta cygnea*, and it seems pretty clear that individuals change their sex: each female produces about half a million glochidia. *Sphaerium* and *Pisidium* are hermaphrodite and evacuate well-grown young, naturally in small numbers. Crowther (**277**) finds usually 6 or 7 in *Sphaerium corneum* but up to 30: Thiel (**182**) has shown at Hamburg that it has two generations a year with free lives from October to August and August to October, producing about 10 young each time, so that the annual increase is about 100. *Paludina* (unisexual) is also viviparous with about 50 young, as is *Paludestrina jenkinsi* (parthenogenetic) with broods of 20 or 30. The other operculates lay eggs, but no one seems to know how many. The pulmonates are all hermaphrodite and lay eggs. *Limnaea peregra, L. auricularia, L. stagnalis, L. palustris* and some *Physa Planorbis* (**217**) and *Ancylus* are known to self-fertilise quite readily (**13**), and they can probably all do so if need arises though they prefer cross-fertilisation. How many eggs are laid in nature is not clearly known, and our information about what happens in aquaria is very imperfect: in some of the accounts (e.g. Rimmer (294)) there is complete confusion between the number of eggs laid and the number per capsule, though I suspect that the two figures are proportionate to one another since both depend on the size of the parent. In captivity some races of *Limnaea peregra* average about 500 and can achieve as many as 3000 (**11**); other smaller races produce 200 or so. Correspondingly Oldham's data (**12**) suggest about 1000 for *Planorbis corneus* while *Pl. nautileus* has about 30 young. Interesting details about egg laying are given for the Indian *Limnaea luteola* by Sechaiya (**215**) and for the American *L. columella* by Baily (**216**).

Length of life. The larger mussels develop slowly and live for many years: if the lines of growth represent annual increments, 10 or 15 years is a common age and 70 has been suggested. Hence destruction of the adults may seriously diminish the population, as has happened with *Unio margaritifer* in the Scotch pearl fishery (**14**) and in Ireland. *Sphaerium* and *Pisidium* appear to be annuals. *Paludina* lives for several years but probably not as long in nature as in captivity, where Oldham (**15**) has kept female *P. contecta* for 5 years and the males (which are smaller) for at least $3\frac{1}{2}$ years. Cleave and Lederer (**22**) say of *P. contectoides* in America that the wild males live about a year and the females up to 3 years, and Annandale and Sewell (**147**) found the same for *P. bengalensis* in India: it has been known since Spallanzani that one impregnation will suffice for more than the current year. *Bithinia tentaculata* often has such well-defined growth marks and *Neritina fluviatilis* is sometimes so thick and encrusted ("gerontic") that it seems probable that they may live 2 or 3 years, but the rest of the operculates are presumptive annuals as *Paludestrina jenkinsi* certainly is. All the pulmonates are annuals with a natural duration of life of 9–15 months or less, except *Planorbis corneus*, which lives and goes on growing for 2 or 3 years and breeds correspondingly often (**12**, **21**); Oldham has kept it in captivity up to 6 years. In hot summers *Limnaea peregra* may get through 2 generations in one season, as it may easily be induced to do in captivity (**11**, p. 57), and it has been found spawning in November in the underground water which comes out at Malham Cove at 46–48° F. all the year round (Percival MS.). Wild *L. truncatula* in Wales (**197**) normally have 2 or even 3 generations in a summer. This may explain why the largest specimens are found early in the spring and in Scotland. In America *L. columella* breeds a new generation about every 2 months in the laboratory (**23**).

I do not understand the statements that in central Europe (**16**, p. 39) and in north America (**17**, p. 51; **18**, vol. 1, p. 412) such species as *L. stagnalis* need 2 or even 3 years to reach maturity. It may possibly be true for places where a severe winter stops growth for several months, but it certainly does not apply to this country where the annual cycle can be clearly seen in wild *L. stagnalis*, *L. auricularia*, *L. peregra*, *Planorbis complanatus*, etc.

Parasitism, etc. In their early stages the large mussels are obligatory "parasites" on fish. Some American species can apparently pass through their metamorphosis in the parent's brood pouch (**214**), and for one the amphibian *Necturus* makes a good host: the claim (**213**) that they can be reared in simple nutrient solutions needs confirmation. In America, too, where a good deal of attention has been paid to mussels for the sake of pearl buttons, there is some (but not much) evidence that certain species have specific relationships with particular fish (**240**, summary and literature in **18**). In Britain, however, I know of nothing to suggest that fish can be dispensed with or that the kind of fish matters very much. Wilson (in **19**) notes the curious point that parasitic Copepods may so occupy the gills as to prevent the attachment of glochidia. No other fresh-water molluscs are dependent for development or in any other way on another animal.

It occurred to me at one time that the widespread discontinuous distribution of some uncommon species might be due to something queer in their life histories, possibly a parasitic phase. But I have bred the three most conspicuous instances—*Segmentina nitida* (from Lewes), *Amphipeplea glutinosa* (Co. Kildare) and *Limnaea glabra* (Leeds, Scotland) to maturity under conditions which excluded fairly satisfactorily the intervention of another animal or any special plant.

(c) *Mortality*

Enemies and parasites. Fresh-water Mollusca have many enemies. Domestic and domesticated ducks are the worst, and they can completely destroy all the Mollusca in a pond or ornamental water, though this drastic effect may be due as much to the putrefactive fouling of the water as to actual eating. I know of no instance where under natural conditions an enemy may be reasonably accused of exterminating any established species: the great majority of animals which prey on snails are more or less omnivorous, and when a snail population is reduced beyond a certain point they turn their attention to other foods which are easier to find: trout, for example, as Pentelow (**33**) and Slack (**34**) have shown, eat what they can get. Rats (**24**, **181**, **244**), water-shrews (**255**) and otters (**155**) eat mussels and snails. Herons and other birds no doubt kill a good many. Peacock (**222**) has occasionally found *Limnaea auricularia* and *Dreissena* on thrush stones, and Carter (**25**) has seen a thrush pick out *Limnaea stagnalis*, smash and eat it: I have watched a blackbird fish out *Planorbis corneus* from a tank in my garden several times, but no attempt was made to eat them. Bellamy (**26**, p. 246) says that in Devon crows pick mussels out of the rivers and drop them on rocks to smash them as gulls do cockles (**63**), and they have been seen eating *Anodonta cygnea* and *Unio pictorum* (**262**) and *Dreissena* (Oldham), which tufted duck will also dive for and then be robbed by gulls (**263**). Thompson (**264**) mentions a grey wagtail full of *Ancylus fluviatilis*. By general consent fish are very fond of snails which are highly esteemed as fish food in trout hatcheries and also for coarse fish: Hall (**27**) specially commends *Planorbis corneus*, *Limnaea peregra*, *L. stagnalis* and *L. auricularia*, and says that the newly hatched young "seem to be the most acceptable of any food to fresh-water fish". Fishing clubs in Yorkshire buy *L. peregra* in quantity for fish food (**30**), and various large species (including even *Dreissena* (**181**)) seem to be moved about a good deal to rivers and lakes where they do not rightly belong. But the interest of fish is not restricted to the fleshy sorts: several observers (**28**, **29**) have found large numbers of *Valvata piscinalis* in trout's stomachs which must be more shell than meat, as must *Paludestrina jenkinsi* (**253**); in the north of Scotland the contents of the trouts' stomachs are often made up almost entirely of *Pisidium* (Oldham), and Burnett discovered *Limnaea burnetti* because he had the curiosity to see what a trout from L. Skene had inside it. In aquaria Krull (**232**), Henson (**245**) and I have found leeches extremely destructive, and gastropods are said to be the natural food of *Glossosiphonia* and *Helobdella* (**31**, **253**), as they are of the rare bug *Aphelocheirus aestivalis* (**265**). Various carnivorous larvae such as *Hydrophilus* (**188**) and beetles such as *Dytiscus* eat eggs and young snails as may caddis worms (**12**); glowworm larvae readily eat *Limnaea* if they get the chance (**266**). The rotifer *Proales gigantea* is parasitic in the eggs of *Limnaea* (**267**). *Limnaea* frequently harbours the larvae of trematode worms, often in immense numbers, and *L. truncatula* is well known as the usual intermediate host of the sheep fluke, but whether these parasites do the snails much harm seems doubtful unless they are present in great excess (**198**): *Valvata* and *Pisidium* may also be infected. In India and Portugal *Bilharzia* larvae definitely injure and kill their *Planorbis* hosts (**199**). Pelsencer (**268**) gives a long list of parasites. The common *Chaetogaster* is probably immaterial.

Mortality in the young. Whatever the precise destructive agents, field experience suggests strongly that those which are effective in keeping the snail populations within reasonable bounds act on the infants: the killing of adults is generally of no great moment and the eggs[1] seem to be fairly safe. One sees a pond, for instance, with vast numbers of capsules of *Limnaea peregra* or *Planorbis complanatus*, and on searching through them one finds that the eggs are developing in a healthy way almost without exception. Yet in two or three weeks' time it may be quite difficult to find the young snails, and it is exceptional to find young ones much more numerous than adults will be later on: the weeding out seems to occur very soon after birth, and the viviparous species are relatively immune. Similarly, if a reservoir goes dry and one can obtain a view of the mussels, the young ones do not seem to be more than enough to maintain the adult population. This infant susceptibility also applies to adverse physical and chemical conditions: eggs are resistant and can be moved about from one sort of water to another with impunity, and those of *Limnaea stagnalis* will develop normally either in distilled water or 5 % salt solution (**32**). But newly born snails have to be treated with a good deal of care, and they are easily killed by a sudden move to different water which older ones do not seem to notice. In nature, therefore, there is an immense "infant mortality". This does not occur if the changes and chances of wild life are excluded, for the whole of a brood of several hundred *L. peregra* may be safely reared in aquaria if they are given room and food enough. The intensity of selection obviously varies greatly in different species: a population of *Anodonta* would be maintained by the survival of less than 1 in a million of the young; *Limnaea peregra* needs perhaps 1 in 500, *Sphaerium* 1 in 10.

(*d*) *Dispersal*

It is possible for many water Mollusca to spread a long way by continuity of their habitats. A map dated 1870 included in the report of the Canal Commission (1909) shows 215 catchment basins in England and Wales: many of them are small coastal areas, but the Thames includes about 8 % of the whole, the Severn 7·5 %, and the Trent 7 %. The canals which were built between 1760 and 1810 joined together all the larger river systems, and the whole canal basin occupies about half of England and Wales (**8**, Fig. 63 and below, p. 173). Similarly in Ireland the Shannon drains 14 % of the country and in Scotland the Tay covers 8 %. *Planorbis acronicus* (**204**), recent and fossil, is found only

[1] In *Neritina* one embryo in each capsule of about 50 eggs eats the others before hatching.

ponds by competition. Similarly, *Planorbis nautileus* is frequently found in drying ponds especially if they are examined in spring when they contain water. But in our local ponds it occurred in 26 of 42 ponds which did not dry and in only 14 of 42 drying ponds[1] and this is in accord with general experience. *Limnaea palustris* is another species which lives sometimes in surprisingly dry places; Adams (**59**), for instance, calls it "amphibious". Ashford (**60**) says it may "lead an aerial life during summer", and Kew (**61**) mentions it in temporary winter water. In Aldenham I have watched it for 17 years (including the 1921 drought) living in thick grass by the roadside, where it got no more water than ran off the road: it was always plentiful until the place was destroyed in building operations. But its toleration of these conditions is in no way compulsory, for it is definitely more common in a variety of good habitats. The same appears to be true of *Pisidium cinereum* which can tolerate drying loci but is much more frequent in better places.

Of these 9 species which can put up with drying ponds, none is restricted to such places as are *Planorbis umbilicatellus* and *Pl. campestris* in northern Canada (Mozley), where melting snow produces ephemeral ponds each year in the same place in which *Limnaea palustris* and *Physa hypnorum* are frequent with *Sphaerium occidentale,* analogous to *Sph. lacustre* (**17**, **18**). Mozley (**250**) gives a good account of the flora and fauna (including 7 molluscs) of a Canadian pond which held water for less than 3 months in each year.

3. The habitats of the various species[2]

(a) *Bivalves*

The four large mussels—**Anodonta cygnea* (Fig. 36), **A. anatina* (Fig. 37), **Unio pictorum* (Fig. 45), **U. tumidus* (Fig. 46)—live in slow rivers, canals, large draining ditches, lowland lakes, reservoirs and large ponds, mostly running habitats though *Anodonta cygnea* and *Unio pictorum* live in some closed marl pits in Kent and *Anodonta cygnea* in marl pits near Manchester (**175**). The deliberate introduction of fish for angling or in times past for food probably explains why *Anodonta* and *Unio pictorum* are so common in reservoirs and ornamental waters, though they are sometimes put in for their own sakes (**174**) and were at one time eaten in Ireland (**181**; **247**, p. 31) and in the Fens (**243**). Thomasson (**239**) attaches special importance to sticklebacks on which he finds the glochidia. Only *cygnea* lives in Ireland, and in Great Britain it has been recorded as far north as Banff; *anatina* extends as far as Caithness, and the two *Unio* are restricted to England. This distribution is probably due in part to the relative rarity of suitable habitats in the north and west as well as to historical and climatic factors. Their essential needs are fish on which they can pass their early parasitic phase and incidentally travel about and a firm muddy bottom in which they can imbed themselves. Why they spend so much of their time two-thirds sunk in the mud I do not know: it seems an extravagant precaution against being swept away by any ordinary current. But a bottom suited to such a life is obligatory. They will not

[1] The corresponding figures for *Sphaerium lacustre* are 15 and 2 but I doubt whether these are really representative.

[2] In the following catalogue the species which are able to live in quite soft water are marked †, calcicole species ** and those which appear to need at least a moderate amount of lime *: the evidence is discussed in more detail below (p. 148).

live either on a hard stony or gravelly bottom or on one which is covered with a thick layer of soft humus in which they would have to disappear before they found firm ground: hence most closed ponds are unsuitable. The four species have similar tastes and may all occur together. *Anodonta anatina* seems to have rather more preference for rivers than *A. cygnea*, and *Unio tumidus* is distinctly the least common and has the most restricted geographical range: it needs fresher, cleaner water than the others and may be a river species which has extended into canals: Lowe (**243**) failed to get it to live in captivity, though *Unio pictorum* did well. *Anodonta cygnea* with or without *Unio pictorum* sometimes abounds in lakes without any pulmonates or operculates (**273**), which illustrates the dependence of the bivalves on the bottom and of the other groups on the water and vegetation.

**Pseudanodonta rothomagensis* (Fig. 61) (if that be really the correct specific name of the English form) is a river species occurring in the Thames and Severn basins and in some of the midland and Yorkshire canals.

The pearl mussel †*Unio margaritifer* (Fig. 14) lives in a well-defined river habitat, though it is a little difficult to specify the essential qualities. As Adams (**59**) points out it occurs only to the north and west of a line from Scarborough to Beer Head,[1] and a full account of its history and distribution is given by Jackson (**71**). It lives in the R. Exe, and passing thence east and north along the coast its next locus is the Whitby Esk in Yorkshire: travelling the other way it is found in Cornwall, all up the west coast and generally in Scotland north of Stirling, in Shetland, Lewis, Isle of Man and generally in Ireland, except in the central limestone plain and the Shannon basin. It is absent from the whole of the midlands and south-east of England. A typical locus is a quick running river up to 3 or 4 ft. deep with a mixture of boulders, stones and sand; it can burrow in fine gravel and particularly likes the sand which accumulates behind large stones: it also lives in the lakes (e.g. L. Earn) through which such rivers flow. Most of its habitats are places in which fishermen would expect to get trout and hope for salmon, though it occasionally (**194**) occurs in meagre streams. As it happens, most of the characteristic rivers contain soft water, and the areas in England and Ireland where it does not occur have hard water. Hence the belief, which I have advocated more than once (**7, 133**), that soft water is the main factor in determining its occurrence.

There is no doubt that the great majority of its habitats contain soft water, and the following list[2] contains such recent analyses as I have been able to get. It is unrepresentative because I have neglected such districts as the west of Scotland (where all the rivers north of the Clyde must surely be soft) and gone out of my way to get samples from known habitats of the mussel in calcareous and dubious districts:

Glengarriff R. (Cork)	1	R. Teign (Devon)	3
R. Spey (Inverness)	2	R. Derwent (Westmorland)	6*
R. Dee (Bala)	2–4	R. Esk (Yorks.)	6
R. Irt (Westmorland)	2*	L. Leane and rivers (Kerry)	7–11
R. Conway (N. Wales)	3	R. Exe (Devon)	10
L. Lubnaig (Perth)	3	R. Taw (Devon)	11

* By the kindness of Dr W. H. Pearsall (see **291**).

[1] "If a line be drawn from Hull to Gloucester and then on to Plymouth, it can be said roughly that all the country to the east and south of it was for Parliament, and everything to the west and north for Charles." *Wales*, by W. H. Davies, 1925, p. 170.

[2] The figures are milligrammes of calcium per litre, i.e. parts per million, which I have always determined by the method given by Thresh and Beale (**148**). Divided by 4, they give approximately the total hardness expressed on the customary scale of parts of $CaCO_3$ per 100,000, and to have a uniform terminology I have converted the hardness figures of the literature to the calcium scale by the same factor, making the necessary correction if they are given in the older scale of grains per gallon (=parts per 70,000). But what is meant by "hardness" or "lime" is not always clear.

R. Tamar (Cornwall)	14	R. Lune (Lancs.)	30
R. Blackwater (Cork)	15†	R. Rede (Northumberland)	32
R. Ithon (Radnor)	17	R. Usk (Monmouth)	49, 51‡
R. Teme (Clun)	19	R. Nore (Queen's Co.)	79
R. Wye (Hereford)	15–33		

† From E. O'Mahony and A. W. Stelfox.
‡ From Dr. H. W. Catto: a third sample higher up 12 years later gave 30.

In contrast with these I give a few figures I have collected which seem to be representative of the rivers in the south of England draining from calcareous strata which do not contain the pearl mussel:

R. Granta (Cambridge)	113	R. Avon (Salisbury)	85
R. Kennett (Suffolk)	115	R. Test (Hants.)	89
R. Gade (Herts.)	104	R. Frome (Dorchester)	70
R. Colne (Herts.)	107	R. Piddle (Weatherbury)	90
R. Thames (Staines)	90	R. Stour (Blandford)	85

West and north the hardness becomes rather less, e.g. R. Axe (Devon) 47, R. Otter (Devon), 37, R. Tees 32 and R. Tyne 34–36: none contain *U. margaritifer*.

The significance of soft water is also supported by the facts: (*a*) it occurs in the upper part of the Dee, above Corwen, where the water is soft (Ca 4) and not in the lower parts where it becomes as hard as 28 (Shrubsole, **65**, **148**); (*b*) similarly in the Teme it lives at Clun, where a sample gave 19, but not below near Ludlow where the hardness rises to 29–35; (*c*) it is common in the Herefordshire Wye (about 20) but not in its tributaries Lug (49), Arrow (41) or Monnow (37). Frierson (**66**) says that it does not occur in calcareous waters in the United States and Geyer (**67**) that it affects soft water in Germany. Further evidence in the same direction was given by McKean (**68**), who found that specimens from the R. Don in Scotland soon died when they were put into the chalky R. Wandle in Surrey, and by Haas (**69**) who says that his specimens died at once when they were transferred from soft to hard water.

The case for soft water is up to a point impressive, but it is difficult to put on one side the instances of the Usk and the Nore or to agree with Phillips (**70**) that the well-grown thick shells from the latter place are a new species. When too I tried Haas' experiment with specimens from the Wye[1] I found (**71**) that they lived happily in various hard waters with calcium 50–130 and finally in the Herts. Colne (Ca about 100) for several months till the winter floods carried them off. It is thus almost equally easy to argue that the thing that is requisite and necessary is a quick-flowing cool river with clean water and the right kind of bottom, and that it is as it were a physiographical accident that such rivers are nearly always soft, though I should have judged by the look of them that such southern calcareous rivers as the Test, Itchen or Otter would have been agreeable to *margaritifer*. It can hardly be the high summer temperature which excludes it from the south-east of England, for it is equally absent from the Shannon basin which is as cool as Wales or Cornwall. The natural host for the glochidia, which are very small and attach themselves to the gills, is the trout (**109**), which is common enough throughout Britain in both hard and soft water: minnows (**110**) also do well and are generally available except in the north of Scotland and parts of Ireland (**72**). Perhaps the solution of this very interesting question may come when someone discovers where the young mussels live after they fall off the fish till they are about 2 in. long—a matter of several years: at present this is quite unknown.

Dreissena polymorpha (Fig. 44) is closely connected with commerce and is found in docks, canals, rivers and reservoirs, anchoring itself to any hard surface by its byssus; it can also live in water mains (**238**), though as it preserves the marine habit of a free-swimming larva its maintenance in running water must be rather precarious, and it is not clear that it would survive in fresh water in this country under natural conditions. It is fond of

[1] It would have been better if they had come from a less calcareous river.

found also in the best. Hence each species can live in any place where its characteristic needs are met by the physical and chemical conditions. The more important features of favourable habitats are (1) cleanliness of water, (2) absence of disturbance, and (3) presence of lime: other factors such as rate of flow, volume of locus, vegetation, etc., are of moment because of their influence on the first two. Bivalves, operculates and pulmonates can each be divided into a group which can live in soft as well as hard water and one which ordinarily needs a fair amount of lime: also into those which can tolerate stagnant water (which include no operculates) and those which need clean and usually running water. With a few exceptions, the needs of the species are so similar that habitats can be classed as good or bad for Mollusca as a whole: the richest places are calcareous rivers, lakes and canals, the poorest rapid streams, mean ponds and mountain lakes.

This paper has, I hope, asked more questions than it has answered. The descriptive phase of the study of the habitats of Mollusca is far from complete, but it has reached the point where it suggests explanations and general principles which are open to analysis, and, though there is still room for collecting at large, field work is likely to be more fruitful if it is planned to throw light on definite problems and guided by some theory. It may centre round the study of particular habitats or of particular species, and since the Mollusca have so little direct relation to one another or to other animals it will mostly be concerned with the investigation of the environment, and ideas which arise in the field may in many instances be tested by experiments in aquaria and by well-considered transplantations.

My information about geographical distribution and localities is largely derived from the accumulation of data made with such devotion by W. D. Roebuck for J. W. Taylor's *Monograph* and for his own *Census of Distribution*, maintained since his death by the Conchological Society. The maps are based on the *Census* records with the addition of a few reported occurrences which seemed sufficiently credible, although no actual specimens have been verified by the Society's referees.

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