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FACTORS THAT LIMIT THE RANGE OF FRESHWATER ANIMALS

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CONTENTS

I. INTRODUCTION

This article is about the factors that limit a species to a certain habitat within its geographical range. How species came to occupy the regions where they occur to-day, a subject discussed at length by Thienemann (1950), is not considered in the article.

There are three stages to this problem: first, taxonomic; second, definition of habitat; and third, experimental investigations of probable correlations that have been revealed during the second stage. Taxonomic studies are not within the scope of this article, a too full account of investigations that have reached only the second stage would not serve a useful purpose, whereas those instances that have reached the third receive the fullest treatment.

Habitats continue to elude exact definition, one reason being that the limiting value for one factor varies according to the intensity of another, and, if several are interacting in this way, the discovery of critical thresholds must be a laborious and difficult task. Moreover, the threshold may not be the same throughout life: adult *Ostrea madrasensis* and *Nereis diversicolor* can live in more dilute water than their young stages can (Remane & Schlieper, 1958), whereas, in contrast, young *Gammarus duebeni* are more tolerant of sudden changes in salinity than older specimens (Kinne, 1954*a*). Competition may prevent a species extending its range to what laboratory experiments on isolated specimens show to be the limits of some chemical or physical factor.

Since the range of each species is limited by a complex of factors, it would be logical to discuss species rather than factors one by one. Research, however, has tended to focus less on species than on factors which, therefore, make better headings under which to present the findings.

II. OVIPOSITION BEHAVIOUR

A species may be absent from a place because conditions, though not unfavourable, are not attractive to the ovipositing female. Among the Ephemeroptera, females of the genus *Baetis* (Percival & Whitehead, 1928; Gillies, 1950; Harris, 1952, and I myself do not agree about which species, but this is not relevant to the present theme) alight on stones and other objects and descend into the water to lay their eggs. Harris (1952) has watched them wander for considerable distances apparently in search of a suitable site. *Habroleptoides modesta* crawls down the side of a stone at the river's brim, and, before laying eggs, appears to test the soil carefully both with its forelegs and with the tip of the abdomen, which by now has lost its cerci (Pleskot, 1953). *Ephemerella ignita* flies upstream and lays its eggs in fast-flowing or broken water (Sawyer, 1950), but this author (1952) also records how a flight which had to cross a bridge on its way upstream mistook the road, which was wet, for a waterway and flew along it. There are numerous records of various species laying their eggs on wet roads and even on dry ones (Gillies, 1950; Verrier, 1954, 1956). No analysis of the responses of an ovipositing female has been attempted but the field observations suggest that, though they may be complex in some species, they are simple in most, and the eventual pattern of the distribution of the nymphs is likely to be due to mortality of those lodged in unsuitable places rather than to maternal selection.

Steiner (1948) has attempted to analyse the responses of *Leucorrhinia dubia* (Odonata), which is confined to moorland and heath ponds. He found that this species, but not one of some twenty others, was attracted to a towel or a white sheet of paper placed on the ground, and suggests that a marked contrast between the light water surface, particularly where *Sphagnum* breaks it, and the dark background is typical of moorland and heath pools and forms a feature that attracts the dragonfly. He found further that 80 specimens visited a dish filled with water from a *Sphagnum* pool compared with 40 going to a similar dish with tap-water, and concluded that the taste of acid peaty water is attractive to the species. Schiemenz (1954) attacks the conclusions rather vigorously. He finds it difficult to believe that moorland and heath ponds offer a greater light and dark contrast than do ponds elsewhere, and he points out that a white surface is attractive to many species; the explanation of Steiner's observations is that *Leucorrhinia* is one of the few genera that settle on a horizontal surface at ground level. Although local pond-water was apparently more attractive in the experiment, many specimens visited tap-water and a specific reaction to taste must be demonstrated more convincingly before it can be put forward as an explanation of the occurrence of *Leucorrhinia*. Other observations (Wesenberg-Lund, 1913, 1943; Gardner, 1950*a*, *b*, 1953; Fraser, 1952; and Moore, 1952) suggest that oviposition of Odonata is less haphazard than that of most Ephemeroptera, but provide no evidence of a precise choice of a place to lay eggs.

In the Culicidae, more highly evolved insects, there is, in marked contrast, no doubt that the occurrence of the larvae of such species as have been investigated is to be explained by the behaviour of the ovipositing females. As long ago as 1922 Lamborn showed that larvae throve when transferred to water from places in which they were never found, and later workers, able to distinguish the eggs, have recorded that these rarely occur in places where larvae do not (Thomson, 1940; Bates, 1940; see Muirhead-Thomson, 1951; and Bates, 1949, for reviews of what is known about mosquito ecology).

Dark places attract the ovipositing females of *Aëdes variegatus* and *A. argenteus* (Buxton & Hopkins, 1927), of *Anopheles minimus* (Muirhead Thomson, 1940) and of *Culex pipiens* (Jobling, 1935). Dampness in addition may be important. In contrast, shade does not seem to attract the females of *Anopheles leucosphyrus* although the larvae are always found in shaded places. When Colless (1956) cut down vegetation round a breeding place, larvae continued to occur for some weeks, and he concludes that it was not absence of shade but some secondary factor associated with it that gradually made the place unattractive to egg-laying females. *Aëdes aegypti* (= *Stegomyia fasciata*) laid more eggs in containers in bushes than in identical ones under houses, and *Culex nebulosa* laid more eggs in containers inside houses (Dunn, 1927*a*, *b*). Buxton & Hopkins (1927) found more eggs in pots 15 cm. in diameter than in pots 10 or 30 cm. in diameter.

Eggs and larvae of *Anopheles culicifacies* disappear from rice fields when the rice grows to a height of 30 cm. or more, though introduced larvae thrive, because rice of this height prevents the female from carrying out over the water a flight without which she will not lay eggs (Russell & Rao, 1942*a*).

Cage experiments are distrusted strongly by Buxton & Hopkins (1927) and by Bates (1949) on the grounds that the females do not behave normally once they have discovered that they are confined, but Muirhead-Thomson (1951), though suspicious, does take note of the results of some. Hecht (1931) provided caged mosquitoes with dishes of water at different temperatures. *Anopheles maculipennis*, whose races are similarly analysed in a later paper (Hecht, 1934), laid most eggs in water at 22–29° C., none in water above 32–34° C. and very few in water below 15° C. *A. claviger*, a palaearctic species confined in the countries of the Near East to springs, wells, and underground cisterns, laid most eggs in water at 12–21° C. The temperature of the pots set out by Buxton & Hopkins (1927) appeared to influence the number of eggs laid in them. *Culex pipiens modestus* and *Aëdes aegypti*, presented with a Petri dish of distilled water and others containing solutions with 1, 2, 3, 4, 5, 6, 7 and 8 g./l. NaCl, laid eggs in all though significantly fewer in 5 g./l. and higher concentrations. Reaction to other simple salts was similar (Hudson, 1956). The purpose of the work was to discover what difference in concentration the female could detect. The author was not concerned with how a breeding place is selected and did not state whether development was possible in all the solutions in which eggs were laid. Kligler & Theodor (1925) showed in similar laboratory tests that three species of *Anopheles* laid decreasing numbers of eggs in increasingly saline solutions and that the higher salinities were lethal to eggs or larvae.

Thomson (1941), whose study of *Anopheles minimus* is the most detailed of any made, concluded that the main factor leading the female to the breeding place was the content of organic matter. Buxton & Hopkins (1927) found grass infusion in pots placed where wild mosquitoes would lay in them more attractive than distilled water, though eggs were laid in that. *Culex fatigans* laid more eggs on hay infusion than on leaf infusion in a cage (Jobling, 1935). *Aëdes aegypti* appeared at a regular stage in a succession which started as peptone in water (Margalef, 1947). Larvae of *Anopheles culicifacies* were abundant in freshly dug pits, but numbers fell steadily as algae and organic matter increased (Russell & Rao, 1942*b*). Physical factors affect the female's choice, but it seems likely that, as several writers hint, though none prove, the main reason why each species has a distinct habitat is that different species are attracted by the odour of a different organic compound.

Distribution of larvae may reflect not only maternal choice but the requirements of the adult. Dragon-flies hawk in places where the vegetational pattern is of a certain type and this selection may affect the distribution of the nymphs (Diver, 1944).

Notonecta maculata (Heteroptera) invariably attaches its eggs to a solid object, preferably a rock or a stone, whereas the other three British species either insert them into plant tissues or stick them on to a surface, and Walton (1936) associates the abundance of this species in tanks or reservoirs where there are cement or stone faces with this habit.

The range of many fish is limited by oviposition behaviour. The buffalo fish (no scientific name given), important in rivers and sloughs of the Mississippi basin, long baffled attempts to induce it to spawn in artificial ponds. Success was eventually achieved by a man who kept the level of a pond low in early spring and then, when the fish were ready to spawn, raised it until water flooded the marginal land. The fish readily moved on to the newly submerged ground and spawned. *Ictalurus punctatus* would not lay in ponds until pieces of pipe were introduced (Coker, 1954). *Esox lucius* spawns in emergent vegetation (Fabricius, 1950), flooded fields (Chimits, 1956), and ditches and swamps at the lake margin (Carbine, 1942). When barred from the usual spawning ground, few pike spawned in a lake that Fabricius had under observation and females resorbing eggs were caught. *Salmo trutta* will retain and ultimately resorb its eggs if it cannot find a suitable stretch of gravel in which to lay them (Stuart, 1953), and there can be no doubt that, in some places at least, its absence is due to lack of spawning places.

Lepomis microchirus, the bluegill, spawns at a temperature of 22·0° C. according to Schultz (1952), though not until 26·7° C. according to Anderson (1948). Various temperatures for pike spawning given by various authors are quoted by Chimits (1951), who (1956) believes that 7° C. is the critical value. The observations of Fabricius (1950) indicate that, for pike at least, there is no absolute threshold and therefore disagreement about its level is to be expected. In Swedish lakes spawning takes place soon after the break-up of the ice, when melting snow causes flooding and the sun may cause a rapid increase in temperature in shallow water. In one lake spawning at one place coincided with a quick rise in temperature to 8° C. At another, temperature remained at 3° C. because the flood water came straight from the snow-fed river; there was spawning here but not until a week later. Fabricius suggests that there are two factors stimulating spawning, the finding of a suitable place and a rise in temperature, and that the two summate.

Stuart (1953) found that trout congregated near the mouths of streams when ready to spawn and entered them when their temperature dropped below that of the lake. Munro & Balmain (1956), on the other hand, found no such relationship in Loch Leven and note that the streams were entered when their flow increased.

Savage (1939) found more frogspawn in ponds richer in potassium than the average and less in ponds where there was less than 3 parts per 1000 of carbonate, but these differences needed statistical tests to demonstrate their significance and spawn was found in a great variety of ponds. He puts forward a suggestion, not backed by experimental proof, that different algae flourish in the different media and that some give off a smell that attracts frogs.

III. ISOLATION

The freshwater ecologist must constantly wonder whether the absence of any species is due to unfavourable or unattractive conditions, or to its failure to reach the place under consideration. The problem is considered from an ecological or small-scale point of view here; the large-scale zoogeographical aspect is dealt with by Thienemann (1950). Freshwater animals may be divided into (1) the very small, which generally have an egg or other resting stage which can be transported by the wind, and their frequently cosmopolitan distribution suggests that they traverse land barriers easily (Gislén, 1948); (2) larger organisms aquatic throughout life; and (3) insects that can fly in the adult stage.

Animals of the second category vary greatly in their ability to get from one piece of water to another. *Mysis relicta* was probably carried into the lakes where it occurs to-day during the Ice Age and appears not to have spread since. It is not found beyond the frontiers reached by the ice (Thienemann, 1950) and is known in only one lake in some regions where there are other lakes apparently suitable, e.g. Ennerdale in the English Lake District and Fure Lake in Denmark (Holmquist, 1959). *Crangonyx gracilis* has invaded the whole of England served by canals in about 30 years (Hynes, 1955*a*). Moon (1957*a*) attributes much of the occurrence of the two species of *Asellus* in Windermere to human interference and concludes (1957*b*) that their presence or absence in other bodies of water in the Lake District shows no correlation with any physical or chemical factor of the environment and that they are where they are because man, intentionally or otherwise, has introduced them. Reynoldson (1961) dissents strongly from this view, and maintains that there is a correlation with calcium and organic matter. In various parts of the country he has found *Asellus* in most water bodies with more than 13 mg./l. of calcium and in very few with less than 5 mg./l. When the concentration lies between these two values, *Asellus* may or may not be present. Distribution in the Lake District, where Moon worked, appears to be without pattern because so many places lie in this intermediate range of calcium concentration. Kreuzer (1940) studied a number of small ponds and records that *Asellus* is generally present in the calcareous ones. The findings of these two authors lead to the conclusion that *Asellus* traverses land barriers between small ponds rather easily.

Boycott (1927) transferred *Planorbis corneus*, which occurred in a nearby river and reservoir, and *Bithynia tentaculata*, which occurred in the river only, to fourteen ponds, of which there were nearly 100 in the neighbourhood. *Planorbis* flourished in about half the ponds but *Bithynia* died out. Boycott concludes that conditions in ponds are unfavourable to *Bithynia* but that the absence of *P. corneus* is due to its inability to reach them. On the other hand, the species that did inhabit ponds, most of which had no outflow, were evidently passing from one to another frequently (Boycott, 1936).

The controversy about the origin of *Hydrobia* (= *Potamopyrgus*) *jenkinsi* is irrelevant here (see Bondesen & Kaiser, 1949). It has invaded most of the British Isles (see Ellis, 1951 for map; and Hunter & Warwick, 1957 for recent Scottish records) in the last 80 years and is spreading on the continent. The history of other invaders, some of which have not spread from the original point of establishment, but many of which have advanced with great rapidity, is recounted by Thienemann (1950).

Many water-mites are parasitic on adult insects, and the leech *Theromyzon tessulatum* may be transported while attached to the throats of birds (Mann, 1954). About the means of transport of other freshwater animals there is only fragmentary information. Ostracods and *Pisidium* have been found clinging to the hairs of water-bugs (Lansbury, 1955). Bondesen & Kaiser (1949) suggest that *Hydrobia jenkinsi* may be swallowed by birds and subsequently vomited. Gislén (1948) records that fresh mollusc spawn was found on the feet of a bird shot in the Sahara many miles from water. Moon (1957*a*, *b*) stresses the importance of human activity. No systematic study of the problem of how freshwater animals that cannot fly are transported across land barriers has been made.

Of insects it must be asked how often they fly, how far they fly and how often they are carried away by wind. Thienemann (1950) excluded insects when discussing the history of the European freshwater fauna because they can fly over what are barriers to other animals, but Illies (1955) maintains that the Plecoptera may be excepted because they fly so little, a view supported by the restricted distribution of many species. There is a considerable amount of rather diffuse information about the various groups and it is possible to list certain species that travel more than the rest. It is not, however, possible to answer the question that is crucial to this section and state that certain species fly so little that years must elapse before they find their way to a new place where conditions are favourable. Jackson (1952, 1956*a*, *b*) has shown that the flight muscles of a number of species of water-beetle are small and the thorax often reduced in such a way that it could never have housed functional muscles; in some species both fully developed and flightless specimens were found, in others all were flightless, but among these a tiny proportion of fliers might elude the most assiduous dissector and yet confer on the species considerable powers of immigration.

How often flying specimens are caught up and swept away is an important question, particularly relevant to the Plecoptera, which rarely take wing, and to the Ephemeroptera, which, unable to feed in the adult stage, have not the reserves for much flying.

There is little information to provide an answer. Hardy & Milne (1937) recorded one caddis and 54 chironomids in nets over the North Sea and (1938) 7 chironomids and one *Helophorus brevipalpis* in a further investigation of 'aerial plankton', but the absence of such groups as Ephemeroptera and Plecoptera proves nothing, as only such a minute fraction of the total volume of air can be sampled. Occasionally small cyclones reach such force that water is sucked up and carried away, inhabitants and all (Gislén, 1948), but such an event is surely too rare to be of much significance.

Nearly all freshwater species—*Dreissena*, the zebra mussel, being the outstanding exception—are without the free-swimming larval stage whereby their marine ancestors got themselves transported and distributed. It is, therefore, noteworthy that Weerekoon (1956), admittedly on rather slender evidence, believes that certain species of Trichoptera are planktonic when very small. It is the most plausible explanation of the occurrence of certain species in shallow water near the edge of Loch Lomond and on a submerged bank but not on the muddy bottom of the deeper water in between.

Various surveys throw some light on the part that chance can play in determining the composition of a population. Bourrelly (1958) deduced from the floral diversity of apparently similar rock pools which filled at high tides and dried out a few days later that the most abundant species was the one which had been the first to re-establish itself when water returned. Thienemann (1950, p. 65) explains the differences in the zooplankton of some recently built reservoirs in the same way. Schachter (1958) found that, when the zooplankton of a somewhat saline pond was annihilated by deoxygenation, its composition after the catastrophe was rarely the same as it had been before. Thienemann (1948) studied for 4 years the population of a small concrete garden reservoir that was drained each winter. Of the 103 species recorded, 10 occurred every year, 14 in three years, 20 in 2 years and the remaining 59 in 1 year only. Two worms and six crustaceans were the only species that could not have made an airborne invasion. Obviously when the fauna is destroyed at frequent intervals, its composition will owe much to chance. How soon, if ever, it reaches stability and how stable it remains is unknown, since no survey comparable to Thienemann's has been made of a place which, once filled, was left undisturbed for years. I have found a stable fauna in a fish pond in which I have been making regular collections for 5 years (unpublished). Godwin (1923), on the other hand, found that the number of species of plants in a series of gravel-pits and an ox-bow was higher the older the pond. In a recent personal communication he maintains his original contention that the chief reason is the time taken by aquatic plants to traverse land barriers, but agrees that conditions will be more varied in an old than in a new gravel pit, which should make a more varied flora possible.

The argument cannot be pushed too far, but it is reasonable to deduce that, if, when a field worker has learnt to detect the habitat of a species, he rarely fails to find it in what appears to be a suitable place, the travelling powers of that species are good. The numerous studies of groups that have been made leave the impression that absences such as those of *Mysis relicta* are not common. The conclusion, which must obviously be guarded, is that chance is not of the greatest importance in freshwater biology.

IV. INTERRELATIONSHIPS

An animal or plant may be absent from a certain place because some other organism eats it, poisons it or ousts it in some less direct way; the first is here referred to as predation, the last as competition. This is the fringe of the vast subject of population dynamics, but, in accordance with the limitation fixed at the beginning, only those instances where numbers are reduced to zero will be considered.

(1) *Predation*

There is probably intense predation in nearly all fresh waters and survival only of those animals whose habits take them to a suitable refuge. Though *Rana temporaria* and *Bufo bufo* lay much spawn in Lake District fishponds, tadpoles disappear soon (Macan, 1949), but in a fishpond without fish they occurred everywhere up to the time of metamorphosis (Macan, unpublished). It was also noted that, in a dry summer when the water level of the fishpond fell until it reached the top of some submerged plants, larvae of *Anopheles maculipennis* appeared in the cover thus provided (Macan, 1949). Ponds in Bengal harbour many larvae of *Anopheles* spp. Malaria control squads remove rooted vegetation breaking the surface and floating mats of algae, and the larvae disappear; it is assumed that they are eaten.

Species that are large and must continue swimming to feed are confined to temporary or extremely saline places. Boone & Baas-Becking (1931), Hedgpeth (1957) and Croghan (1958*a*), state that *Artemia salina* could live in sea water but is confined to places where there are no fish to eat it. Lundblad (1921) put foward the same explanation for the occurrence in temporary places of other phyllopods. Stuart (1941) suggests that the chironomid *Cricotopus fucicola*, which he reared in fresh water, is found in nature only in pools too saline for the carnivores which could easily catch its sluggish larva. This observation is not confirmed by experiment and the distribution could be due to selection by the ovipositing female.

The converse case is the limitation of predators to places where there is suitable prey. Noland (1925) concludes that this is an important factor determining the occurrence of certain species of ciliates. Hetherington (1932) shows that a hungry *Stentor coeruleus* will eat *Gonium pectorale*, *Euglena* sp. and *Trachelomonas* sp. sparingly, but most ciliates avidly. Other ciliates eat only some bacteria, failure to appreciate which fact has led some authors to attribute their decrease in bacterially rich cultures to other factors when it was probably due to exhaustion of the food supply, the bacteria remaining not being suitable (Johnson, 1941). The most complete story is that related by Fauré-Fremiet (1950, 1951). Where anaerobic bacteria that produce hydrogen sulphide are growing on rich black mud in shallow running water, colourless sulphur bacteria flourish. The fall in pH attracts two species of *Colpidium*, which feed on the bacteria without much reducing their numbers. The arrival of predators causes a reduction in the numbers of *Colpidium* and then of all the ciliates. Two more species come in and eat all the bacteria and finally *Coleps hirtus* appears and devours everything left. Nothing is known of how such changes affect later links of the food chain.

The cladocerans *Leydigia leydigii*, *Macrothrix laticornis* and *Ceriodaphnia rotundus* thrive on organic particles of vegetable origin, *Simocephalus vetulus* is one of the few species that can make use of algae with a hard cell wall, and *Daphnia pulex* and *Moina brachiata*, which cannot, require algae without such a covering. The nature of the food supply is one of the factors determining the natural occurrence of these species (Pacaud, 1939). In the laboratory *Simocephalus vetulus* and *Daphnia obtusa* did not survive in water with leaves but lived a long time when snails were also present. *Planorbis corneus* was kept alive for 8 months on a diet of cigarette paper and a small population of *Daphnia* lived with it. None survived 17 days with cigarette paper and no snail. It is thought that bacteria decomposing the snail's faeces provided food for the Cladocera (Pacaud, 1949). Hutchinson (1932), investigating the absence of cladocerans and scarcity of rotifers, two typically freshwater groups, in Lake Tanganyika, suggests that this lake may be more like the sea than others on account of its great size and may lack something, such as fine organic debris, bacteria or the smallest nannoplankton, which these animals feed on; the suggestion has not been investigated further. Boone & Baas-Becking (1931) record that *Artemia* may disappear with increasing salinity because the tolerance limits of its food, not its own, have been surpassed.

Larger animals appear generally to have a wide range of food, though little is known about what most feed on when very small; lack of suitable prey for that stage may be the cause of absence. Thienemann (1950, p. 102) states that the chironomid *Eucricotopus brevipalpis* feeds only on *Potamogeton natans*, and this is perhaps the most appropriate place to mention his observation (1950, p. 106) that the caddis *Ptilocolepus granulatus* uses only the leaves of certain mosses to make its case.

A brief résumé of the extensive Russian work on food and feeding of aquatic invertebrates is given by Gajevskaja (1958).

(2) *Organic substances*

Algae, bacteria and fungi may produce substances that encourage or inhibit growth of other organisms; they may also inhibit their own growth (Lefèvre, Jacob & Nisbet, 1952). A number of species of algae would not grow in water from a canal where the alga *Amphanizomenon gracile* and little else was abundant but throve in water from the springs feeding the canal (Lefèvre, Hedwig & Nisbet, 1951). The phytoflagellate *Prymnesium parvum* produces a substance that rapidly kills fish (Reich & Aschner, 1947). Toxic properties of other algae are mentioned by Shelubsky (1951) and Gajevskaja (1958). The rate at which *Daphnia* filters decreases after it has eaten *Chlorella* (Ryther, 1954) and its oxygen consumption also drops (Vollenweider & Ravera, 1958). Three varieties of *Paramecium aurelia* are able to kill other varieties by means of a toxin (Sonneborn, 1939). *Limnaea pereger* can produce a toxin which is rapidly fatal to fish, but only in a concentration of at least 5 g./l. (about twenty specimens), which is unlikely to be reached in nature (Wundsch, 1930). Carp fry placed in small hatchery ponds with eggs of *Esox lucius* all died (Chimits, 1951) but more critical experiments are required to prove a connection between the two. Lucas (1947) and, more recently but more shortly, Friedrich (1952) have reviewed this field.

(3) *Competition*

There are various instances where absence of one species appears to be related to the presence of another. Numerous attempts to introduce *Salvelinus fontinalis* and *Salmo irideus* into France have been unsuccessful, and the significant features of the few places where they have been established seem to be isolation and absence of other fish (Vivier, 1955). Introduced into North America, *Salmo trutta* appears unable to compete with the native *Salvelinus fontinalis* except in a few places where it can profit by its ability to tolerate slightly higher temperature (Dymond, 1955). In some lakes in the north of Sweden, Nilsson (1955) caught most specimens of *Trutta* in shallow water where they fed on the bottom fauna all through the year and most *Salvelinus* in deeper water where they fed on bottom fauna in summer. In a troutless lake there were two recognizable forms of char, a larger living in the shallow water and feeding mainly on bottom fauna and a smaller living in deeper water and behaving as did all the char where trout were present. The stonefly *Diura bicaudata* occurs in lakes and high up in stony streams in England, and *Perlodes mortoni* occupies the lower reaches of the streams. In the Isle of Man *P. mortoni* is absent and *Diura bicaudata* occupies the entire lengths of stony streams (Hynes, 1952). *Planaria montenegrina* occupies the upper parts of Balkan stony streams, *P. gonocephala* occurs below it, and there is a fairly sharp dividing line between them at a point where the temperature reaches 13–14° C. *P. gonocephala* extends down to a point where the temperature is 21–23° C. Beauchamp & Ullyott (1932) found some streams where one or the other occurred alone and then *P. montenegrina* extended down to a point where the temperature was 16–17° C. and *P. gonocephala* up to the spring. A similar relationship between the western European species has been described by many authors, but Beauchamp & Ullyott found that it depended also on the rate of flow, both species occurring in the upper reaches of slower streams. Leloup (1944) does not find these species to be related ecologically in the way that other authors have described.

Young *Salmo salar* and *S. trutta* seize territories at an early age and Kalleberg (1958) has watched this and the aggressive way in which they drive off trespassers in a tank. Further examples are given by Gerking in *Biological Reviews* (1959). Frank (1952) cultured *Daphnia pulicaria* and *Simocephalus vetulus* separately and together. The reproductive rate of both species drops to a low level as the density of population increases, that of *Simocephalus* more rapidly. Moreover, whereas the population density of *Simocephalus* has little effect on the reproductive rate of *Daphnia*, the reverse is not true. Frank believes that this is why eventually *Daphnia* is always the survivor in mixed culture, but he doubts whether natural populations are ever dense enough for these effects to manifest themselves. Hynes (1954, 1955*b*) believes that *Gammarus pulex*, a more recent arrival, is driving *G. duebeni* out of England and attributes its success to a higher rate of reproduction. It is also favoured by greater resistance to a parasite which causes sterility. It is less easy to see how competition between some other animals, flatworms, for example, acts.

Many of the limiting factors about to be discussed do not act directly because, as the limits for a species are approached, competition curtails its range. The two species of *Planaria* illustrate this point exactly.

V. PHYSICAL FACTORS

(1) *Water movement*

Water movement, whether it be flow or wave action, has great indirect effect on freshwater communities because its intensity determines the nature of the substratum. This section is about its direct effect on animals, particularly in the zone where it is strong enough to remove everything but stones.

The Simuliidae undoubtedly and the Blepharoceridae probably are morphologically adapted to live in a current. The Ecdyonuridae and *Ancylus fluviatilis* are morphologically adapted to cling to hard flat substrata, and some flourish in still water. Other animals show no particular morphological adaptation, and adaptation of behaviour is probably the key to their success (Ambühl, 1961).

The most thorough investigation of the relation between species and current is that of Dorier & Vaillant (1954), who discovered for each species: (1) the strongest current in which it was found in nature, (2) the strongest current it would ascend, and (3) the current speed at which it was washed away. The significance of these figures is not always clear, for most stream animals live among the stones or in the moss or alga which grows on the steepest rock faces and are exposed to slight current only. Moreover, Ambühl (1961) states that in the swiftest current there is a layer over a flat surface which is hardly moving and its thickness is about the same as the height of most of the animals.

Certain species (e.g. Ephemeroptera, Macan, 1957; and *Simulium*, Grenier, 1949; Zahar, 1951) are confined to the slower parts of stony streams, but whether they are washed away by faster currents, and if so, at what stage in the life history this happens, are unanswered questions. Huet (1942) attributes the scarcity of *Gammarus* in rivers compared with streams to the drag of the greater weight of water in the former, but *Gammarus* beneath the stones of a stable bottom cannot be affected by the weight of water flowing overhead and predation seems a more likely cause (Macan & Mackereth, 1957).

Species of *Simulium* (Grenier, 1949) and other animals (Ambühl, 1961) select a place where the current is running at a certain speed, but it should be noted that the first author dwells on the difficulty of measuring the current to which specimens in the wild are exposed and the second gives only a preliminary account of his work.

Philipson (1954), who made measurements similar to those of Dorier & Vaillant, observed that some of the net-spinning caddis larvae would make their nets only in flowing water and that *Hydropsyche* started in a slower current than *Wormaldia*.

(2) *Substratum*

That a substratum must provide a refuge from predators has been mentioned above and that it must also provide a vantage point for feeding is obvious, but an exact analysis of what Andrewartha & Birch (1954, p. 513) call 'a place in which to live' has not been made for any freshwater animal. Picken (1937) found that the range of certain ciliates was more restricted than that of their food, apparently by suitable substratum. Some, once established in a tuft of alga or filamentous bacterium, would not leave it, though whether this was brought about by a response to contact or to a steep chemical gradient at the edge of the tuft remained uncertain. Herbivores feeding on diatoms epiphytic on the filaments were followed by carnivores and by detritus feeders and the association remained together until the tuft decayed. A relationship between the occurrence of certain species and the nature of the substratum has been noted by Hynes (1941), Linduska (1942), Macan & Mackereth (1957), Nielsen (1942), Percival & Whitehead (1929) and Scott (1958). Bovbjerg (1952) showed that 88% of specimens of a crayfish that lives in stony streams settled on a cinder bottom when presented with a choice of that or mud in an aquarium; 60% of a species from a muddy environment settled on the mud. The fact that neither figure is 100% suggests that distribution in nature is not to be explained wholly in terms of selection of a particular kind of bottom. Other factors, though not ones which explain this anomaly, are high temperature and low oxygen concentration, to which the mud-dwelling species is more tolerant. It is also the only one of the two able to burrow into the substratum and survive drying up. Some plants have a much more varied rotifer fauna than others (Edmondson, 1944) and presence or absence of planktonic species may depend on whether certain algae on which they lay their eggs are present or not (Vollenweider, 1948). *Ancylus fluviatilis* is a tolerant species, which has been found even in a small quarry pool fouled by cattle, but it is confined to places with a hard substratum (Macan, 1950). Leeches are only exceptionally met with in biotopes where there are no suitable substrata for adhesion (Boisen Bennike, 1943). The most plausible explanation of all these observations is that the behaviour of the species brings it to places where certain conditions obtain.

Popham (1941) showed that *Corixa distincta* in an aquarium tends to choose a background which it matches and that it is less restless on one of the same intensity as itself than on one darker or lighter. He also states that 'it is a matter of common experience that, if specimens of *Arctocorisa distincta* be placed in an aquarium the colour of which differs greatly from their own, the insects become very restless and attempt to fly away', but in one of his experiments more specimens that did than did not match a bottom flew away. If his assertion, which in general is supported by the observations of Lindberg (1944), be true, this cannot be the whole story, for muds of different chemical nature are inhabited by different species (Macan, 1938) and there is sometimes little difference in colour between them. Popham (1941, 1943) also showed that a corixid not matching its background in an aquarium was more likely to fall a prey to fish. In a field experiment (1944) he found that the individuals of three species of corixid showed less variation after fish had been introduced than before and he concludes that those least like their background had been eaten, but in view of his previous findings there is the alternative that they had flown away.

(3) *Desiccation*

A species able to build up a population quickly in a pool that was dry but has refilled can take advantage of a period in which it is free of competition and predation.

The best known inhabitants of temporary water are mosquitoes, particularly those of the genus *Aëdes*, and phyllopods. The fullest account of such places and their fauna is that of Kreuzer (1940). Mann (1955) states that the leech *Dina lineata* is characteristic of temporary ponds.

Not all the mosquito eggs hatch when a pool fills, presumably an adaptation to ensure that disappearance of the water before a generation has been completed does not annihilate the population. Gillett (1955*a*, *b*) found that the eggs in a batch laid by *Aëdes africanus* varied in their sensitivity to hatching stimuli and that this was due to an inherited factor transmitted by both parents. Hall (1953, 1959) has investigated the hatching of the eggs of *Chirocephalus diaphanus*, and finds that time taken for development within the egg varies with the depth, eggs lying in 2 cm. or more developing hardly at all.

Hynes (1958) has described the fauna of a stretch of stream that dried up during a fine summer. Many animals survived by burrowing into the substratum, the eggs of others survived, provided that the time for hatching did not arrive during the drought, and some did not survive at all whether in the egg or the active state. When, in lakes dammed to provide hydroelectric power the level remains high in summer and low in winter, the plant zones are finally narrower than they were before interference with the water level (Quennerstedt, 1958). Hynes (1961) describes the extensive change in the littoral fauna of such a lake.

(4) *Miscellaneous*

Gerris najas is common in boathouses in Windermere but only in those with stone walls. If the wall be smooth the bug is absent, because, suggests Brinkhurst (1959), the crevices between stones provide it with a refuge in which to hibernate.

This is a suitable point at which to mention one of the few pieces of work in which an attempt to evaluate all the factors has been made, and it is kept together even though some of the factors belong to other Sections. Trickling filters purifying sewage have a simple fauna of larvae of chironomid, psychodid and cordilurid flies and of enchytraeid worms somewhat like that of the wrack zone of the sea shore. At one sewage works two mainly carnivorous chironomids in the genus *Metriocnemus* were absent, there was in consequence less predation, and a greater abundance of psychodids was attributed to this. The absence of the predators appeared to be due to the practice of resting the beds for a fortnight, which let the surface, where the larvae were wont to pupate, dry up (Lloyd, 1937). *Lumbricillus lineatus* is successful in trickling filters because it attaches its eggs to a surface, which other enchytraeids do not. *Enchytraeus albidus* was absent from beds with smooth stones, presumably because the eggs were washed out, but occurred where the material was angular or pitted. In some beds it was the only worm, owing to its greater tolerance of certain trade wastes. It bred in the winter but never reached great abundance because, in the spring, the psychodid larvae became active, their feeding loosened the bacterial-fungal mat on the stones and much of this was washed away, taking many of the worms with it (Lloyd, Graham & Reynoldson, 1940; Reynoldson, 1947, 1948, 1957).

VI. TEMPERATURE

(1) *Tolerance limits and optimum*

Many species are confined to high altitudes, high latitudes or to cold springs, others occur in the plains and extend further south. Temperature is obviously involved but papers describing exactly how it acts are scarce in the vast literature.

Thanks to the work of the Canadian school more is known about *Salvelinus fontinalis* than about any other species. The technique for discovering lethal limits was described by Fry, Brett & Clawson (1942), who worked with small *Carassius auratus* (goldfish). The fish were kept at various temperatures before the experiments and then placed in a tank at a constant temperature for 14 hr. All fish kept at 1–2° C. beforehand were alive after 14 hr. at 26° C. and all were dead at 30° C.; 50% died in that time at 27° C. The corresponding figures for fish kept at or, in the Canadian terminology, acclimated to, 10° C. were 29, 33 and 31° C. The temperature at which 50% of the fish died after 14 hr. was regarded as the lethal temperature. For acclimation temperatures rising from 0–36·5° C. the lethal temperature rose from 27 to 41° C., roughly 1° C. for each 3° C. rise in acclimation temperature. Acclimation above 36·5° C. would not raise the lethal temperature but did increase the time until death.

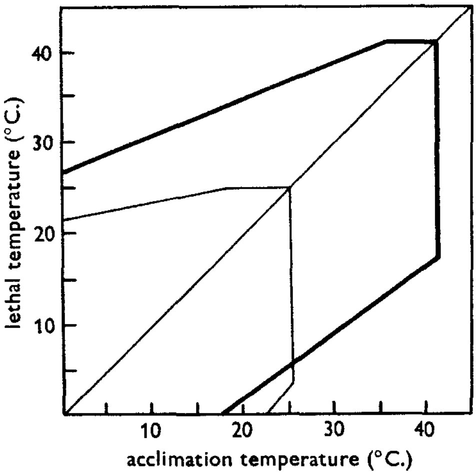

Fig. 1. Relation between acclimation and lethal temperature. Thick line: *Carassius auratus* (Fry, Brett & Clawson, 1942); thin line: *Salvelinus fontinalis* (Fry, Hart & Walker, 1946).

Fish acclimated to 41° C. died in water at 17° C. 3° C. change in acclimation temperature produced a 2° C. drop in lethal temperature, and fish kept at temperatures below 17° C. survived in water at 0° C.

Lethal temperature is plotted against acclimation temperature (Fig. 1). A horizontal line runs from the point where increase in acclimation temperature leads to no increase in lethal temperature to the point where the two are the same. Thence a perpendicular drops to the line showing lower lethal temperature. The five-sided figure so formed encloses 1220 square degrees. *Salvelinus fontinalis* has a lower maximum lethal temperature, 25·3° C.; less acclimation, an increase of 1° C. lethal temperature requiring an increase of 7° C. in the acclimation temperature; and a figure enclosing a number of degrees squared just half that of *Carassius* (Fry, Hart & Walker, 1946).

Placed in a gradient, *Salvelinus* from a temperature below 14° C. will choose warmer water, and if from water above 19° C. it will choose cooler water. Otherwise it will select in the gradient the temperature from which it has come (Fry, 1951).* The temperature selected may vary with the season, being lower in winter (Sullivan & Fisher, 1953).

These laboratory findings agree well with field observations. *Salvelinus fontinalis* is rarely found in waters warmer than 19° C. though it can survive 27° C. if not exposed for too long to that temperature (Creaser, 1930). Huntsman (1946) records mortality in two streams when temperatures ranged from 25·4 to 31·4 and 23·6 to 31·1° C. Elson (1942) noted fish leaving a lake and running up a stream as the temperature approached a value of 21° C.

The optimum temperature has been investigated in various ways. The consumption of oxygen by a quiescent fish rises steadily up to 25·3° C., the lethal temperature. That of a fish kept swimming constantly in a rotary chamber reaches a peak at 19° C. and then drops. The greatest difference between the two values is at 16° C. The fish swam fastest at temperatures between 15 and 20° C. (Graham, 1949). Food was eaten in greatest quantity and used most efficiently at 13° C. (Baldwin, 1957). The longest dart produced by an electric shock was at 10° C. (Fisher & Elson, 1950), a figure which is lower than the others, possibly because all the fish tested were kept at 4° C.

No other animal has been studied as thoroughly as *Salvelinus fontinalis*. Comparable data for other fish, also due mainly to the Canadian school, are generally available only for one aspect of relation to temperature. Hart (1947) and Brett (1944) give information about thermal tolerance for a number of species. Most have a higher lethal temperature than *Salvelinus* but a similar pattern, except *Lebistes reticulatus* (the guppy) whose lethal temperature seems to be unaffected by acclimation temperature (Gibson, 1954). All can tolerate a temperature of 0° C. Fry (1947) discusses the subject more generally and Brett (1956) briefly reviews the field of effect of temperature.

Selection of a position at a given temperature by a fish introduced into a temperature gradient has been studied by Ferguson (1958), Garside & Tait (1958), Pitt, Garside & Hepburn (1956), and Schmeing-Engberding (1953), the last of whom, however, did not take into account the temperature at which the fish had been kept previously. *Cyprinus carpio* (carp) acclimated to 35° C. chose a temperature of 32° C. but from 30° C. and lower temperatures it moved into warmer water. Other species had various preferred temperatures, generally between that of *Cyprinus carpio* and *Salvelinus fontinalis*, though that of the salmon *Oncorhynchus tschawytscha* was lower. *Salmo gairdneri* was unusual in selecting warm water when acclimated to cold and *vice versa*.

Difference between oxygen consumption of an active and a passive fish reaches a

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* This paper gives an excellent review of the work on *Salvelinus* but is unfortunately cyclostyled and scarce. It is cited here only because the original data are in a degree thesis and therefore even more inaccessible.

maximum before the lethal temperature in *Salvelinus namaycush* (Gibson & Fry, 1954) and *Carassius auratus* (Fry & Hart, 1948), but continues to increase right up to the lethal temperature in *Ameiurus nebulosus* (Fry, 1947) and *Salmo trutta* (Fry, 1957).

Growth of *Lebistes reticulatus* was faster at 23 and 25° C. than at 20 or 30° C. Many of the specimens reared at 25° C. were malformed (Gibson & Hirst, 1955). Morawa (1958) showed that the accumulation of fat by *Coregonus albula* in summer was greater in productive lakes but could be brought to an end when disappearance of oxygen from the lower layers of the lake confined the fish to the unfavourably warm upper layers.

A temperature effect not recorded by the authors mentioned is described by Fish (1948). The effects of a myxobacterium, *Chondrococcus columnaris*, grew worse with rising temperature; unimportant below 16° C., it infects wounds at higher temperature, and unharmed tissue, often with fatal results, above 21° C. A poor run of blueback salmon (no scientific name given) in an unusually warm year was attributed to the ravages of this parasite, though confirmation from the examination of dead fish does not seem to have been obtained.

Other studies of invertebrates have been less elaborate. For example, Muirhead-Thomson (1951, chap. 10) discovered the lethal temperature of mosquito larvae by raising the temperature 1° C. every 5 min. until it reached a value at which larvae died within that period of time. Nonetheless, he did find a correlation between the lethal temperature and the maximum likely to be encountered in nature. Whitney (1939) kept various nymphs for 24 hr. in tap-water and then transferred them to constant temperature for 24 hr. The lethal temperature, defined as that at which 50% died in this time, was lower for stream animals than for those inhabiting ponds: 20–21·3° C. for *Baetis rhodani* and 28·5–30·2° C. for *Cloeon dipterum*.

Steinböck (1942) denies that *Planaria alpina* is a cold-water species, having found it in a pool which, fed by snow-melt water, reached 22° C. in the afternoon of a day in August. At night, however, temperature was much lower than this. Schlieper & Bläsing (1952) made some experiments and found that it could easily tolerate such a temperature if not exposed to it too long; 25° C. could be tolerated without ill effect for about 12 hr. in winter and 48 hr. in summer. Beauchamp (1935) showed that this species cannot tolerate indefinitely temperatures above 12° C. and (1937) that above this level its reaction is always to travel against the current, which would presumably generally take it into cooler water. According to Dahm (1958) it never breeds in water warmer than about 12° C.

There is less information about lower lethal limits, but 48 hr. exposure to $-5{\cdot}5°$ C. kills all the eggs of *Aëdes aegypti* and exposure to 0° C. kills some (Davis, 1932). Development is most rapid at 32° C. and there is heavy mortality at 14° C. (Bar-Zeev, 1958).

Pacaud (1948) studied the rate at which *Calopteryx splendens*, and *Erythromma* sp. (Odonata), *Notonecta glauca* (Hemiptera) and *Gammarus pulex* (Crustacea) devoured chironomid larvae in temperatures ranging from 5 to 28° C. The maxima and the rate of change with increasing temperature varied greatly. Efficiency of conversion of food was not studied. It will be difficult to judge the significance of his results until many more species have been studied in the same way.

Rate of growth was studied by Blunck (1914, 1924), whose work is noteworthy on account of its thoroughness and the comparison of two closely related species. The eggs of *Dytiscus marginalis* take 48 days to hatch at 7° C., and an increasingly shorter time at progressively higher temperatures. The greatest number hatch between 10° C., at which temperature development takes 27 days, and 15° C., at which it takes 11 days. At higher temperatures development is quicker but mortality is higher and some of the eggs which do hatch give rise to malformed larvae. Lower temperatures do not affect the eggs directly but increase their chances of death due to fungal attack or to the dying of the plants in which they lie (Blunck, 1914). Young larvae do not grow below 10° C. and are so sluggish that ultimately they die, apparently of starvation. The first instar is completed in 42 days at 11° C. and 10 days at 15° C. after which increasing temperature increases rate of growth more slowly. Above 27° C. there is mortality and the production of monsters. Later instars have a similar but not identical rate of development. *Dytiscus semisulcatus* differs in that development starts at 5° C. or a little below; the upper lethal temperature is only about 2° C. lower than that of *D. marginalis*. The larvae of *D. semisulcatus* are found from November to June, those of *D. marginalis* in summer (Blunck, 1924).

Rate of development at different temperatures of a number of other animals has been studied. Data for various species of mosquito are given by Bates (1949) and Muirhead-Thomson (1951). Brown (1927, 1929) gives figures for the temperatures at which various Cladocera die and at which they grow most rapidly, and finds that northern species have a lower temperature range than southern ones. Elster (1955) gives figures for the rate of development of *Eudiaptomus gracilis*, and Clemens (1950) for *Gammarus fasciatus*. This American species reaches maturity in 59 days at 18° C. and in half that time at 25° C. *G. duebeni* has a lower range; prolonged exposure to 26° C. is lethal and shorter exposure brings egg production to a permanent end. It is reduced at 20° C. and temperature between 4 and 16° C. seems to be optimal. Frequency of moulting increased up to 20° C. and then decreased (Kinne, 1953, 1954*a*).

Moore (1939, 1949*a*, *b*) found a zonation of species of *Rana* from the north to the south of America. The further south a species occurs, the higher its threshold for growth at both ends of the range and the higher the temperature at which growth is fastest. The figures are constant throughout the range of each species. *R. pipiens* is an exception, for it has a much wider geographical range and a higher temperature range the further south it is found. Experiments showed that the species consists of races each adapted to the temperature of the latitude where it lives. The races are generally inter-sterile. Moore is interested in the evolutionary rather than the ecological implications of these findings.

All the species mentioned, and presumably every species, has a temperature optimum, which, however, is not easy to define. In *Salvelinus fontinalis* it was slightly different according to what aspect was considered. The work of Pratt (1943) on cultures of *Daphnia magna* illustrates this point, though it is doubtful whether conditions comparable to those in his experiments are found in nature. At 12° C. cultures soon died out; at 25° C. they generally died out, because the rapid reproduction soon produced crowding which caused heavy mortality and reduced reproduction; at 18° C. the populations survived at a steady level because, with less rapid reproduction, crowding started to depress the rate of reproduction before it increased mortality much. It is probably better to refer to an optimum zone that merges gradually into one of unfavourably high and one of unfavourably low temperature.

(2) *Temperature as a limiting factor*

Temperature influences organisms in various ways; freshwater animals have diverse life-histories, and the result is that any account of how temperature limits range is bound to be complicated. A high temperature range for development does not necessarily mean that the species is confined to warm regions; it may reproduce only during the warm season and hibernate during the winter. The larva of *Dytiscus marginalis* dies of starvation below 10° C., but that does not prevent the species extending well into the Arctic Circle. The larvae occur in summer and the adults are able to overwinter. Other animals are able to lie quiescent when it is cold and resume activity as soon as the temperature rises again. For example, young *Salmo salar* remain inactive in pools when the temperature is below about 7° C. (Allen, 1940) and *Neomysis vulgaris* rests on the bottom while the temperature remains below 3° C. (Vorstman, 1951). The physiology of this phenomenon has not been investigated.

Conversely cold-water species may tide over the summer in a stage more resistant than the others. *Rhithrogena semicolorata* emerges earlier and hatches later in warmer streams and presumably is more resistant to high summer temperatures in the egg than in the nymphal stage (Macan, 1960). The emergence of *Baetis rhodani*, generally continuous throughout the summer, is interrupted at the hottest time in the warmest streams (Pleskot, 1958).

There are three main ways in which animals are prevented from invading warmer water. (1) It is lethal: *Salvelinus fontinalis* and *Planaria alpina* provide good examples. (2) They come into competition with another species whose optimum and range of tolerance is different; predation or parasitism may curtail range if rising temperature favours the predator or parasite. (3) The water is never cold enough to stimulate reproduction.

Cold-water species spawn in winter (*Salmo trutta*) or only at temperatures well below the lethal level (*Gammarus duebeni*). Schlieper & Bläsing (1952) postulate that this might account for certain absences of *Planaria alpina*, which, they believe to be able to live at a temperature well above that at which they will reproduce, but this, as noted above, is not in accord with the findings of Beauchamp, to whose work they do not refer. In any case in most climates there can be few waters so constant in temperature that they are not cold enough for the most exigent species at some time of year.

Species may be barred from colder water in the following ways:

(1) Temperature reaches a lethally low level at some time of year. The inability of *Aëdes aegypti* to tolerate low temperatures is probably why this circumterrestrial species is confined to warm latitudes.

(2) The threshold for development or some other activity is not exceeded or not exceeded soon enough or for long enough. Ide (1935) and Sprules (1947) account for the occurrence of species in the lower but not the upper reaches of rivers in this way, but I doubt whether the explanation can be as simple and as comprehensive (Macan,

1957). Davies & Smith (1958) postulate that *Simulium hirtipes* does not occur above about 450 m. because temperature is too low for development in winter and then rises to a lethal level before development can be completed, but they do not demonstrate this with actual measurements. Berg (1941) finds that in Denmark *Acentropus niveus* (Lepidoptera) feeds only at temperatures above about 11° C., though Palmén (1953) records a lower limit in Finland.

(3) Competition. The two flatworms already mentioned illustrate the curtailing of range at the lower as well as the upper end of the scale.

(4) It is never warm enough for reproduction. *Micropterus dolomien* (small-mouth bass) is stimulated to spawn by a sudden rise of temperature to 16° C., and thereafter temperature must remain a little above that level for 3 weeks or the males will desert the nests and the eggs will die. Rawson (1945) found that an untimely fall in temperature wiped out the generation in 2 years out of 4 in some lakes into which he had introduced this species and concludes that it is near the northern limit of its range. This topic was touched on in the Section on oviposition.

(3) *Analysis of the effect of temperature*

The permeability of certain peritrich ciliates increases with temperature and this is likely to be of ecological significance (Kitching, 1948). Temperature is of importance to the inhabitants of brackish water, but its influence can more usefully be discussed in the section on that subject.

The tolerance by an animal of a wide temperature range depends on the extent to which its metabolism is influenced by temperature. The oxygen consumption of *Salmo iridaeus*, about the same as that of the more eurytherm *Squalius cephalus* at 5° C., rises much more rapidly as temperature rises. Similarly the oxygen consumption of *Planaria alpina* rises fast to reach a peak at 15° C., and that of *P. gonocephala* rises to a peak of about the same height but does not reach it till the temperature is 20° C. Eurytherms are also more resistant to changes in pH and salt concentration, to poisons and to X-rays (Schlieper, 1952*a*, *b*). Schlieper, Bläsing & Halsband (1952) demonstrate that, with increasing temperature, the rate of oxygen consumption of *Salmo iridaeus* and *P. alpina* goes up more slowly in water to which calcium and magnesium have been added. Moreover, they survive a lethal temperature longer. Conversely, potassium depresses resistance. This information is given by Halsband (1953) who finds that *S. iridaeus* survives 3 weeks at 27·5° C. in tap water containing additional sodium, magnesium and calcium salts, whereas controls in untreated tap-water lived but an hour or two at this temperature. He adds that the respiration increases faster with rising temperature in *S. iridaeus* than in *Squalius cephalus*. Bläsing (1953) repeats much of the information about the two flatworms and records that *P. gonocephala* can and *P. alpina* cannot survive a sudden increase in temperature of 10° C. This caused a big rise in the oxygen consumption of *P. alpina* followed by a drop to the level at the same temperature reached gradually, whereas that of *P. gonocephala* did not overshoot in this way. Further the oxygen consumption of *P. alpina* dropped more rapidly and reached a lower level than that of *P. gonocephala* when the concentration in the medium was low.

Pleskot (1953) observed that the emergence of *Habroleptoides modesta* (Ephemeroptera) was restricted to spring and was earlier in warmer water. Eggs soon hatched and small nymphs were present throughout the summer, from which she deduces that the temperature is not lethal, but that, as just before emergence metabolic activity is high and the transport of oxygen to the tissues difficult, the oxygen requirements at this stage cannot be met when the water is too warm.

Large *Limnaea pereger* can respire through the surface while the temperature is below 12° C., but must come up to fill the respiratory chamber with air when the temperature is above this. In summer, therefore, it is restricted to shallow water (Hunter, 1953). In warmer water there is not only a greater demand by the tissues for oxygen but there is less of the gas in a saturated solution. The most recent measurement of saturation concentration at different temperatures is that of Mortimer (1956).

VII. OXYGEN

(1) *General requirements*

The water of the upper reaches of a stream is likely to be almost saturated with oxygen all the time, but lower down in slower reaches the respiration of organisms and decomposition of organic matter reduces the oxygen concentration by night (Hubault, 1927; Butcher, Pentelow & Woodley, 1930). Unproductive standing water always contains plenty of oxygen; Laurie (1942), making 24 hr. observations in an upland pond at different times of year, found a minimum of 66% saturation. Under richer conditions, though the water may be supersaturated by day, the respiration or decomposition of a dense population of phytoplankton may cause a marked reduction in oxygen concentration by night. In small bodies of water seasonal and diurnal fluctuations may be considerable. In one pond oxygen ranged between about 9 and 11 ml./l. in April, and was below 1 at every hour during twenty-four in September (Whitney, 1942). In cold regions oxygen depletion under ice is usual (Greenbank, 1945; Rawson & Ruttan, 1952). Local effects have been observed near the mud-surface (Brundin, 1951) and in clumps of rooted vegetation (Buscemi, 1958).

In lakes that are rich and shallow, but deep enough to stratify in summer, the concentration in the lower layers may drop to a low value, even nil, which bars them to a number of animals (e.g. snails, Alsterberg, 1930; fish, Morawa, 1958; Hubault, 1955; *Mysis*, Theinemann, 1950; Holmquist, 1959). A few specialists, notably certain species of chironomid, may be abundant (Harnisch, 1951).

Other effects of oxygen are less obvious because they are bound so closely with temperature and organic matter and because concentration can vary so much in a short time. To arrange a series of stations in order of oxygen concentration would require a continuous record throughout the life of the species to be studied. This has never been done and, if it had, there would remain the question of whether the average or the minimum concentration was the significant one. Nonetheless, Dodds & Hisaw (1924) show a correlation between the oxygen content of the water and the ratio of gill area to weight of seven species of Ephemeroptera. The oxygen values represent the average of several determinations, but on the critical question of how it was decided when to take the samples there is no information. They studied nymphs that were quite or nearly fully grown and do not consider the concentrations to which younger stages were subjected. Though he did not work with any of the same species as Dodds & Hisaw, Wingfield (1939) has shown that the 'gills' of some species are not places of oxygen uptake, but assist respiration by driving water over the surface of the rest of the body. I believe that the relation between oxygen concentration and gill area found by Dodds & Hisaw was fortuitous and without ecological significance.

Much of the work on oxygen has consisted of comparing the consumption of a species from running water with that of a similar one from stagnant water, though not all observers have realized that there are three precautions that must be taken.

(1) The specimens must be in the same physiological state. *Ancylus fluviatilis* kept at the same temperature for a year consumes more oxygen in spring and early summer than during the rest of the year. Berg, Lumbye & Ockelmann (1958) attribute this rise to reproduction. The oxygen consumption of *Daphnia obtusa* increases at maturity and then falls; it is increased by crowding and decreased by starvation and by senescent *Chlorella* (Vollenweider & Ravera, 1958). In *Rhodnius*, a land bug, oxygen consumption rises to a peak at the time of moulting; the resting level is about the same in each instar but the peak is higher in each succeeding instar (Zwicky & Wigglesworth, 1956). Consumption varies considerably at different stages in the development of fish eggs (Lindroth, 1942).

(2) The activity must be controlled. The oxygen consumption of a nymph of *Ephemera danica* in a flask with sand on the bottom is, at 15° C., rather more than twice what it is at 5° C., but, if there is nothing on the floor, it is about ten times (Wautier & Pattée, 1955).

(3) Specimens must be compared at several temperatures. At 5° C. *Planaria alpina* consumes less oxygen than *P. gonocephala*, at 8° C. the same amount, and thereafter up to 15° C. more, considerably more at the higher temperatures (Bläsing, 1953; Schlieper, 1952*a*, *b*).

In fish it might be expected that the dissociation curve for haemoglobin would give a good indication of oxygen requirements. In *Esox lucius*, *Anguilla anguilla* and *Cyprinus carpio* the haemoglobin is still 95% oxidized at an oxygen pressure of 10 mm Hg., whereas that of *Salmo trutta* is 50% dissociated at that pressure (Harnisch, 1951). Fry (1957) points out, however, that there is enormous variation in the dissociation curves according to the temperature and that, until many more measurements at different temperatures have been made, there will not be enough data for useful comparisons. He and his co-workers have found it more valuable to discover at different temperatures the amount of oxygen used by a resting fish and one exerting itself to the full, to which he applies the terms standard metabolic rate and active metabolic rate. The standard metabolic rates of *Savelinus fontinalis* and *Carassius auratus* are shown in the upper part of Table 1. The lower part of the table shows the lowest oxygen pressures and the concentrations at which the fish are able to obtain this amount of oxygen, in other words the pressures and concentrations at which no activity over and above what is necessary for the maintenance of life is possible. Fry calls it 'the level of no excess activity'. Graham (1949, fig. 10) finds that the lethal

Table 1. *Standard metabolic rate. Consumption of oxygen by a resting fish at different temperatures and the minimum oxygen pressure at which it is possible (level of no excess activity)*

	° C.										
	5	9	10	15	16	20	23·5	24·5	25	35	
Salvelinus	27	—	59	85	—	140	198	—	—	—	ml. O_2/kg./hr.
Carassius	8	—	24	50	—	85	—	—	140	225	ml. O_2/kg./hr.
Salvelinus	30	32	—	—	50	59	—	79	—	—	mm. Hg, O_2
Carassius	4	—	8	10	—	18	—	—	17	25	mm. Hg, O_2

Data for *Salvelinus fontinalis* from Graham (1949, tables 1 and 3); for *Carassius auratus* from Fry & Hart (1948), table 2.

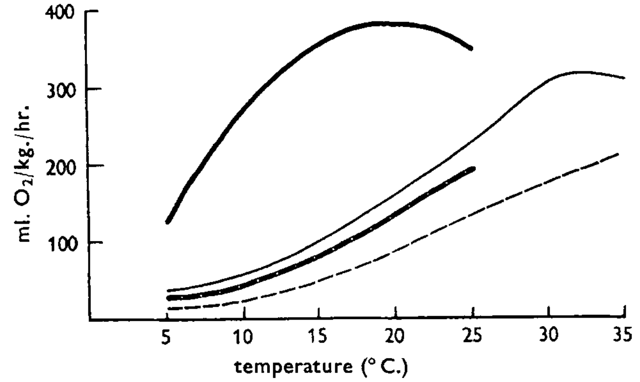

Fig. 2. Oxygen consumption by active fish (continuous line) and resting fish (broken line): *Salvelinus fontinalis*, thick line (Graham, 1949) and *Carassius auratus*, thin line (Fry & Hart, 1948).

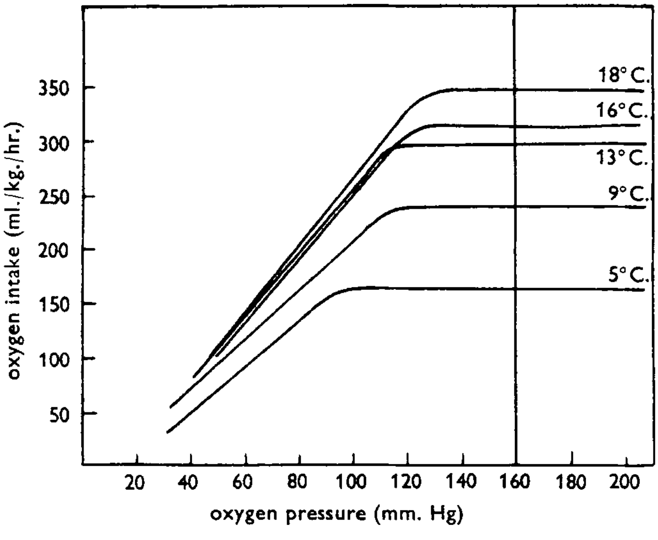

Fig. 3. Oxygen consumption by *Salvelinus fontinalis* at different pressures and temperatures (Graham, 1949).

concentration at all temperatures is a little below the level of no excess activity, presumably because a resting fish in an experiment is not quite as immobile as it could be. Shepard (1955) found that the lethal concentration could be reduced a little by acclimation. At 9–10° C. 95 % of *S. fontinalis* survived 5000 minutes in an oxygen concentration of 1·9 mg./l., 50 % in 1·75 and 5 % in 1·5 mg./l. After acclimation a concentration of 1·05 mg./l. could be tolerated.

Table 2. *Effect of oxygen concentration on the activity of* Salvelinus fontinalis *at different temperatures. The figures show the consumption of oxygen by active fish expressed as a percentage of the consumption at a concentration where oxygen is not limiting activity*

temp. (° C.)	oxygen concentration as % air saturation			
	100	75	63	50
5	100	100	100	64
10	100	100	82	53
15	100	96	65	50
20	100	73	51	25
25	100	57	10	lethal

The table is based on the work of Graham (1949) but taken from Fry (1951).

It is evident from these figures that *Salvelinus fontinalis* is much less tolerant of low oxygen concentration than *Carassius auratus*. It also requires much more oxygen for full activity (Fig. 2). Both requirements are of obvious ecological significance but possibly more important is the concentration of oxygen which limits activity. Above a certain concentration activity is not dependent on oxygen and is presumably limited by something in the transport system, a question discussed by Fry (1957) and Lindroth (1941). Below the point where the lines on Fig. 3 bend, the incipient limiting level, the degree of activity falls as the concentration of oxygen falls. Table 2, an arrangement by Fry (1951) of the data given by Graham (1949), shows that at the higher temperatures activity is reduced very soon by falling oxygen concentration. The incipient limiting levels for *Carassius* are (Fry & Hart, 1948):

5	10	15	20	25	35	° C.
15	21	29	34	39	40	mm. Hg

This is the most striking difference between the two species; in waters where there is barely enough oxygen to keep *Salvelinus* alive, the activity of *Carassius* is not limited. Of the fish that have been studied, *Carassius* is the least, *Salvelinus* one of the most exigent in its oxygen requirements (Fry, 1957).

Gasterosteus aculeatus reacts immediately to water of low oxygen concentration, turning away or backing at 20° C. but not at 13° C. (Jones, 1952).

There are different oxygen demands among invertebrates, too, but they have not been studied as thoroughly as those of fish. Fox & Simmonds (1933) found that the consumption of oxygen by *Baetis rhodani*, which occurs only in flowing water, was at 10° C. four times and 16° C. three times that of *Cloeon dipterum*, which is common in ponds. *B. rhodani* had a faster heart beat, and a shorter survival time in low oxygen concentration. The animals were anaesthetized, so the figures give the standard metabolic rate, and 150 were used in each experiment, which should have cancelled out any differences due to physiological condition. Since there was no key to the nymphs of *Baetis* at the time, the workers could not have been certain that they were using only *B. rhodani*, but this is unlikely to be a source of serious error. They found also a similar relationship between *Molanna* (identified as *Limnophilus vittatus* in the next paper) from a pond and *Hydropsyche* sp. from a stream. Similar results for other species of Ephemeroptera were presented by Fox, Simmonds & Washbourn (1935). Fox, Wingfield & Simmonds (1937) measured the oxygen consumption at various oxygen concentrations. The temperature was 10° C., the animals were not anaesthetized, and, as the bottle they were in was turned upside down every 5 min., it was probably something approaching the active metabolism that was measured. The consumption of oxygen by small nymphs of *Baetis* sp. dropped steadily with decreasing concentration even when the water was supersaturated to start with. *C. dipterum* consumed oxygen at a steady rate down to a concentration of about 1·5 ml./l., when there was a marked incipient limiting level. Other species were intermediate. Walshe (1948) obtained similar results with two pairs of chironomids, one from a stream and the other from a ditch. Mann (1956), experimenting at 20° C. and a maximum oxygen concentration of 6 ml./l., found an incipient limiting level at about 2 ml. of oxygen per litre in two species of Hirudinea generally taken in stagnant water but none in three others most common in running water. Herbert (1954), using 50% survival in 4 hr. as a criterion, found that pond Cladocera had a lower lethal level of oxygen than species from lakes. According to Pacaud (1939) *Daphnia pulex* and *Moina brachiata*, typical of very polluted ponds, can flourish in them because they are tolerant of oxygen lack and less susceptible than other species to interference by bacteria which settle on the feeding limbs. Both do well only when naked algae are available as food. *Moina* is associated with ducks apparently because the clay which their activities keep in suspension favours it in some unknown way. *Ceriodaphnia rotunda* shows a close and unexplained association with *Lemna* ponds, is the most tolerant of oxygen lack and is one of the few species able to do well on a diet of vegetable debris. Pacaud suggests that other species are barred from such places by inability to tolerate low oxygen concentration, settling of bacteria on the feeding limbs or the toxicity of certain organic compounds. He does not mention competition. *Macrothrix hirsuticornis* can live only in cool water. Other species are probably limited by certain food requirements which have already been mentioned.

Berg (1951, 1952) compared *Ancylus fluviatilis* (Mollusca), which he regards as principally a running-water species, with *A. lacustris*, which is generally found in stagnant water. *A. lacustris* survives serious oxygen lack longer, but its incipient limiting level is higher, which is unexpected. The rate of oxygen consumption by the two species is about the same at 16° C. Possibly these results are due to a faulty ecological premise, for, working in a more rocky part of the world than Berg, I find that the main requirement of *A. fluviatilis* is a hard substratum, and have collected it in a small pool in a disused quarry (Macan, 1950).

Oxygen studies are complicated by the adaptation of certain species to the conditions in which they find themselves. *Asellus aquaticus* from a swift stream used 1½ times as much oxygen as specimens from a slow stream (Fox & Simmonds, 1933). Fry of *Salmo trutta* reared in a slow current consumed significantly less oxygen than fry from conditions identical except for a faster current (Washbourn, 1936). Berg (1953) compared the oxygen consumption of specimens of *Ancylus fluviatilis* from a stream where the temperature ranged about 11° C. and a lake where it ranged about 18° C. Tested at both temperatures, the specimens from the warmer water consumed more oxygen, the reverse of what was expected.

Of two crayfishes, the one that lived on a muddy bottom was more tolerant of a low concentration of oxygen than the one that lived on a stony bottom (Bovbjerg, 1952). Wundsch (1922), Pacaud (1944) and Berg (1948) all invoke oxygen concentration to explain the distribution of *Gammarus*. Thienemann (1950, p. 25) points out that *G. pulex* can tolerate down to about 2·7 ml. of oxygen per litre but its epizooites cannot, and they disappear in water in which the host can still just thrive.

Ambühl (1961) shows that the consumption of oxygen by the ephemerid larva *Rhithrogena semicolorata* increases as the speed of the current increases. This is likely to be why this species is confined to running water, whereas the similar *Ecdyonurus*, whose oxygen consumption is not particularly high (Fox, Simmonds & Washbourn, 1935), inhabits stony lake shores as well. The so-called gills of some Ephemeroptera, *Cloeon* for example, serve to keep a current of water flowing over the body and the lower the oxygen concentration the faster the gill-beat. The gills of *Baetis* beat little and those of *Rhithrogena* are used as a sucker. Many other invertebrates have no means of changing the water around them when the oxygen concentration is low, and those that have a high oxygen demand are doubtless confined to running water not so much because of the actual concentration of oxygen, but because the flow makes available more oxygen than could be obtained from the concentration in still water.

Fox &Taylor (1955) found that *Chironomus* and *Anatopynia* larvae, an ostracod and young *Tubifex* survived longer in water 1/5 saturated with air than when fully aerated, and that *Chironomus* larvae and *Tubifex* grew more rapidly in the former water. This must influence the localities in which these, and no doubt other, burrowing invertebrates are found. *Bodo sulcatus* (Flagellata) assembles in a zone of preferred low oxygen concentration (Fox, 1921); this has subsequently been found with other flagellates, and must influence the situations where they concentrate. *Simulium* larvae moving upstream in an experimental trough will choose whichever of two arms has the more oxygen, if the concentration is below 25% saturation (Phillipson, 1956).

Oxygen demand in relation to salinity is discussed in the section on brackish water.

(2) *Life without oxygen*

Chironomus anthracinus, *bathophilus* and *plumosus* larvae live in the mud of rich lakes at depths where there may be no oxygen for several months. *C. thummi* also occurs in rich lakes but in shallower water where oxygen lack, though it may be complete, is never prolonged. They obtain energy by splitting carbohydrates into simpler compounds such as lactic acid and fatty acids, but the first three species can rely more completely on this process than can *C. thummi*, for they do not, whereas it does, show a big increase in rate of oxygen consumption when oxygen becomes available after a period of absence (Harnisch, 1951, 1958). Walshe (1947) found a similar but small repayment of an oxygen debt by *C. plumosus*, but showed that the debt amounts to no more than 0·5 % of the oxygen that would have been used if available. Lactic acid appears in the water in which *C. plumosus* has been kept without oxygen and the debt is probably the oxygenation of the small amount that has not been excreted. Walshe suggests that *C. bathophilus* may be more efficient at eliminating the products of anaerobic respiration. Brand (1944, 1945), in reviewing anaerobiosis, mentions butyric and caproic acid in *C. thummi*.

The chironomids named and many others are brightly coloured with haemoglobin throughout life. Exposure to low concentration of oxygen stimulates production of haemoglobin in *Daphnia* (Fox & Phear, 1953), in *Artemia* (Gilchrist, 1954) and in various other Cladocera and Phyllopoda, in two chironomids, and in young but not adult *Planorbis corneus* (Fox, 1955). Fox, Gilchrist & Phear (1951) show that haemoglobin increases survival in *Daphnia* at low concentrations of oxygen, and enables it, moreover, to feed more rapidly and produce more eggs. Gilchrist found a higher consumption of oxygen at low concentrations by *Artemia* with haemoglobin.

Pause (1919) found the survival time of *Chironomus gregarius* deprived of oxygen to be 5 hr. in the first instar, 8 hr. at the beginning of the second rising to 25 hr. at the end, and up to 54 hr. in later instars. Haemoglobin appeared during the second instar. The larvae left their tubes at night and swam up to oxygenated layers to charge their haemoglobin which could then act as a store while oxygen was absent near the bottom. Leitch (1916), however, calculated that the oxygen would not last more than 12 min. and Walshe (1950), watching *Chironomus plumosus* under a spectroscope, noted that the haemoglobin became reduced 9 min. after undulatory respiratory movements stopped.

She concludes that the function of haemoglobin is to transport oxygen when it is in short supply, which enables the larva to feed and to respire aerobically at levels lower than would otherwise be possible and to recover from lack of oxygen more quickly and at a lower threshold.

The reduction of feeding rate with decreasing oxygen concentration in pale chironomid larvae is not greater as a result of treatment with CO, which leads Walshe (1951) to suggest that they may have a different respiratory enzyme system.

(3) *Excess oxygen*

Fox & Taylor (1955) kept *Chironomus* larvae of the *plumosus* group, *Anatopynia varia*, *Heterocypris incongruens*, *Tubifex* sp., *Planorbis corneus*, *Limnaea stagnalis* and *Artemia salina* in flasks with 100, 21 (air saturation) and 4 % oxygen. The last-named species survived in all concentrations, all the others except *L. stagnalis* survived best in 4 % and/or 21 %. Woodbury (1942) records mortality of fish in a lake coinciding with supersaturation, Mann (1952) attributes death of fish in transport containers to too much oxygen and Harnisch (1951) states that supersaturation may be toxic to fish. Mann notes that supersaturation may send the pH up to 10·5. On the other hand, Wiebe & McGavock (1932) subjected fish to supersaturated water for 20 days during 9 of which the supersaturation exceeded 300% and found no ill effects.

VIII. WATER OF HIGH SALINITY

Mixohaline water* is inhabited by species from the sea and by species from fresh water and the numbers of both drop rapidly with decreasing and increasing salinity respectively. There are a few true mixohaline species, all with close relatives in the sea or in fresh water, and one or two that live in one and migrate to the other to breed. The best known are the eel, *Anguilla anguilla*, and the mitten crab, *Eriocheir sinensis*, which breed in the sea, and the salmon, *Salmo salar*, which breeds in fresh water. Mixohaline water has attracted the attention of many ecologists and physiologists, and the problems besetting its invaders have been reviewed many times (Krogh, 1939; Harnisch, 1951; Beadle, 1957, 1959; Remane & Schlieper, 1958). Segerstråle (1958) gives a bibliography of the world literature.

Invasion from the sea is only of marginal interest to us but must be mentioned because some freshwater animals came in through this route. Some species can tolerate considerable changes in the concentration of salts in the body fluids, others can maintain a concentration higher than in the medium by various means; salts may be taken in against the gradient either at some point on the surface or in the excretory system and the permeability may be reduced. Species that have gone right through to fresh water have generally become less permeable and have reduced the osmotic pressure of the blood (see Beadle & Cragg (1940) in addition to the reviews quoted above and Potts (1954) for a theoretical discussion).

Aëdes detritus, the salt-marsh mosquito, is the mixohaline animal of freshwater ancestry about whose physiology most is known and it can be compared with the freshwater *A. aegypti*, a tropical species popular because easily cultured. Wigglesworth (1933) showed that the so-called anal 'gills' of a mosquito larva are not respiratory but are the only part of its surface readily permeable to water, which is entering all the time and being removed by the Malpighian tubules. Later (1938) he showd that more than half the osmotic pressure of the body fluid of *Culex molestus* and *A. aegypti* is due to amino acids, and that chloride can be absorbed from dilute solutions. Treherne (1954*a*) showed that labelled sodium is taken up mainly through the anal papillae though some enters by the gut and the body surface. The species can increase the amount of chloride in the body fluid in a concentration of 0·006% NaCl, but has little power to prevent concentration rising in solutions more concentrated than the blood. As the outside concentration approaches 1% NaCl all control is lost and any further rise in the medium is followed by a similar rise inside and the larva dies (Beadle, 1939). The fluid in the Malpighian tubules is slightly more concentrated than that of the blood, but contains less sodium in dilute media. These organs have, however, no power to remove excess sodium (Ramsay, 1951). Both sodium and potassium

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* It was recommended at a symposium held in Venice in 1958 that the term brackish water should be dropped because it had been used in too many different ways.

are absorbed from the rectal fluid, the former only when there is little in the external medium (Ramsay, 1953).

Larvae of *Aëdes detritus* are recorded by Beadle (1939) in salinities corresponding to 32–286% sea water. That they are not found in more dilute water is probably not due to physiological reasons, for they can take up chloride from a dilute solution though their lower limit is higher than that of *A. aegypti*. The tissues continue to function though the concentration of the blood changes, the range being from the equivalent of 0·8% NaCl in distilled water to 1·4% in 6% NaCl, which is 200 % sea water. The control mechanism has not been fully investigated but what *A. detritus* can and *A. aegypti* cannot do is to make the rectal fluid more concentrated when in a saline medium (Ramsay, 1950).

Larvae of *Helodes* (Coleoptera) absorb chloride through anal papillae as well as through the gut (Treherne, 1954*b*), but *Sialis lutaria* (Neuroptera) appears to have no mechanism for the active uptake of ions. It can tolerate distilled water because it is highly impermeable (Beadle & Shaw, 1950).

Gammarus duebeni occurs in fresh water (Hynes, 1954) and in water more saline than the sea (Kinne, 1954*a*). The rate of development of the eggs, the upper limit of temperature that they can tolerate, the mortality of the eggs, the mortality of the young and the behaviour of copulating adults all indicate an optimum at a salinity of about 10‰. Growth was fastest between 5 and 20‰ salinity. At 10‰ eggs can develop at a temperature of 22° C., at 2‰ the lethal level is 16–17° C. and at 40–50‰ it is under 13° C. (Kinne, 1953, 1954*a*). The toleration of salinity by *Nereis diversicolor* also varies with temperature (Kinne, 1954*b*). Panikkar (1940), finding that certain prawns were more tolerant of low salinity in summer, suggests that high temperature favours tolerance, which is why animals tend to penetrate into more dilute water in the tropics. Kinne believes that the temperature for optimum tolerance is different in each species and that, whereas in temperate regions tolerance will be much reduced at some time of year by high or low temperature, in the tropics a smaller temperature range during the year enables animals to maintain themselves in more dilute water.

Corixa lugubris, a salt-marsh species, consumes least oxygen at 6‰ salinity, *C. fossarum* and *C. distincta*, freshwater species, at a much lower salt concentration. Up to about 25‰, when it is thought that the control mechanism breaks down, the oxygen consumption of *C. lugubris* rises steadily but the freezing point of the blood remains unchanged up to a value of 17‰ in the medium. The freshwater species are not able to keep the internal concentration constant in similar circumstances and their oxygen consumption does not increase to the same extent. Claus (1937) concludes that the increased oxygen consumption by the mixohaline species is a direct measure of the work that it is having to do to maintain constant internal concentration against a gradient. Remane & Schlieper (1958), however, point out that the relation is probably not as simple as this, and that big changes in the rate of oxygen consumption are often revealed by observations continued for a longer time than those of Claus. The rate of respiration of *Astacus fluviatilis* transferred to water of 15‰ salinity sinks for 3 weeks before reaching a steady level. They believe that changes in rate of respiration are related to changes in the protoplasm which take place gradually after a change of salinity.

Lagoons in which sea water is concentrated are inhabited by marine species that can tolerate the high salinity, though high temperature and chemical changes resulting from stagnation may be limiting factors too (Beadle, 1959; Hedgpeth, 1959; Schmitz, 1959). Absence of predators may enable animals such as phyllopods to establish themselves, and isolation is another factor that must sometimes be considered. *Artemia salina*, the brine shrimp, appears to be the only member of this community about whose physiology something is known (Croghan, 1958*a–d*). The tissues can continue to function though the concentration in the body fluids rises and falls with that of the medium. The rise and fall is, however, controlled and does not exceed an osmotic pressure equivalent to 2·5% NaCl in very concentrated solutions. The mechanism is situated in the first ten pairs of branchiae and it can, it is suggested, take sodium chloride up or pass it out according to requirements. Water is absorbed from the gut but there is some doubt about the water exchange (cf. Croghan, 1958*d*, *e*). The animals survive only in solutions in which there is more sodium than calcium, magnesium and potassium, and the more total salt there is the greater the proportion of sodium necessary (Boone & Baas-Becking, 1931; Jacobi & Baas-Becking, 1933).

The animals in saline water in which the proportions of the ions are not as in the sea belong to typically freshwater groups and maintain themselves, as far as the few observations show, by virtue of a low permeability and an excretory system that can keep the concentration of the body fluids low (Beadle, 1959).

IX. CALCIUM

There is hardly a group of freshwater animals in which the distribution of some species has not been related to calcium and here a selection from the records is presented. In some groups most of the species are found in calcareous water and the number of them falls as the concentration of calcium decreases, but in others species characteristic of waters poor in lime contrast with those which, frequently closely related, are found only in calcareous waters. Of the first category, the molluscs are divisible into hard-water species rarely found in waters where there is less than 20 mg. Ca/l. and those which can tolerate less than this (Boycott, 1936). Hubendick's (1947) extensive collecting in Sweden confirms this, though some species there have a calcium limit higher or lower than in Britain. Frömming (1936, 1938) is the one worker who considers calcium unimportant to molluscs. Boisen Bennike (1943) and Mann (1955) have worked on Hirudinea, Reynoldson (1958) on triclads. The latter finds that further south each species penetrates less calcareous water.

Data for Crustacea are more controversial. Couégnas (1920) claimed that, in a granite region, crayfish occurred only in streams affected by a calcareous rock, but Nygaard (1955) noted that *Astacus fluviatilis* throve and multiplied in a lake with only 1·8 mg. Ca/l. The experiments of Schumann (1928) showed that *Gammarus pulex* requires 5 mg. Ca/l., somewhat less than the limit which Wundsch (1922) had set as a result of field observation. Steusloff (1943), covering the same ground, concluded that the limit found by Wundsch was coincidence not correlation, the real one being lower, and *G. pulex* has been recorded from a tarn in which the calcium fluctuated between 1·8 and 2·6 mg. Ca/l. (Macan & Mackereth, 1957). According to Moon (1957*b*) the distribution of *Asellus* spp. is not correlated with any known physical or chemical factor, but Reynoldson (1961) finds it rarely in places with less than 5 mg. Ca/l., sporadically in places with up to 13 mg. Ca/l. and generally in waters with more than that. Kreuzer's (1940) results are similar. Tucker (1948) finds the highest number of individuals and of species of molluscs, leeches, flatworms, *Asellus* and *Gammarus* in the most calcareous of fifteen ponds, though examination of his data suggests several other factors likely to play a part.

In the second category, nymphs of *Heptagenia* occur on stones in running water and in lakes; in the calcareous lakes of central Ireland the species is *H. sulphurea*, in the lime-poor lakes in the mountains it is *H. lateralis* (Harris, 1952). Similar relationships are recorded among the Culicidae (Macan, 1939, 1951), among the Cladocera (Pacaud, 1939; Smyly, 1958), and among Corixidae (Macan, 1954). Jewell (1939) relates the distribution of freshwater Porifera to the calcium content of the water. Bates (1939), experimenting with culture media for larvae of various species of *Anopheles*, found that *A. superpictus* survived only when there was a moderate amount of calcium.

Little is known about how calcium affects distribution. Snail shells are thinner in softer water but nobody has demonstrated that a thin shell is a disadvantage in the struggle for existence, nor explained why some species require 20 mg. Ca/l. and others much less. Calcium is essential to animals that have to reduce their permeability. *Gunda* (= *Procerodes*) *ulvae*, an inhabitant of the intertidal zones of streams, absorbs soft water till it bursts, but survives in hard water (Pantin, 1931). Schlieper, Bläsing & Halsband (1952) and Halsband (1953) show that in water with plenty of calcium the rate of respiration of *Planaria alpina* and *Salmo trutta* increases less rapidly with rising temperature than in soft water and they survive exposure to a lethal temperature longer. Robertson (1941) reviewed the function of calcium in invertebrates.

Where subterranean water comes to the surface heavily charged with calcium bicarbonate and, flowing away as a stream, precipitates calcium carbonate on its bed, certain psychodid larvae and chironomids that build calcareous tubes are abundant and the usual Plecoptera, Ephemeroptera and Trichoptera scarce (Geijskes, 1935; Thienemann, 1950, p. 85).

X. OTHER CHEMICAL FACTORS

A piece of water may lack a certain species because, containing too much or too little of something, it is toxic or unattractive. The difference between too much and too little may not be great; copper is toxic in quite small amounts, but all animals must have some (Fox & Ramage, 1931) and those whose respiratory pigment is haemocyanin need more.

Attempts to explain the distribution of species in terms of chemical differences have been numerous, but, except where conditions are extreme, mostly fruitless.

There are great differences in the numbers and species of algae in the various Lake District lakes, but chemical analysis has so far shown quite small differences between them (Mackereth, Lund & Macan, 1957). I relate the mollusc population to size, amount of vegetation, presence of dead leaves and situation, and find a correlation only with calcium out of the seven ions whose concentration Mackereth has measured. Whether results of this kind are due to absence of correlation, failure to test for the important ion or to inability to measure very small concentrations is not known. Edmondson (1944) examined a large number of lakes and arranged them in higher and lower ranges according to the pH, calcium, magnesium, bicarbonate and conductivity. He then saw how often each of a number of species of rotifers occurred in each range and tested the difference statistically. He dwells on the difficulty of determining exactly what limits the range of any species from an analysis of this kind. Using the same sort of approach Jewell (1935) concludes that silicate, conductivity, organic matter and flow all influence the occurrence of sponges.

Attractive substances can be important only to animals which can fly away if they are not there, that is the beetles and bugs. Species of Corixidae succeed one another as organic matter accumulates and the species are different according to whether decomposition is proceeding well and the vegetation is progressing towards fen or whether there is poor decomposition with the formation of bog (Macan, 1938). This has not been explained and it is speculation to record these facts under this heading.

Certain molluscs cannot take up chloride from waters where there is less than 3 mg./l. of it (Krogh, 1939) and this could be a limiting factor, though it has never been shown to be so. Where there are few ions, peat tends to form and 'humic acids' drain from it into the water. These are said (e.g. Thienemann, 1950, p. 40) to be unfavourable to some species but again no critical experiments have been made. Tucker (1958) and Reynoldson (1961) record poorer populations with decreasing amounts of dissolved organic matter as well as of calcium.

Whether there is too much of any substance generally depends on what else is present not on the absolute amount. The work on *Artemia* has already been described. Similarly *Daphnia magna* is killed by potassium, calcium and magnesium chlorides in distilled water, but survives if quite small amounts of sodium chloride are added. By means of such experiments, Harnisch (1951) is able to arrange anions and cations in an order of toxicity. The effect of the heavy metals is greater in soft than in hard water (Water Pollution Research, 1957). Carpenter (1926) described in a stream polluted by a lead mine four stages according to the concentration of lead. First there were no animals, then there were insects except Trichoptera, then these and planarians came in, and finally the fauna was completed by the appearance of fishes and molluscs. Further surveys were made by Laurie & Jones (1938) and Jones (1958), who believes that zinc is a more important polluting substance than lead, but that it had been overlooked by the earlier workers. He studied the flora and the food and concluded that some absences, Trichoptera for example, could have been due to scarcity of food and not to direct toxic effects. Hutchinson (1932) cultured species of *Daphnia* in pond water containing 13·5 mg./l. SiO_2, 16·5 mg./l. Ca, 1·7 mg./l. and 2·6 mg./l. Cl. Varying amounts of magnesium chloride were added together with hay infusion as food. The lethal concentration ranged from 30 mg./l. for *D. thomsoni* to 240 mg./l. for *D. magna*, a result which indicated that the absence of the genus from Lake Tanganyika was not due to its high content of magnesium. On the other hand, the restricted fauna of Devil's Lake was attributed to its 844 mg./l. Mg, and the absence of Cladocera in Bear Lake to its 0·65 mg./l. Zn.

Every swan that takes up its abode on Ullswater dies and Moon (1938) attributes this to lead, which, brought in from the spoil heaps round the mines, is accumulated in the plants which the swans eat.

Dittmar (1953) suggests that the absence of *Gammarus* from certain places is due to an excessive amount of magnesium relative to the amount of calcium.

Toxic substances arising from aquatic animals and plants have been discussed in the Section on interrelationships. Of terrestrial plants, *Thuya occidentalis* is said to produce a humus from which a toxin finds its way into streams (Ebeling, 1930).

XI. HYDROGEN ION CONCENTRATION

Spirostomum ambiguum congregates at pH 7·4 when placed in a gradient and that is the value at which it shows greatest activity. The range in which it can live is about pH 6 to 7·6 (Saunders, 1924). The rate of feeding and movement of *Colpidium* rise rapidly as pH rises from 5 to 7, and fall to a minimum at pH 8, after which there is a slight rise. The change of viscosity of mucus at different levels of pH may account for this (Mills, 1931).

There are many studies of distribution in which ranges of species and ranges of pH are found to coincide and Edmondson's (1944) study, quoted in the last Section, may be mentioned as an example, but it is impossible to determine whether the animal is limited by hydrogen or hydroxyl ions, or by the factor that causes one or the other to preponderate, or by something independent of either. Hutchinson (1941) doubts whether the range of any animal except *Spirostomum* has been shown unequivocally to be due to hydrogen ion concentration.

XII. DISCUSSION

Lakes are transitory features of the landscape in terms of geological time and small bodies of water may last no more than a few decades. There are few places which have existed long enough for the development of an indigenous fauna and therefore it is to be expected that ability to traverse land barriers should be possessed by many freshwater animals. Insects are obviously well suited to be successful colonists, but among the animals without a flying stage this ability certainly appears to be widespread, though there is still little known about how overland journeys are accomplished.

Fresh water is more discontinuous than land and much more variable in what it contains than any other medium; in particular the content of oxygen may fall from air saturation or above to nil in a few hours. Fresh water can never be as cold as the land or the sea and in general temperature is its most stable feature, though some springs are so hot that nothing lives in them. All these extremes have been colonized by at least a few pioneers, which are found in waters with high salinity and marked ionic unbalance compared with the sea, waters with very low ionic content, waters with no oxygen, and waters with temperature far above the lethal level for most animals. In general this has been achieved by physiological adaptation and quite a lot is known about the mechanisms involved. Species become fewer as conditions become more extreme, which is no doubt partly attributable to the limitations of the adaptability of protoplasm; the rarity of places offering extreme conditions and the remoteness of many of them must also be taken into account. Yet a third consideration is the predator-prey relationship. Though a water surface acts as a trap for land animals on which aquatic species may feed, an animal cannot colonize a lake in appreciable numbers until a plant has done so. There is then a danger that the animal population eats all its food and it may be surmised that the colonization of extreme conditions may involve the overcoming of the physiological difficulties not by one species only, but by several that make up a balanced community.

There exists always a danger that the ecologist lays on these inhabitants of extreme conditions a stress out of proportion to their numerical significance. Their habitat is easy to define, the effect of the feature characteristic of it can be examined in isolation, and the inhabitants are simpler to study than what may be called ordinary species. The range of these is generally limited by a complex of factors, each one changing its threshold as the others vary in intensity. Understanding of this complex would be easier if something were known about the past of each species, in other words to what conditions it is adapted. In fact little is known and probably never will be, but a certain amount of speculative reconstruction of the probable course of events is not without its value. The first invader of a new lake colonized a wide variety of substrata. It might be driven off some of these by later comers, but, if it remained widespread, descendants on different substrata would gradually become different species—it is not necessary here to join in the controversy about how this may or may not have taken place. Gradually the number of species would increase and there would be many that became adapted to a narrow range of conditions, though these are probably few relative to the number of adaptable species in comparison with the proportion elsewhere, owing to the transitory and variable nature of fresh water. The steady progress of this process would make the establishment of a newcomer increasingly difficult.

If, during this time, temperature remained fairly uniform, the animals might become accustomed to it and lose the power of living outside a comparatively narrow range. This might be of considerable importance if there was a general change of conditions and greater facilities for spread of freshwater animals, such as happens at the end of an ice age.

These events take place slowly and man can see little during his working life except sometimes when a newcomer transported from another zoogeographical region proves more successful than an autochthonous species and replaces it, or demonstrates the existence of a niche that is uncolonized or only partly colonized by the native fauna. Otherwise the systems are in equilibrium, fluctuating, of course, but about a mean that changes little. Many species are clearly confined well within the range of the physical and chemical conditions that they could tolerate and are prevented from extending their ranges by other species. A stage has been reached where competition and other interrelationships are the most potent factors acting on the various species.

For members of such a community, adaptation of behaviour in relation to a particular structure of the substratum, either vegetable or inanimate, is of the first importance. Each species will flourish best on that substratum where its peculiar behaviour pattern enables it to effect the best compromise between obtaining food and being cropped too heavily itself. There may be a particular time, notably immediately after hatching, when the behaviour pattern is highly critical, and it is well established that the distribution of some aquatic larvae depends entirely on the reactions of the mother at the time of oviposition.

The range of a species thus depends, first, on historical events linked with its ability to cross barriers, secondly, on its physiological requirements, and thirdly, on its behaviour pattern.

XIII. SUMMARY

1. Factors that limit a species to a certain habitat within its geographical range are the subject of the article.

2. The responses of an ovipositing female of some species of Ephemeroptera are not very precise and eggs are laid in places unsuitable for the nymphs. Oviposition in the Odonata is less haphazard but does not always result in eggs being laid in places where the life history can be accomplished. Occurrence of mosquito larvae is determined entirely by maternal choice. Various physical factors are important and it is likely, though unproven, that different odours attract different species. Certain species of fish will not spawn unless they can find certain physical conditions.

3. Small animals often have a resting stage that can be blown about. Many freshwater animals are insects that can fly, though not much is known about the extent of their travels. Of the larger invertebrates that are not insects, some rarely succeed in traversing land barriers but most do this quite often. On the whole, the impression is that absence is generally not due to failure of the species in question to reach the place concerned.

4. All species are probably limited to places that offer refuges from predators, unless they live in waters which, because they are temporary or offer extremes of some factor such as salinity, harbour few or no predators. Some ciliates and cladocerans are limited to places where a particular food is plentiful, but most animals have a wide range. Algae produce substances which may inhibit or encourage the growth of other organisms, and animal toxins too are known. The range of one species is often curtailed by the presence of another; fish have aggressive behaviour, *Gammarus pulex* owes its success to its higher reproductive rate, but the mechanism of competition is not always possible to explain.

5. The adaptation of most inhabitants of running water is one of behaviour not structure and they live among stones or in vegetation where there is little current. Some are found only in the slower reaches but little is known of the reason. Many species are confined to a particular kind of substratum, possibly because they select it.

There are adaptations to life in temporary waters. The occurrence of *Gerris najas* is related to the presence of conditions suitable for hibernation.

6. Data relating to lethal, optimal and preferred temperatures are reviewed. Cold-water species do not invade warm water because it kills them or because they cannot compete with some species whose temperature range is higher. The reverse processes keep warm-water animals out of cold water, though inability to tolerate temperatures near freezing point can obviously only affect animals living outside the temperate regions. They may also be excluded from cold water because the temperature does not rise above a threshold level for development, breeding or some other activity.

7. Rate of oxygen consumption at full activity and at rest, and the concentration of oxygen required before full activity is possible, vary greatly from species to species. Some invertebrates with a high oxygen demand are probably confined to running water because they have no mechanism for causing water to flow over the respiratory surfaces.

Anaerobic respiration enables certain chironomids to live in places where oxygen may disappear. Some animals live better in water not saturated with air. The haemoglobin of many animals that live where oxygen may be scarce is an important transporting agent at low oxygen concentrations. Too much oxygen can be unfavourable.

8. Adaptation to mixohaline (brackish) water by a freshwater organism involves toleration by the tissues of a fluctuating concentration in the body fluid and the ability to get rid of unwanted ions. Oxygen consumption is generally lower in mixohaline water. Toleration of salt concentrations outside the optimum range is reduced the further the temperature is from an optimum.

9. Calcium appears to be favourable for all the species of some groups and the less there is the fewer the species. In others there are species typical of soft and species typical of hard water, and they may be closely related. Calcium enables some mixohaline-water animals to tolerate extreme dilution and makes certain sensitive species more tolerant of unfavourable conditions, but nothing is known of how it affects distribution. Deposition of calcium carbonate may affect the fauna by altering the substratum.

10. The poor fauna of two lakes is attributed to excessive quantities of zinc in one and magnesium in the other, and pollution resulting from lead mining annihilates or impoverishes a fauna according to its degree, but attempts to explain distribution in terms of small chemical differences has not had much success. The toxic level of any substance is much influenced by the concentration of other substances.

11. Some protozoa are the only animals known to be affected by the concentration of hydrogen and hydroxyl ions.

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XV. ADDENDUM

A full account of Ambühl's work has become available since the above article was written. Ambühl (1959) constructed a tank the bottom of which, made of plaster of Paris, was traversed by ridges like flat stones sloping downwards from the upstream end. Water containing acetyl-cellulose powder was run through the tank and cinematographed under A.C. illumination. Each speck of powder appeared as a series of dots, from the distance between which the speed of the particle could be calculated. There was a stagnant zone before and behind each stone and a layer in which flow was much reduced just above the surface. It was a few millimetres thick, that is, of such a height that most animals on the surface of a stone would be subjected to slight current only.

Ambühl made some field collections, and started with the assumption that places where the bottom appeared to be identical but over which the current was flowing at different speeds would offer conditions that differed only in rate of flow. This is not quite sound because, as soon as any difference does come into being, biotic effects immediately become a possibility; and it may also be surmised that stones of the same size and shape could differ in texture, which might be important. Ambühl found that *Gammarus pulex*, *Ephemerella ignita*, *Habroleptoides* sp., *Ecdyonurus* sp. and *Helmis maugei* were scarce at the very low speeds, most abundant at 10, 20 or even 30 cm./sec. and then decreased with increasing velocity though all persisted to the fastest current measured which was 100 cm./sec. The distribution of other species was similar, except that their greatest abundance was in faster water: *Baetis vernus*, *Neureclipsis bimaculata* and *Simulium* sp. at 40 cm./sec., *Hydropsyche angustipennis* at 60 cm./sec. The significance of these results is far from clear. Ambühl had shown