

Sektion II. Hauptreferat 2

A review of running water studies

T. T. MACAN (Ambleside, England)

With 8 figures and 3 tables in the text

It would be unconventional for anyone to address this association at length without mentioning classification. I shall begin by suggesting that, before any elaborate scheme is drawn up, it is profitable to examine the extent of the material to be classified. I make also an initial assumption that the species is the basic unit in ecology. This restricts the material at our disposal. For example, the work of BRINCK (1949), HYNES (1941) and ILLIES (1955b) on the taxonomy of nymphal Plecoptera could not circulate till the war finished. My own paper (MACAN 1950) on *Baetis* was, I believe, the first attempt to separate the nymphs of that genus and was the first of a series of studies of immature Ephemeroptera, studies with the defect of being confined to the British fauna. Clearly pre-war work cannot be compared with that of the last decade, and it is to this that I propose largely to confine myself.

One turns first to Denmark, the home of comprehensive surveys, where BERG (1948) and his colleagues have made a detailed study of the Susaa. Unfortunately there is little with which comparison can be made. Turning next to the extreme headwaters, we have VAILLANT's (1955) work on the fauna of thin films of water. This too stands unique. Most popular have been comparatively small stony streams, studied by JONES (1949), whose investigation of some other Welsh streams has unfortunately to be ignored because collections were made only in the summer; by ILLIES (1952 Die MÖlle, 1953a Die Fulda); by ALBRECHT (1953 Die Plane); and by DITTMAR (1955). This is not much on which to found any scheme of classification.

There are more ecological data if single animal groups are considered. To give a list of selected references would be an invidious task, and I mention here only those studies about which we have heard at this congress; POMEISL on Plecoptera, PLESKOT on Ephemeroptera, SCHWOERBEL on mites, MIKULSKI on chironomids, and DORIER on *Simulium*.

Schemes of classification of running waters

BERG (1948) and SCHMITZ (1955), and doubtless others, point out that we can classify only parts of a river system and not the whole. There are two main approaches:

1. The biological, where collections are made at random, the stations are grouped according to the species found, and then factors common to all the stations inhabited by a group are sought (e. g. table 2).

2. The physical, where the collector starts with an arbitrary division of the area into what appears to him distinct biotopes and samples typical stretches of each (e. g. table 1).

Two soil-ecologists, AGRELL and GISIN, have engaged in a bitter polemic about the merits of these two approaches. I submit that both are valuable.

The following schemes of classification have been put forward:

(1) ILLIES (1952) and DITTMAR (1955), in a physical approach, divide their streams according to the annual temperature range:

Quellgebiet	under 5° C per annum
Oberlauf	5—10° C per annum
Mittellauf	10—15° C per annum
Unterlauf	over 15° C per annum

SCHMITZ (1955) prefers to use the difference between the temperature of the water and the air. I see objections to this scheme:

1. Any one of these classes may include both stony swift and slow muddy weedy biotopes,
2. only some animals are limited by temperature,
3. for these, annual range is probably not the significant aspect of temperature.

(2) ILLIES used a biological approach in his next paper (1953 a). He counts the total species at any one station and then makes a graph showing how many of them occur at the other stations up and down stream (fig. 1). The point at which a line begins to drop more steeply is probably where a biocoenosis ends. The individual species are lost sight of in this method, but it is obviously one, further application of which will be awaited with interest.

SCHMITZ (1957) took ILLIES' analysis further and concluded that invertebrate biocoenoses corresponding to the fish zones used for many years (see HUET 1949 for a recent contribution) could be recognized. Here I cannot follow him; within a fish zone the substratum can vary a good deal and moreover, as MÜLLER (1955, 1956) has shown, two stretches of water otherwise identical will harbour different zoocoenoses if there is a lake above one and not above the other.

(3) MARLIER (1951), in another biological approach, attempted to discover the animal associations. He writes: "Chaque synusie est bien délimitée; ce qui trompe

l'observateur, c'est qu'il cherche toujours à distinguer des communautés de grande étendue, alors qu'en eau douce courante, le peuplement constitue une réelle mosaïque de petites synusies." This, if true, as it may well be, is discouraging, for, if only small associations can be distinguished, the whole scheme is likely to become so complex that it defeats its own ends, which are to marshal ideas on a simple plan from which further advance can be made.

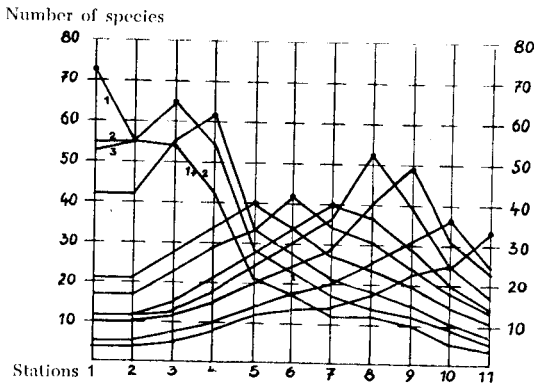


Fig. 1. Population of the Fulda River (ILLIES 1953).

The total number of species (in four groups) at each station is shown and the number of these found at every other station plotted.

MARLIER quotes no figures and leaves unanswered the questions of how distinct these "synusies" are and how abrupt the transition between them is. This being so, I cannot agree with his confident statement that "les méthodes synécologiques sont celles de l'avenir". They may be, but it is too early to know yet. MARLIER contrasts the great strides forwards of plant sociologists with the lack of comparable progress in zoology. One must ask whether this is not due to a fundamental difference. Almost all plants require light, and one of the most important ecological factors, if not the most important, is the nature of the dominant species. Generally, from one point to another along the gradient of some factor, it is able to maintain itself; then it disappears rather suddenly and is replaced by another dominant, which determines the structure of another phytocoenosis. There is nothing comparable to the dominant plant among animals, and the possibility exists that every species in a community has a different range along any gradient. Animal and plant communities can perhaps be likened to two rollers. The animal one is round but the plant one is polygonal and therefore stable only when resting on a side. The transition from one side to another represents the transition from one phytocoenosis to another. The animal one, in contrast, is stable at any point if nothing is pushing it. Should further work show this to be true, the fruitlessness of attempts to define zoocoenoses will be evident.

(4) Reverting to the physical approach, we must notice schemes based on the

substratum. Fig. 2 shows a highly simplified section through a Lake District valley. Near the head there are deposits of material brought down by glaciers or by the stream itself, and this yields an unstable bottom of round stones. Lower down an outcrop of bare rock yields a substratum of flat slate-like stones much less easily moved by the current. HYNES (1941) noted differences in the Plecoptera of the two kinds of substratum (see also MACKERETH 1957). PERCIVAL and WHITEHEAD (1929) found differences between different types of substratum (table 1). *Ancylus* is almost confined to fixed stones, that is stones whose lower parts are buried in a matrix of smaller stones and gravel; it may be surmised that

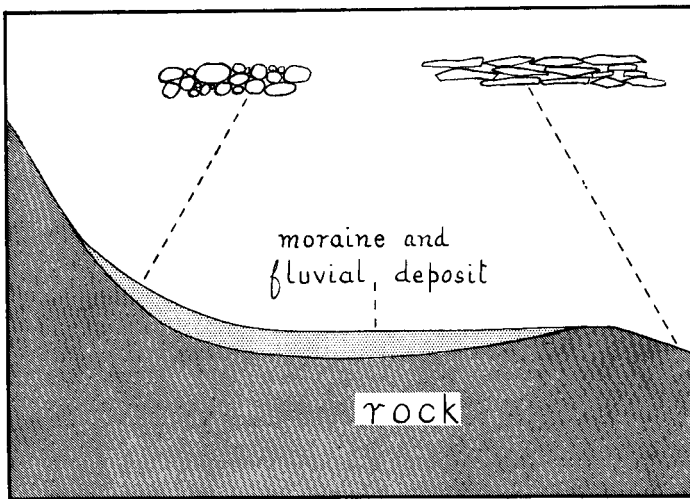


Fig. 2. Diagrammatic section along a valley.

there may be a correlation between this and the animal's inability to flee when a less stable bottom starts to roll. *Rhithrogena* is absent from and *Baetis* scarce on the fixed stones, perhaps because they cannot seek shelter beneath them. KAJ BERG (1948), discussing the classification of the Susaa, rates the nature of the substratum as the most important factor after rate of flow. LINDUSKA (1942) is another worker who attaches great importance to nature of substratum, though mention must be made of the shortness of the period during which he collected. SCOTT (1958) showed that *Glossosoma* is commonest on medium-sized stones, other Trichoptera on large stones.

EINSELE (1957), whose observations on the productivity of different types of bottom, though unsupported by figures or references, are important, notes that, in the Stauen of Austrian rivers, the slack current and muddy bottom favour species of the barbel region, the low temperature and good oxygenation species of the grayling; both flourish. This illustrates nicely the dangers into which anyone tied by too rigid a scheme of classification could run.

Table 1. Number of specimens per square decimetre of different types of substratum. A selection from the data given by PERCIVAL and WHITEHEAD (1929).

	Loose stones	Fixed stones	Stones, gravel	<i>Cladophora</i> on stones	Moss
<i>Baetis</i>	4	0,2	0,7	0,5	25
<i>Rhithrogena</i>	4	—	3	—	1
<i>Ephemerella</i>	3	5	—	45	39
<i>Hydropsyche</i>	0,4	—	—	0,5	305
<i>Glossosoma</i>	2	2	1	—	—
<i>Agapetus</i>	10	14	7	0,2	2
<i>Rhyacophila</i>	0,2	0,1	—	0,2	13
Chironomidae	6	2	2	176	1455
<i>Ancylus</i>	—	4	1	—	—
Hydracarina	0,1	1	0,2	0,1	204
<i>Gammarus</i>	0,2	—	0,2	—	8

Studies of groups

ILLIES (1953 b) pointed out the poor powers of dispersal of the Plecoptera, which has resulted in marked differences in the species lists of different parts of Europe. Possibly his specialization in this group makes him (1955 a) over-despondent about the possibility of finding any method of classifying European running waters.

Nothing can be done with the Trichoptera until methods of identifying the larvae have been worked out.

Simulium, mites and flatworms must be passed over for lack of time. The names of those who have presented papers on these groups to this congress have been listed above.

Table 2 shows an arrangement of the Ephemeroptera records of various authors. The last seven species are not found in Britain (on the slide shown in the lecture, they were omitted). The collections are arranged in groups according to the species as explained above. Characteristic of the first group are *Ameletus inopinatus* and *Baetis vernus* or *tenax*, which I have never been able to distinguish. Both are small streams at altitudes of 800—1000 m. Incidentally, since PLESKOT (p. 410) records *Baetis vernus* from the warmest part of the Schwachat, there is probably here a taxonomic knot that has still to be unravelled. (During the excursions Dr. PLESKOT demonstrated the fauna of alpine streams higher than any considered here and none of the species seen are in table 2. There appears to be no published account of this fauna, though PLESKOT [1951] discusses some of the species.) The second group comprises similar streams at lower altitude; *Paraleptophlebia submarginata* and *Centroptilum luteolum* are found only in the slowest stretches. The waters of the third group are also fast and stony but larger; the species from the group before persist and there are several newcomers. In the fourth group there is a disappearance of ecdyonurids

and the appearance of a few new species and this is correlated with slower current and the establishment of weeds. These data are taken from all over Europe, and it does seem that, in a general way, river systems can be divided

Table 2. Records of Ephemeroptera from running water. *Caenis*, *Ephemerella*, *Leptophlebia* and *Habrophlebia* are omitted.

	WINKLER 1956	CLEHILL 1960	BRINKHURST 1957	HYNES MS	HARKER 1953	DITTMAR 1955	MACAN 1957	ILLIES 1952	HYNES MS	refs. in MACAN 1957							
										Lake District Rivers	R. TEES	R. RHEIDOL	R. AIRE, NIDD and WHARFE	R. AVON	R. KENNET	R. SUSAA	
<i>Ameletus inopinatus</i>	×	×															
<i>Heptagenia lateralis</i>	.	×	×	×	×	×	×	.	×	×	×	×	×				
<i>Ecdyonurus venosus</i> , <i>torrentis</i>	.	v	v.t	v	t	v	tv	v	v	tv	v	v	v				
<i>Rhithrogena</i> <i>semicolorata</i>	×	×	×	×	×	×	×	×	×	×	×	×	×				
<i>Baetis tenax/vernus</i>	×	×	×	×	.	2	.	.	×	.	×	.	.	×	×	×	
<i>Baetis rhodani</i>	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	.	
<i>Baetis pumilus</i>	.	×	×	×	.	×	×	×	×	×	×	×	×	×	.	.	
<i>Ephemerella ignita</i>	.	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
<i>Paraleptophlebia</i> <i>submarginata</i>	×	×	×	.	×	×	×	.	×	×	.	
<i>Centroptilum</i> <i>luteolum</i>	×	×	.	×	×	.	.	×	×	×	
<i>Ecdyonurus dispar</i>	.	.	×	×	×	
<i>Baetis scambus</i> , <i>bioculatus</i>	(s) ²	.	s	s	b	s	b	b	bs	b	
<i>Heptagenia</i> <i>sulphurea</i>	×	×	.	×	×	.	×	
<i>Procloeon rufulum</i>	×	×	.	.	×	×	.	
<i>Baetis niger</i>	×	×	×	.	
<i>Cloeon</i> spp.	×	(×) ²	×	
<i>Siphonurus</i> <i>lacustris</i>	× ¹	.	.	×	.	×	(×) ²	×	.	×	×	×	
<i>Habroleptoides</i> <i>modesta</i>	×	.	×	
<i>Baetis alpinus</i>	×	
<i>Baetis gemellus</i>	×	×	
<i>Epeorus assimilis</i>	×	.	×	
<i>Ecdyonurus forcipula</i>	×	
<i>Torleya major</i>	×	
<i>Chitonophora</i> <i>krieghoffi</i>	×	

¹ *S. aestivalis*. ² Single specimens in a large collection. ³ Also *R. haarupi* and *Centroptilum pennulatum*.

according to the ephemeropteran fauna. The question is whether divisions based on other groups fall at the same points. A lot more data are necessary but such as there are suggest that they do not (cf. SCHWOERBEL, p. 355).

Factors limiting range

Current is of primary importance in determining the main types of substratum (stones, sand, mud etc.) (NIETZKE 1938), but here its influence within the zone where it is fast enough to remove everything but stones is to be considered. DORIER and VAILLANT (1954) made numerous measurements and record (table 3) for each of a number of species:

1. the current that it withstands in nature;
2. the maximum current that it will ascend;
3. the current speed at which it is washed away.

Table 3. Current speed in cm/sec. 1. maximum withstood in nature, 2. maximum against which the species will ascend, 3. speed at which the species is washed away. A selection from the data given by DORIER and VAILLANT (1954).

	1	2	3
<i>Agrion</i> sp.	10	54	77
<i>Gammarus pulex</i>	40	44	99
<i>Planaria alpina</i>	14	140	143
<i>Baetis rhodani</i>	30	102	177
<i>Rhithrogena semicolorata</i>		125	182
<i>Heptagenia lateralis</i>	28	140	188
<i>Chloroperla</i> sp.	24	177	240
<i>Ancylus fluviatilis</i>	24	109	240
<i>Rhyacophila</i> sp.	125	100	200
<i>Simulium ornatum</i>	114	117	240

It is not wholly clear how they determined what speed of current a species may occasionally venture into and the second set of measurements demands the assumption that all the animals tend to move against the current, which BEAUCHAMP (1933) has shown not to be so. The work is undoubtedly an important contribution, but the exact significance of the results is difficult to evaluate. This applies also to the work of PHILIPSON (1954), apart from his observation that some of the net-spinning Trichoptera will not make a net unless the current is above a certain speed, and that the threshold is higher for *Wormaldia* than it is for *Hydropsyche*.

The ideas that AMBÜHL (p. 390) put before this congress appeal to me strongly. He states that most stream animals spend their lives down among the stones where there is little or no current, and that even those that do crawl onto the surface find themselves in a comparatively still layer of water over which the rest is flowing. Adaptation to stream life is primarily an adaptation in behaviour.

This is well exemplified by *Gammarus*, which is a poor swimmer without any obvious morphological adaptations for life in running water. If it is exposed by the lifting of a stone, it tends to swim against the current and to get underneath something as quickly as it can. The possession of the right reactions is no doubt why it is such a successful stream animal, which in the English Lake District, for example, occurs in the steepest streams.

Nevertheless some species are confined to the slower parts of the stony region; *Paraleptophlebia submarginata* and *Centroptilum luteolum* have already been quoted as examples and *Habrophlebia fusca* may be mentioned too. The problem, like many in ecology, is possibly one of natural history that will be solved by studying the species and discovering the details of the life history and the reactions at all stages. One may remark that all the work quoted has been done on rather large larvae; the ovipositing adult, the egg, and the newly hatched larvae are all stages that could be critically affected by current speed.

FONTAINE (p. 400) has shown that current may have an effect on the physiological state of an organism.

Some ancillary effects of current require mention:

1. Water regime. KRESSER has (p. 417) described how a glacier-fed stream has one regular flood at the time of maximum melt in contrast to the rain-fed stream where periods of high and low water occur quite irregularly. I know of no attempt to correlate faunistic differences with this, though MIKULSKI (p. 372) has made a start.
2. Drought was discussed by HYNES (1958) at the last congress.
3. Turbidity. GESSNER (1955) noted in S. America a contrast between the rich fauna of the clear mountain streams and the paucity of life in the permanently turbid rivers lower down. HAMILTON (p. 435) found fauna unaffected by sand-pit washings. There is no doubt room for further investigations.
4. Food. MÜLLER (1955, 1956) shows how the plankton washed out of a lake leads to changes in the fauna and particularly to a great increase in the net-feeders belonging to Trichoptera, Simuliidae and Chironomidae. In two other papers (1954) he showed that the stream animals themselves are continually being washed down and this is the main source of food for *Trutta*. KALLEBERG (1958) reaches just the same conclusion studying fish. The absence of specific names in MÜLLER's work is, to a large extent, made good by ILLIES (1956).

Oxygen. Studies of oxygen consumption demand three preliminary considerations.

1. It may change at different times of year as shown by BERG, LUMBYE and OCKELMANN (1958) (fig. 3).

2. Steps must be taken to control the activity of the animal in the experiment (WAUTIER and PATTÉE 1955) (fig. 4).
3. The difference between two species may change greatly with changing temperature (SCHLIEPER 1952 [fig. 5] and SCHWOERBEL p. 355 above).

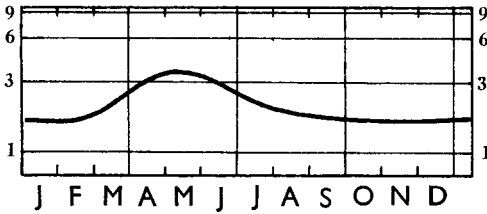


Fig. 3. Oxygen consumption in $\mu\text{l/hr/individual}$ of 20 mg of *Ancylus fluviatilis* kept at a constant temperature of 11°C throughout the year (after BERG, LUMBYE and OCKELMANN 1958).

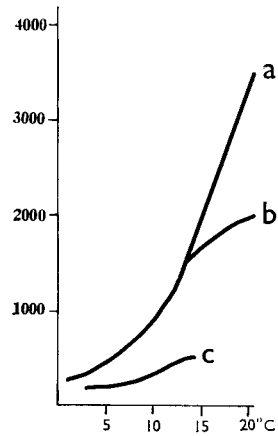


Fig. 4. Consumption of oxygen with increasing temperature by *Ephemera danica* in a flask with a, no substratum, b, some pebbles, c, sand. Figures are $\text{cmm O}_2/\text{hr/g}$ of animal's dry weight (after WAUTIER et PATTÉE 1955).

A resting *Salvelinus fontinalis* (speckled trout), a species of flowing water, requires more oxygen than a resting *Carassius auratus*, the familiar goldfish of ponds and bowls (fig. 6.) *Carassius* can extract oxygen for its minimum needs from water containing distinctly less than the amount necessary to keep *Salvelinus*

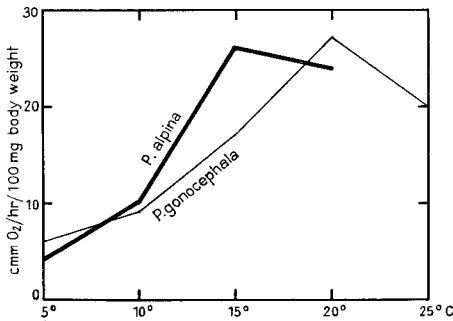


Fig. 5. Consumption of oxygen at different temperatures by *Planaria alpina* and *P. gonocephala* (SCHLIEPER 1952).

alive (GRAHAM 1949, FRY and HART 1948). An active *Salvelinus* requires much more oxygen. Possibly the most significant aspect of oxygen is the tension at which it begins to limit the activity of a fish. At 20°C this happens to *Salvelinus* almost as soon as the level drops below saturation (159,5 mm Hg); at 5°C

activity is uninfluenced by oxygen tension until about 95 mm Hg (fig. 7). The incipient limiting levels for *Carassius* are 15 mm Hg at 5° C and 40 mm Hg at 35° C.

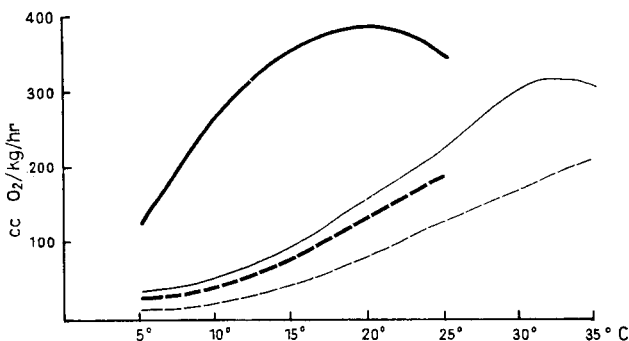


Fig. 6. Oxygen consumption by active fish (continuous line) and resting fish (broken line). *Salvelinus fontinalis* — thick line (GRAHAM 1949) and *Carassius auratus* — thin line (FRY and HART 1948).

Work on invertebrates has not been as detailed as that of the Canadian school on fish and in some of it not all the precautions set out above have been considered. None the less it is clear that the oxygen demand of stream-dwelling animals is significantly greater than that of close relatives living in still water (FOX & SIMMONDS 1933). An important contribution to this subject is that of

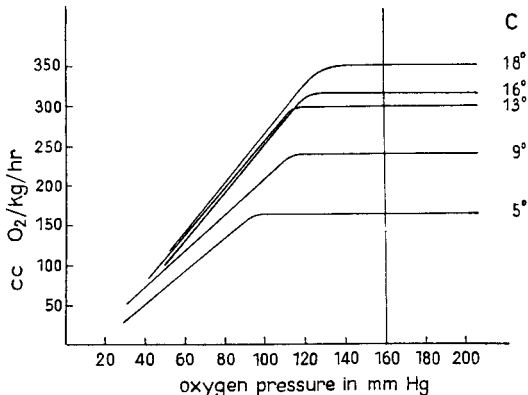


Fig. 7. Oxygen consumption of an active *Salvelinus fontinalis* at different temperatures and different concentrations of oxygen (GRAHAM 1949).

AMBÜHL (p. 390) who finds that the oxygen consumption of certain species increases as rate of flow increases. But I note that, in the experiments about which he talked, the temperature was 18° C, which seems to me excessively high and, I believe, near the lethal level for *Rhithrogena semicolorata*. This work certainly confirms the idea that some species are confined to running water by their oxygen requirements.

Other chemical factors. On the whole the study of running waters has not revealed much difference between streams of different chemical composition, though SCHWOERBEL (p. 355) finds calcium a factor affecting the distribution of mites. Addition of calcium and magnesium to water decreases the rate at which *Planaria alpina* and *Salmo irideus* consume oxygen with rising temperature, and enables them to tolerate a lethal temperature for longer (SCHLIEFER, BLÄSING and HALSBAND 1952).

Pollution. This, an ecological factor all too common in many countries, is too large a subject to be treated here. Attention may be drawn to a recent work by HYNES (1960) and to the current appearance of a second volume of LIEBMANN's (1951) book.

Temperature. Some animals are confined to the headwaters of river systems because they cannot tolerate the temperatures reached lower down. *Planaria alpina*, for example, behaves continuously above 12° C in a way in which it behaves only when stimulated at lower temperatures (BEAUCHAMP 1935). STEINBÖCK (1942) claims that it is not a cold-water stenotherm, having found it in a pool that reached 22° C during the day, but SCHLIEFER and BLÄSING (1952) point out that it can tolerate high temperatures if not exposed to them for too long (e. g. 23° C for 12 hours in winter and 2 days in summer). The contention that laboratory findings and field observations do not coincide does not seem to be substantiated. The work of BEAUCHAMP and ULLYOTT (1932) and BEAUCHAMP (1933, 1935, 1937) is also relevant and is mentioned here because so many have overlooked it. PLESKOT (1951) correlates with temperature the distribution of various species of Ephemeroptera in the streams around Lunz. *Rhithrogena alpestris* occurs in the coldest water, *R. hybrida* and *R. semicolorata* at higher temperatures.

The detailed work of the Canadian school has established that the lethal temperature for *Salvelinus fontinalis* is 25,3° C (FRY, HART and WALKER 1946), though, if it can, it will avoid water several degrees colder than this. That of *Carassius auratus* is 41° C (FRY, BRETT and CLAWSON 1942). Fish were tested after being kept for some time at a constant temperature (acclimated) and it was found that the raising of the acclimation temperature from 0 to 36,5° C raised the lethal temperature from 27 to 41° C. These figures are plotted on fig. 8. From 36,5° C, acclimation above which does not make the lethal temperature any higher, the line is taken horizontally to the point where lethal and acclimation temperatures are the same. A vertical line is dropped to meet the line showing the relation between acclimation temperature and lower lethal temperature. Fish acclimated at 41° C die at 17° C and it is not until the acclimation temperature is down to 17° C that they can survive exposure to 0° C. The figure obtained in this way encloses 1220 degrees centigrade squared, the comparable figure for *Salvelinus* about half that number.

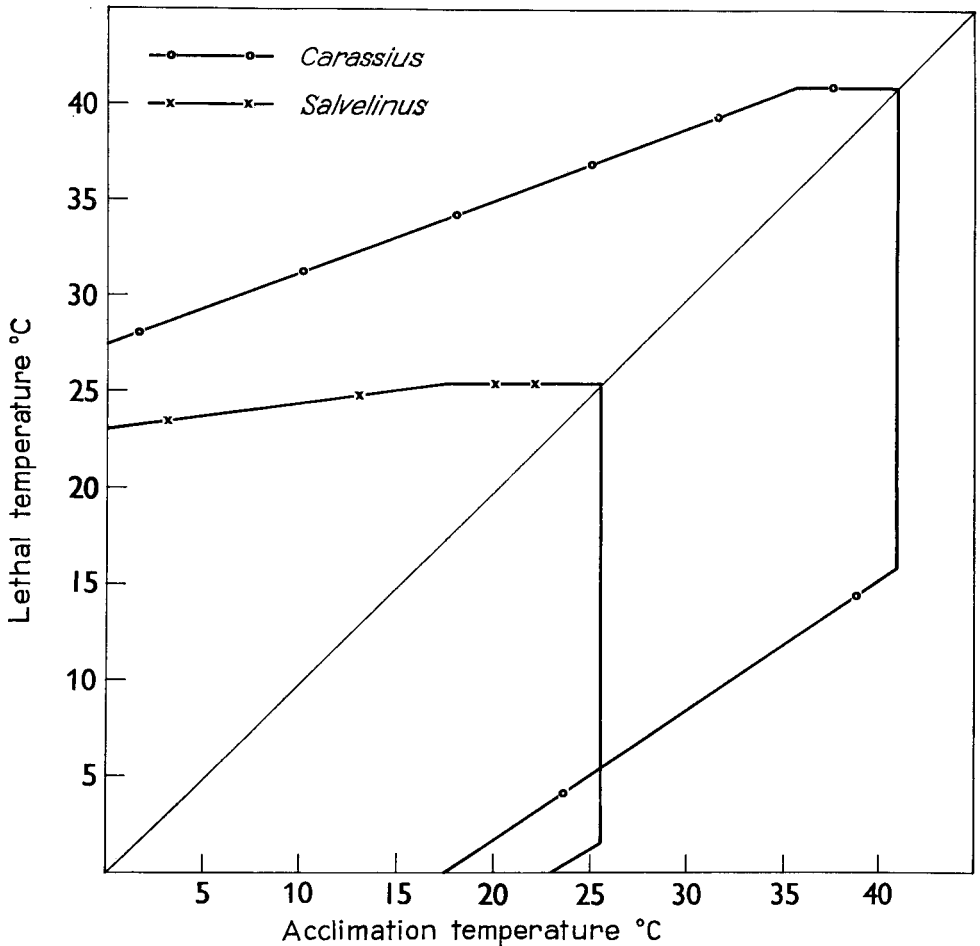


Fig. 8. Relation between lethal temperature and acclimation temperature in *Salvelinus fontinalis* (FRY, HART and WALKER 1946) and *Carassius auratus* (FRY, BRETT and CLAWSON 1942).

It is not always clear whether high temperature affects the animal directly or through the oxygen demand (SCHLIEPER 1952 [see fig. 5], PLESKOT 1953 and SCHWOERBEL p. 355).

Range into warmer water may be curtailed by competition. *Planaria montenegrina* extends down a stream to a point where the temperature is 16–17°C when it is alone but stops at 13–14°C when *P. gonocephala* is present (BEAUCHAMP and ULLYOTT 1932).

SCHLIEPER and BLÄSING (1952) assert that *Planaria alpina* can tolerate in the laboratory temperatures higher than any found in its natural range, which could be due to the fact that the species will only breed in cold water or to competition.

Cold-water species generally breed in the winter. Whether, in the absence of competition, they could adapt themselves and their breeding habits and spread to warmer regions, is a question that cannot be answered at the moment.

Temperature may also influence the life history considerably (PLESKOT 1951 and p. 410). This is of the utmost importance in productivity studies. Stony streams are inhabited mostly by winter-growers; in warmer streams summer-growers, often with several generations, are more important. A stream could perhaps be too warm for one and too cold for the other and therefore less productive than one colder as well as one warmer.

Other species may require water warmer than that of the headstreams, being adversely affected because:

1. The temperature is too low to enable it to complete development or to complete it soon enough.
2. It cannot compete successfully with a species that develops faster at the temperatures prevailing.
3. An absolute lethal temperature is reached at some time of the year.

The last possibility is unlikely to be of much importance in our latitudes where nearly every piece of water reaches a temperature near 0° C in winter, but may well be further south where frost is occasional. The other two are likely explanations not at present confirmed by experimental work. The first is invoked by IDE (1935) to explain distributions that he observed.

4. Adults can live but the temperature is not high enough to stimulate reproduction or to enable egg development to be completed. RAWSON (1945) describes an example of this. Spawning of *Micropterus dolomieu* (small-mouth bass) is stimulated by a quick rise in temperature to the neighbourhood of 16° C. A period of two to three weeks with a temperature of about 18° C is required for successful development. Any drop much below this causes the males to desert the nests and the eggs to die. As this happened in two out of four years in a Canadian lake to which RAWSON had introduced them, he concluded that they were near the northern limit of their range.

That an animal may move out of a place just because, if unscientific terminology may be permitted, it does not like the conditions, must not be overlooked. Carp select warmer water up to 35° C, the exact temperature chosen being dependent on that at which they have been living previously (PITT, GARSIDE and HEPBURN 1956). Data on the temperature selected by various species of fish placed in a gradient are given by SCHMEING-ENGBERDING (1953).

It is not necessary to point out that there is much still unexplained; STARMÜHLNER (p. 404) showed how snails become suddenly very abundant in a stream when a warm tributary comes in, but he did not explain why.

Size. The number of species of Ephemeroptera increases as a stream grows larger (table 2). I suggest that this is because special places such as sandy bays become larger as everything increases in scale and eventually large enough to support a viable population.

Conclusion

I have presented pros and cons and delivered few definite opinions. That is because I believe that the subject is not yet ripe for them. I shall conclude with two: First we need more facts. Secondly we need freedom of thought and if anyone succeeds in confining the ideas of a large number of other workers within a rigid framework, and after all a framework makes a cage, that person will be doing science a grave disservice.

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