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EGGS OF EPHEMEROPTERA

J. M. ELLIOTT & U. H. HUMPECH*

Introduction

The life cycles of Ephemeroptera vary considerably between species (see Macan 1979), and are often complicated by an overlap of cohorts (a cohort is a group of individuals that were born at the same time, or in practice born over a short period of time). These cohorts must be recognized and separated before estimates can be made for growth rates, mortality rates and production. Information on eggs, especially their rates of development, facilitates the identification and separation of cohorts, and is therefore an essential part of quantitative studies on the life cycles of Ephemeroptera.

Several workers have described the swarming and mating behaviour of European Ephemeroptera (see references in Savolainen (1978)). Degrange (1960) describes the morphology of the eggs of 51 species from Europe, whilst Koss (1968) describes the eggs of 60 species from North America. The eggs of most species have a length of between 150 and 200 μm and a width of between 90 and 150 μm , but the eggs of the larger species may be 250-300 μm long by 150-200 μm wide. Various attachment structures ensure that the eggs adhere to submerged objects or the substratum. The eggs of some species have an external adhesive layer that swells on contact with water, whilst eggs of other species have their surface covered with suckerlike discs or plates, adhesive projections or coiled or uncoiled threads that often have terminal knobs. Species in a third group have polar caps at one or both ends of their eggs. Each polar cap swells on contact with water and releases a large number of threads with terminal knobs.

This short review summarizes information on the fecundity, oviposition behaviour, egg hatching and parthenogenetic development of Ephemeroptera. The emphasis is on British species, but other European and North American species are mentioned where necessary. The nomenclature follows Macan (1979) for the British species, Illies (1978) for the other European species, and Edmunds, Jensen & Berner (1976) for the North American species. Fishermen's names for British species are listed by Kimmins (1972).

Fecundity

Fecundity is usually defined as the number of ripening eggs in the female prior to oviposition. Although information on fecundity is available for twenty-four of the forty-seven species in Britain (Table 1), most of this information is for only a few females of each species and usually the size of

* Limnologisches Institut der Österreichischen Akademie der Wissenschaften, Berggasse 18/19, A1090 Wien, Austria.

TABLE 1. FECUNDITY OF EPHEMEROPTERA OCCURRING IN BRITAIN.

1. Up to c. 1200 eggs per female.
Caenis horaria, *C. macrura*, *C. moesta* (5), *Ephemerella ignita* (3,5,7,9,12), *Habrophlebia fusca* (8), *Leptophlebia vespertina* (11), *Paraleptophlebia submarginata* (8,12,14), *Cloëon dipterum* (5), *Baëtis niger* (5), *B. fuscatus* (14).
2. Up to c. 2500 eggs per female.
Ecdyonurus dispar (5,10), *Heptagenia lateralis* (5), *Leptophlebia vespertina* (5,8,12,14), *Siphonurus lacustris* (5), *Centroptilum luteolum* (5,12), *C. pennulatum* (5), *Baëtis muticus* (5,12).
3. 2000-3500 eggs per female.
Cloëon simile (4,5), *Ecdyonurus insignis* (10).
4. Up to c. 4500 eggs per female.
Baëtis rhodani (1,2,6,9).
5. Up to c. 6000 eggs per female.
Ephemerella danica (5,9,12), *E. vulgata* (12), *Ecdyonurus venosus* (10,13).
6. 5000-8000 eggs per female.
Ecdyonurus torrentis (10).

References: 1, Benech 1972b; 2, Bohle 1969; 3, Bohle 1972; 4, Davidson 1956; 5, Degrange 1960; 6, Elliott 1972; 7, Elliott 1978; 8, Grandi 1960; 9, Harris 1956; 10, Humpesch unpublished; 11, Kjellberg 1972; 12, Landa 1969; 13, Rawlinson 1939; 14, Schoenemund 1930.

the females is not given. This is unfortunate because fecundity increases with increasing size of the female (Fig. 1). The relationship between fecundity (Y eggs per female) and body length (L mm from front of head to tip of abdomen) has been shown to be well described by the power law:

$$Y = aL^b \quad (1)$$

or $\log_e Y = \log_e a + b \log_e L$

where a and b are constants. Such a relationship has been found for *Baëtis rhodani* (Benech 1972b; J. M. Elliott, unpublished; see Fig. 1), and for the North American species *Leptophlebia cupida* (Clifford 1970; Clifford & Boerger 1974), *Hexagenia limbata* (calculated from data in Hunt 1951), and *Ephemerella simulans* (calculated from data in Britt 1962). The value of b in these studies is close to 3 (range 2.66-3.04). Sweeney (1978) found that fecundity was a linear function of dry body weight in three North American species.

When there is a long flight period, the females that emerge early are larger and more fecund than those that emerge later, e.g. *Baëtis rhodani* (Benech 1972b; see also Fig. 1), *Ecdyonurus venosus* (U. H. Humpesch, unpublished). Sweeney & Vannote (1978) have proposed that similar changes in North American species are due chiefly to temperature that apparently affects adult size and fecundity by altering the larval growth rate and the timing and rate of adult tissue development.

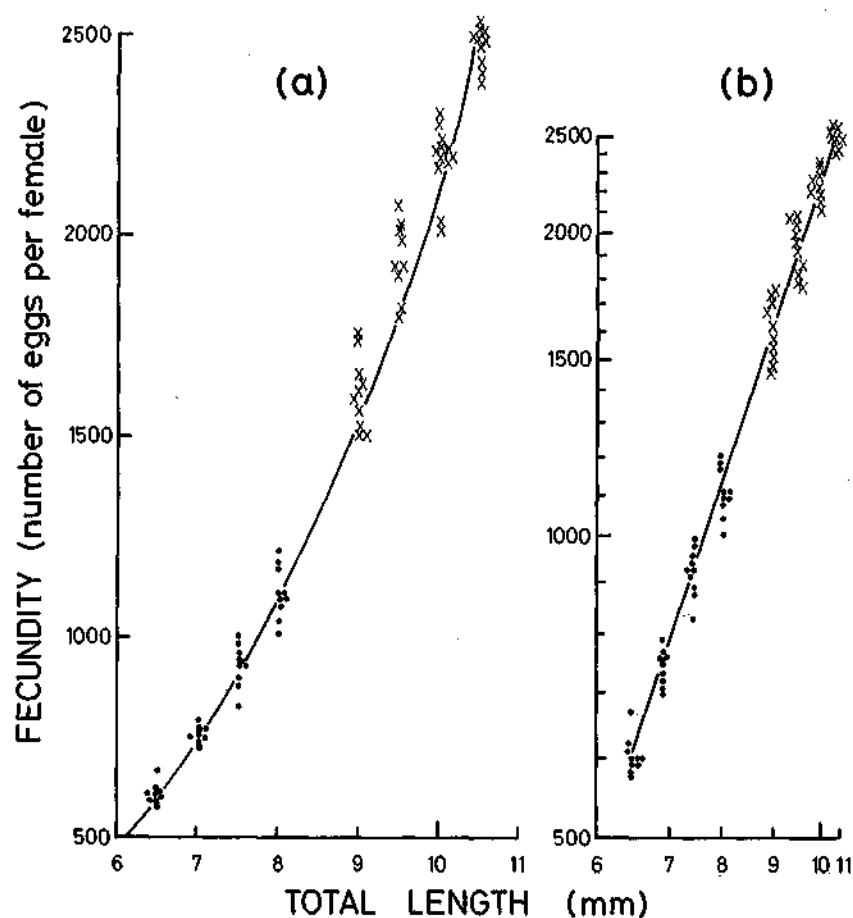


FIG. 1. Relationship between fecundity (number of eggs per female) and total length (mm) of *Baëtis rhodani*, using data from a summer generation (●) and a winter generation (x): (a) On arithmetic scale with curvi-linear regression line; (b) On log/log scale with linear regression line.

Oviposition behaviour

Most females fly in an upstream direction before ovipositing in streams and rivers. The eggs are always laid in the water, but they hatch immediately on contact with water in the ovoviviparous *Cloëon* spp. Information is available for twenty-six of the British species (Table 2). The following five basic types of oviposition behaviour occur but there is some disagreement over the category to which some species belong:

TABLE 2. OVIPOSITION BEHAVIOUR OF EPHEMEROPTERA OCCURRING IN BRITAIN
(a ? indicates that the observation is doubtful).

1. Female goes underwater and eggs laid on substratum.
Baëtis rhodani (1,2,5,9,15), *B. vernus* (2), ?*B. muticus* (9,17), *B. fuscatus* (14,18), *B. scambus* (1,9).
2. Female rests on stone above water and eggs laid on substratum underwater. *Ecdyonurus dispar* (10), ?*E. venosus* (20), ?*Rhithrogena semicolorata* (14).
3. Female flies down to water surface and eggs released in one mass.
Ephemerella ignita (see refs in 6), *E. notata* (9), *Centroptilum luteolum* (9,12), ?*Ephemera danica* (9), *Siphonurus armatus* (18), *S. lacustris* (20), ?*Paraleptophlebia submarginata* (20).
4. Female flies down to water surface and eggs released in batches.
Ephemera danica (4,17), *E. vulgata* (14,20), *Ecdyonurus venosus* (18,19,20), *E. insignis* (20), *E. torrentis* (7), *Heptagenia sulphurea* (9,16), *Rhithrogena semicolorata* (7,11,14,16,20), *R. germanica* (16), *Leptophlebia vespertina* (13,20), *Habrophlebia fusca* (20), *Caenis macrura* (14), *Baëtis muticus* (8,15), *B. fuscatus* (9,20), *Cloëon simile* (4).
5. Ovoviviparous species.
Cloëon dipterum (see refs in 3).

References: 1, Benech 1972a; 2, Bohle 1969; 3, Degrange 1959; 4, Degrange 1960; 5, Elliott 1972; 6, Elliott 1978; 7, Elliott unpublished; 8, Gillies 1950; 9, Harris 1956; 10, Humpesch unpublished; 11, Humpesch & Elliott 1980; 12, Kimmins 1972; 13, Kjellberg 1972; 14, Landa 1969; 15, Macan 1957; 16, Mosely 1938; 17, Percival & Whitehead 1926; 18, Percival & Whitehead 1928; 19, Rawlinson 1939; 20, Schoenemund 1930.

1. Female goes underwater and eggs laid on substratum.
Baëtis rhodani belongs to this category (Elliott 1972). The female lands on a partially submerged stone in rapidly-flowing water, folds her wings along the abdomen, then walks under the water and searches for a suitable oviposition site, usually on the underside of the stone. She always faces the current and swings her abdomen from side to side until a row of eggs is laid in an arc. The female moves slowly forward and thus lays contiguous rows of eggs to form a flat semi-circular plate with its concave edge facing the current (Plate 6). When oviposition ceases, the female may walk out of the water and fly away, but she is usually swept away downstream.

Only *Baëtis* spp. are known to show this type of behaviour but some *Baëtis* spp. may lay their eggs in a different way; e.g. *B. muticus* belongs to this group according to Percival & Whitehead (1928) and Harris (1956), but not according to Gillies (1950) and Macan (1957). North American *Baëtis* spp. also belong to this type (Edmunds et al. 1976).

2. Female rests on a stone above water, and eggs laid on substratum under water.

There are no detailed descriptions for British species, but the oviposition behaviour of *Habroleptoides modesta*, a European species absent from Britain, has been described in detail by Pleskot (1953). The females search for stones that are partially submerged and near the banks. When a suitable stone is found, the female walks backwards until the tip of the abdomen is just under the surface of water in wet areas between stones and gravel. The eggs are laid amongst the gravel but the female is never totally submerged. The tails (setae) are usually broken off before oviposition starts.

3. Female flies down to the water surface and eggs are released in a single mass.

Ephemerella ignita belongs to this category (Elliott 1978). Swarming for oviposition usually occurs in the late afternoon and evening. The egg mass forms a spherical greenish ball that is carried at the genital aperture with the posterior abdominal segments curved downwards and round the ball to hold it in position. Eggs are laid in fast-flowing and turbulent water, usually where moss is present. The female flies upstream and descends to the water surface, releasing the egg-ball on contact with the water. After ovipositing, the female usually falls on the water surface. The egg mass separates immediately on entering the water and each egg has a polar anchoring cap that attaches it to the substratum.

Species in the genera *Ephemerella*, *Centroptilum* and *Siphonurus* are known to show this type of behaviour. *Ephemera danica* also belongs to this type according to Harris (1956), but *Ephemera* spp. are placed in the next category by all other authors. North American *Ephemerella* spp. also belong to this type (Edmunds et al. 1976).

4. Female flies down to the water surface and eggs are released in several batches.

Rhithrogena semicolorata belongs to this category (Humpesch & Elliott 1980). The female flies upstream and descends to the surface of the water, releasing a few eggs by dipping the tip of her abdomen at intervals whilst flying over the water, or by actually settling on the water surface for short periods. The eggs sink to the bottom and are dispersed over a wide area. After several visits to the water surface, all the eggs are released and the spent female usually falls on to the water.

Most species belong to this category, including the North American species in the families Ephemeridae, Heptageniidae and Leptophlebiidae (Edmunds et al. 1976).

5. Ovoviviparous species

Cloëon dipterum is the only British species known to be in this category. The females rest for 10-14 days after copulation, and then lay their eggs on the surface of the water. As soon as the eggs come into contact with the water, they hatch and the larvae swim away. Some authors claim that the eggs can hatch inside the abdomen of the female, but this is unlikely (see review by Degrange 1959). The closely related *C. simile* is definitely not ovoviviparous according to Degrange (1959, 1960).

North American species in the genus *Callibaëtis* are also ovoviviparous (Edmunds et al. 1976). Therefore ovoviviparous species are known only in the family Baëtidae.

Hatching of eggs

Detailed studies have been made on the hatching of eleven species and nineteen populations of European Ephemeroptera, including eight species occurring in Britain (Table 3). Most species hatch within the range 3-21 °C, but *B. rhodani* has a higher upper limit of 25 °C whilst in *R. semicolorata* the lower limit is between 4.5 °C (no hatching) and 5.9 °C (4-11% hatching). The maximum percentage of eggs hatching in the laboratory is over 90% for the two *Baëtis* species and *E. ignita*, but is less

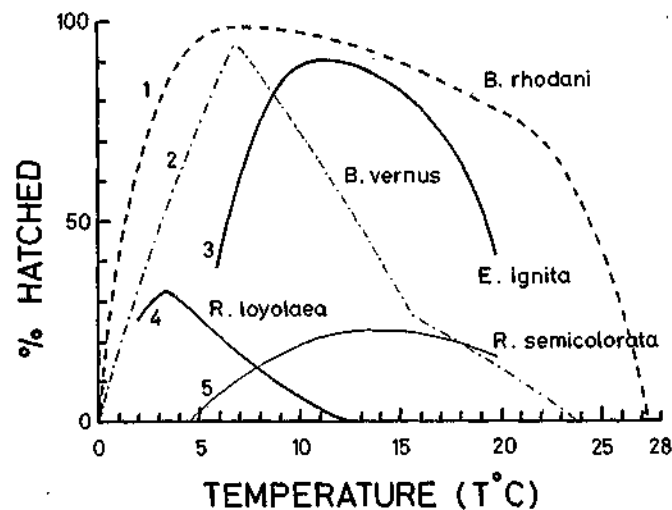


FIG. 2. Comparison of the percentages of eggs hatching at each temperature for European species of Ephemeroptera: (1) *Baëtis rhodani* (combined data; Bohle 1969; Elliott 1972; Benech 1972); (2) *B. vernus* (Bohle 1969); (3) *Ephemerella ignita* (Elliott 1978); (4) *Rhithrogena loyolaea*; (5) *R. semicolorata* (Humpesch & Elliott 1980).

TABLE 3. INFORMATION ON EGG HATCHING OF EPHEMEROPTERA OCCURRING IN BRITAIN.

Approximate temperature range over which eggs hatched, mean values for the maximum percentage of eggs that hatched, equation relating hatching time to temperature, whether or not equation has been tested in the field, and mean number (with 95% CL) of days for 50% of the eggs to hatch at 5 °C and 10 °C.

Species	T °C	Max % hatched	Equation	Tested in field	Days for 50% hatch at 5 °C	Days for 50% hatch at 10 °C	Reference
<i>Baëtis rhodani</i>	3.0-25.0	99	power-law	yes	66(64-68)	26(25-27)	1,2-4
<i>B. vernus</i>	6.8-20.0	>94	not known	yes	154(148-160)	41(40-42)	7
<i>Rhithrogena semicolorata</i>	5.9-19.9	28	power-law	yes	180(170-191)	52(50-54)	6
<i>Ecdyonurus dispar</i> (lakes)	3.9-20.3	38	power-law	yes	—	—	6
(rivers)	4.4-20.1	21	not known	no	—	—	6
<i>E. insignis</i>	8.7-19.9	13	power-law	no	138(124-154)	48(47-49)	6
<i>E. torrentis</i>	3.9-19.6	29	power-law	no	166(157-176)	39(37-41)	6
<i>E. venosus</i>	3.6-20.6	48	power-law	no	603(526-744)	45(43-47)	6
<i>Ephemerella ignita</i>	5.9-19.8	>90	hyperbola	yes	—	134(117-165)	3,5

References: 1, Benech 1972a; 2, Bohle 1969; 3, Bohle 1972; 4, Elliott 1972; 5, Elliott 1978; 6, Humpesch 1980a; 7, Humpesch & Elliott 1980.

than 50% for *R. semicolorata* and the four *Ecdyonurus* species. This low hatching success probably also occurs in the field and must be taken into account in the interpretation of life cycles and population dynamics. There is a clear relationship between hatching success and water temperature in some species (Fig. 2), but not in *Ecdyonurus* spp. The Central European species, *R. loyolaea*, is included in Fig. 2 as an example of a species with a very narrow range of temperature for hatching.

The relationship between hatching time (Y days after oviposition or fertilization) and water temperature (T °C) could not be described by an equation in four populations, two of which had a diapause in the egg stage, namely *Baëtis vernus* and one population of *Ephemera ignita* (Bohle 1969, 1972) (diapause is a period of suspended development or growth with a greatly decreased metabolism). In all other populations, the relationship has been well described by a hyperbola or power law, e.g. British species in Table 3. Both models are summarized in the general equation:

$$Y = a/(T-t)^b \quad (2)$$

where a , b and t are constants. If $t=0$, then the equation is a two-parameter power law. If $b=1$ and t is the threshold temperature at which the development rate is theoretically zero, then the equation is identical to the two parameter hyperbolic curve with the constant, a , equal to the number of degree-days above t °C required for hatching. Equation (2) has been successfully fitted to data for ten species and fifteen populations of European Ephemeroptera, including seven species occurring in Britain. A hyperbolic curve was the best model for *E. ignita* whilst a power law was more suitable for the remaining six species (Table 3). An example of the good fit of the power-law model is given in Fig. 3. The power-law equation was also fitted to data on hatching in the North American species, *Tricorythodes minutus* (Newell & Minshall 1978), but the value of b was one and therefore a hyperbolic curve would be an equally good fit. A logistic equation has been used to describe the relationship between temperature and the days required for the start of hatching in the North American species, *Hexagenia rigida* (Friesen, Flannagan & Lawrence 1979).

The usefulness of the models summarized in equation (2) increases considerably if they can be used to predict the time of hatching in the field. This has now been tested successfully for six species, including four British species (Table 3). Hatching times vary considerably between species (cf. values for 50% of eggs to hatch at 5 °C and 10 °C in Table 3). There are also intraspecific differences for some species (e.g. *Ecdyonurus picteti*, *E. venosus*) but not for others (e.g. *Baëtis rhodani*, *Ecdyonurus dispar*, *Rhithrogena semicolorata*). More general intraspecific differences in egg development have been found in populations of *E. dispar* from lakes and rivers (Humpesch 1980a), and populations of

Ephemera ignita in France, Germany and England with an obligatory diapause in the eggs of the German population (Thibault 1969; Bohle 1972; Elliott 1978). These differences may be genuine but it is also possible that the work was on different species that were not recognized because of taxonomic inadequacies.

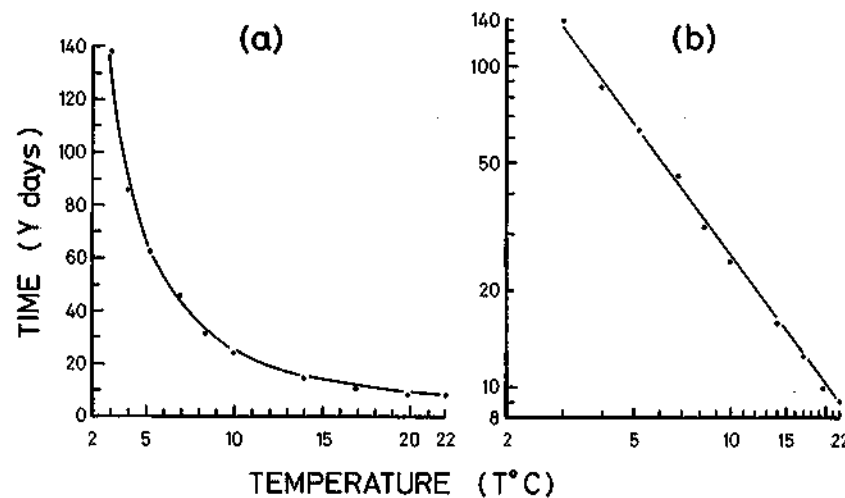


FIG. 3. Relationship between the time required (Y days) for 50% of the eggs of *B. rhodani* to hatch and temperature (T °C) in the laboratory: (a) On arithmetic scale with curvi-linear regression line; (b) On log/log scale with linear regression line.

Once the eggs start to hatch, the period over which hatching occurs may be remarkably short in some species, e.g. between 10% and 90% of eggs hatched in less than ten days in *Rhithrogena* spp., *Baëtis rhodani* (if $T > 5$ °C), and *Ecdyonurus* spp. (if $T > 10$ °C) (Elliott 1972; Humpesch 1980a; Humpesch & Elliott 1980). Tiny nymphs of these species occur over several months and this observation has often been interpreted as an indication of a long hatching period. It is now obvious that this interpretation is probably incorrect and the most likely explanation is that some nymphs grow very slowly after hatching. This is one example of the value of information on hatching times, and emphasizes its importance for the interpretation of life cycles.

Parthenogenesis

Degrange (1960) obtained unfertilized eggs from 51 European species and found that they could develop parthenogenetically in 26 species. Fourteen of the latter species occur in Britain, namely: *Caenis*

moesta, *Ephemerella ignita*, *Ecdyonurus insignis*, *E. dispar*, *Heptagenia lateralis*, *H. sulphurea*, *Leptophlebia vespertina*, *Siphonurus lacustris*, *Centroptilum luteolum*, *C. pennulatum*, *Cloëon simile*, *Baëtis niger*, *B. muticus*, *B. scambus*. Humpesch (1980b) has recently found that eggs can develop parthenogenetically in two species of *Rhithrogena* and five species of *Ecdyonurus*, including the British species *E. dispar*, *E. insignis*, *E. torrentis* and *E. venosus*. For the last two species and for the Central European species, *E. picteti*, there were sufficient data to show that the relationship between hatching time and water temperature was well described by a power law (equation (2) with $t = 0$). As males are known for all the European species, the parthenogenesis is not obligatory. Unfertilized (parthenogenetic) eggs were found to develop more slowly than fertilized ones, and fewer of them hatched (Degrange 1960; Humpesch 1980b). In some species (e.g. *Cloëon simile*) the unfertilized eggs produced only females, whilst in other species (e.g. *Centroptilum luteolum*) males were also produced but only in low numbers.

Parthenogenesis has been confirmed for thirteen North American species (see references in Mingo (1978); Bergman & Hilsenhoff (1978)) and one South American species (Froehlich 1969). As males are very rare or absent in five of these species, their parthenogenesis may be obligatory.

Conclusions

This short review has shown that, for the forty-seven species of Ephemeroptera in Britain, information is now available on the fecundity of twenty-four species, the oviposition behaviour of twenty-six species, the hatching of eggs of eight species and the potential for parthenogenetic development in fourteen species. There is clearly a need for similar information on the remaining species. This information is essential for the interpretation of life cycles, the identification of cohorts, the study of spatial pattern and movements, the construction of life tables, and the estimation of rates of growth, mortality and production.

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STUDIES OF CHEMICAL SPECIATION IN NATURALLY ANOXIC BASINS

W. DAVISON

Introduction

This article attempts to convey the flavour of some of my work at the FBA. It is concerned with chemical speciation of both metals and non-metals, the use of polarographic techniques, and applications to the study of the chemistry of anoxic waters. The first part of the paper tries to explain unfamiliar terminology and to give the reader a feeling for the subject. An example of simple lake chemistry is then presented to illustrate why the concept of speciation is necessary.

Cations and anions cannot exist in water as single entities. They are complexed, either by water molecules or inorganic/organic ligands. The aquo complex for a metal ion, M, may be represented as $M(H_2O)_z^{+y}$ where z is the charge of the molecular complex and y is the number of co-ordinated water molecules (usually six). Sometimes a convention which effectively discounts water as a complexing ligand is adopted and then the aquo complex is referred to as the free metal ion. The distribution of a metal ion among its various water-soluble complexed states is referred to as its speciation, and each molecular configuration which can exist in true solution is called a soluble species. Constants which define the strength of complexation of each particular ligand are variously called stability, equilibrium, dissociation, or association constants. They refer to an equilibrium state and are therefore thermodynamic quantities. Most natural systems are not at true equilibrium and so kinetic factors play an important role in determining species distribution at any given time. The interconversions between species may be controlled by chemical kinetics, but often the driving force which changes the equilibrium in natural systems originates from living processes. The rates themselves may also be controlled by biological factors because enzymes and 'microbes' may be operationally regarded as catalysts. An extreme case is that of nitrate and ammonia interconversion which takes place readily in a natural and microbially influenced environment. If the interconversion was solely dependent on chemical kinetics, the rates would be so slow that the two forms would be virtually stable.

In natural waters it is essential to try to define, as unambiguously as possible, the concentrations of all individual chemical species because it is at this molecular level that chemical reactions occur and living organisms take up both nutrient and toxic elements. Therefore only by a thorough understanding of chemical speciation can we hope to understand the detailed mechanisms of the chemical and biological processes.

Recognition of the above facts prompted me to embark on a study of chemical speciation with particular reference to the study of the hypolimnia of local lakes. This involved a good deal of basic work in theory and