ADAPTATIONS TO A MARINE CLIMATE ILLUSTRATED BY EPHEMEROPTERA

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The climate of the Pacific Coast of the Northwest U.S. is characterized by mild winter temperatures (Fig. 1), by heavy rainfall in autumn, winter, and spring (Fig. 2), and by warm dry summers. As a result of this combination of climatic factors, numerous ice-free aquatic habitats are established which exist 5 to 7 months of the year, but which become completely dry each summer. This paper is a discussion of the mayflies which were regularly found in these temporary habitats in the Willamette Valley, near Corvallis, Oregon.

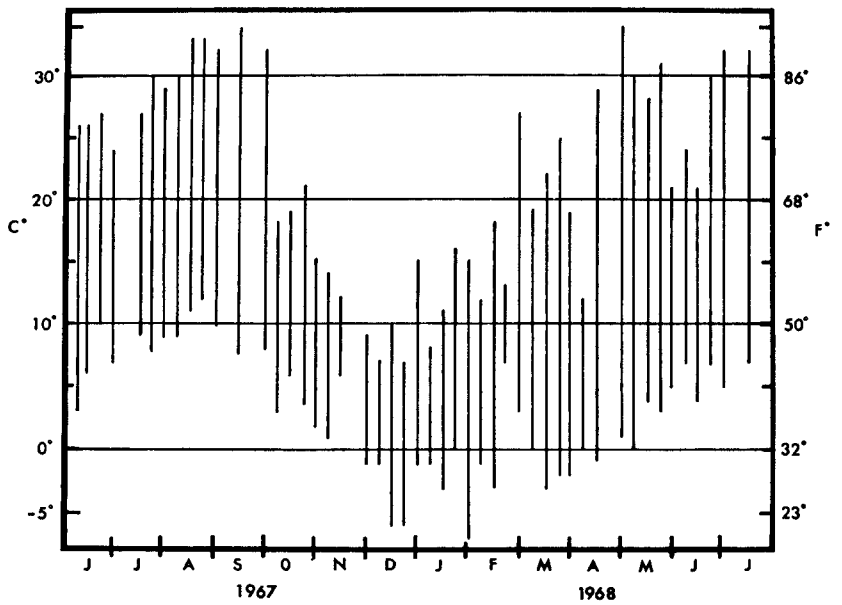

FIGURE 1. Weekly air temperature extremes near Corvallis, Oregon

Two areas were chosen for study. The first, a stream, contained water from late October to early May and was located about 10 miles north of Corvallis. The stream was located in an open grassy field (Plate Ia), was 1-3 feet wide, 3-8 inches deep, and had a slow current of clear water (Plate Ib). The stream was fed from seepage from the surrounding high ground.

The second study area, a pool, was located about 6 miles south of Corvallis and contained water roughly the same period as the stream. The pool consisted of a roadside ditch and the adjacent low ground (Plate Ic). The water was up to 2 feet deep, and the substrate varied from grasses and sedges to gravel and mud.

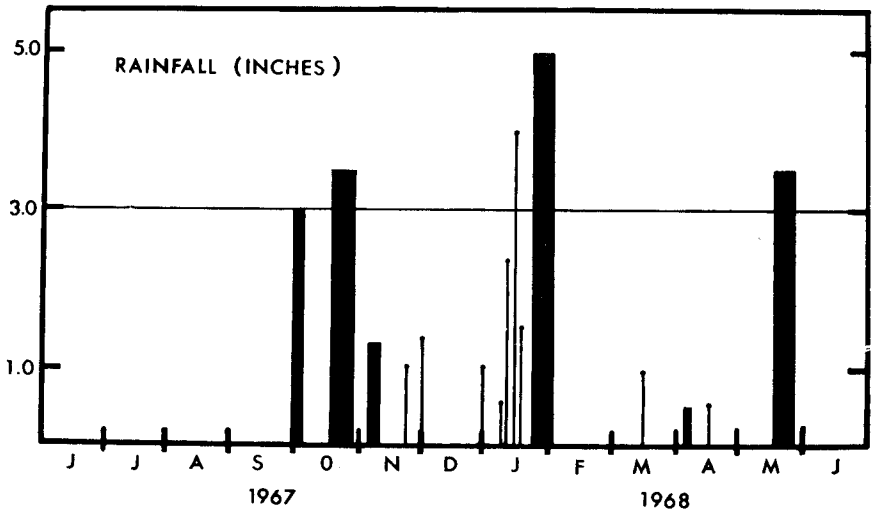

FIGURE 2. Rainfall near Corvallis, Oregon

A number of taxa of aquatic insects including Coleoptera, Trichoptera, Plecoptera, Diptera Odonata, and Megaloptera, as well as Ephemeroptera, were found in the habitats. Taxonomic keys and descriptions however were lacking in nearly all cases. Thus, the Ephemeroptera were chosen for detailed study; nymphs were reared to the adult stage to obtain specific identifications, and extensive collections were made from various habitats in the area in order to learn the local distribution of the species.

Monthly samples were taken to determine the development of the immature stages and to determine the emergence period of the adults.

THE LIFE CYCLES

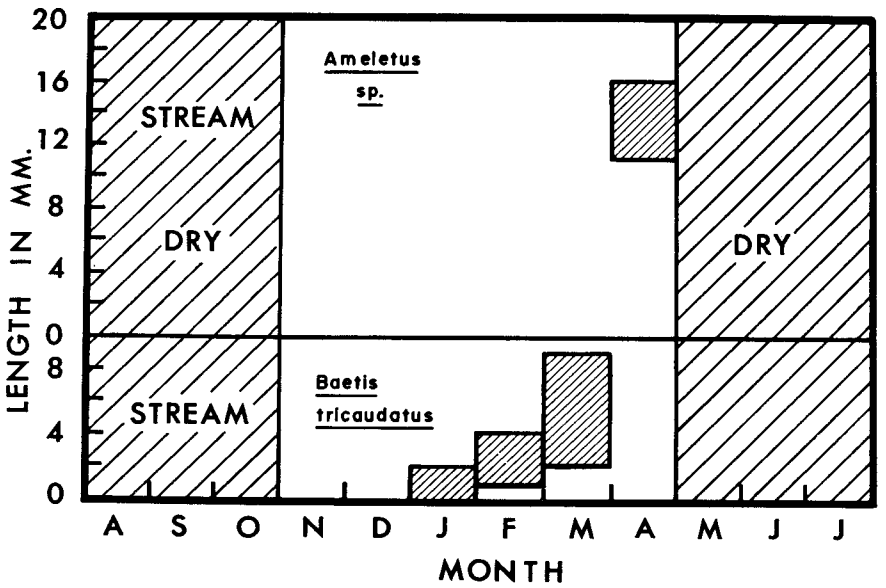

FIGURE 3. Size class distribution of two species in the temporary stream

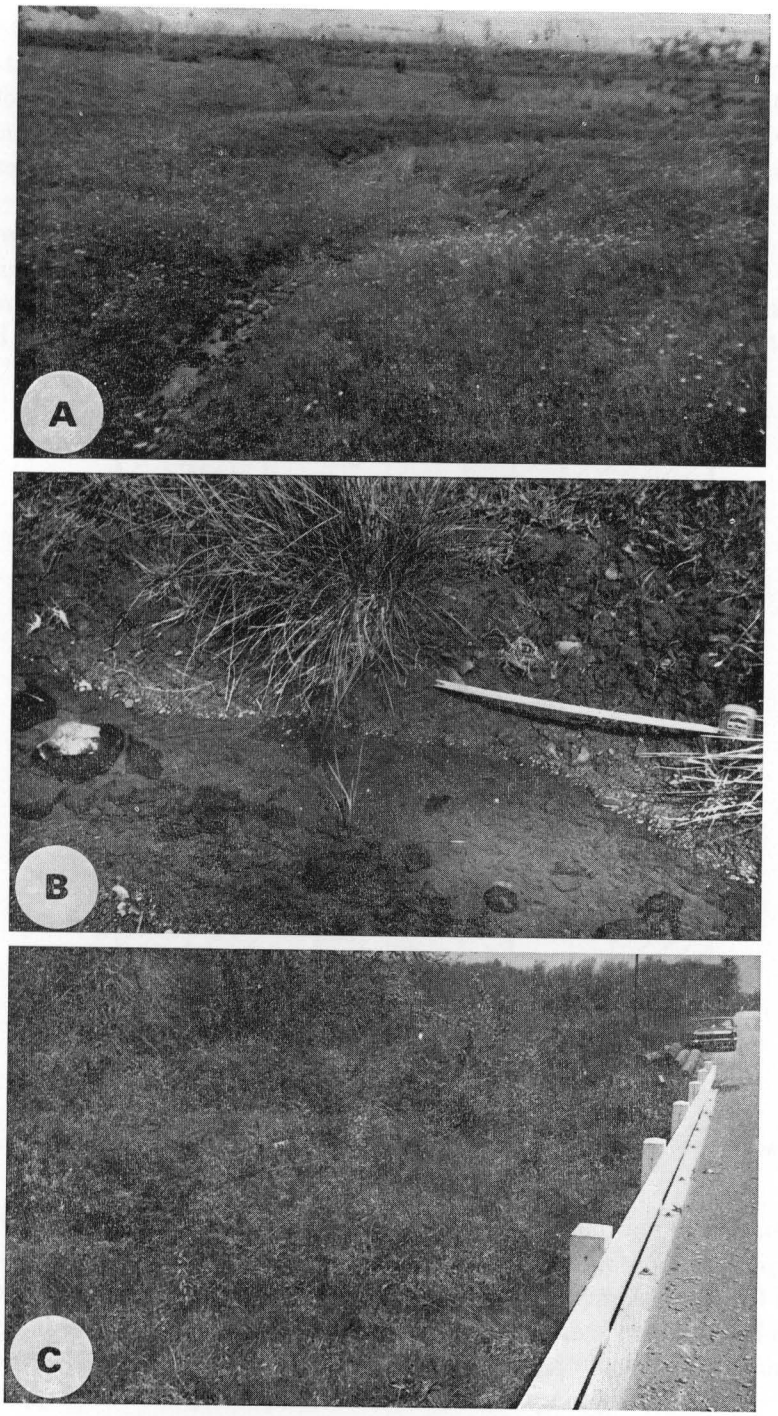

PLATE I

a, b. Temporary stream, near Corvallis, Oregon

c. Temporary pool, near Corvallis, Oregon

Two types of life cycles were found in the Ephemeroptera. The first type is illustrated by two species in the stream (Fig. 3). *Ameletus* sp. (possibly a new species) and *Baetis tricaudatus* DODDS were not found in the stream until several months after it had filled with water. Both species were found in permanent waters close to the temporary stream, and both were collected as adults during the early winter months. Eggs laid in the stream by these winter adults may account for the presence of these nymphs in the stream. Upstream migration from permanent water is a possible, but unlikely, explanation.

A contrasting type of life cycle is illustrated in Fig. 4 by two species from the pond and one from the stream. In this type, nymphs were present and well developed within a short time after the pond or stream filled with water. These nymphs must have originated from eggs

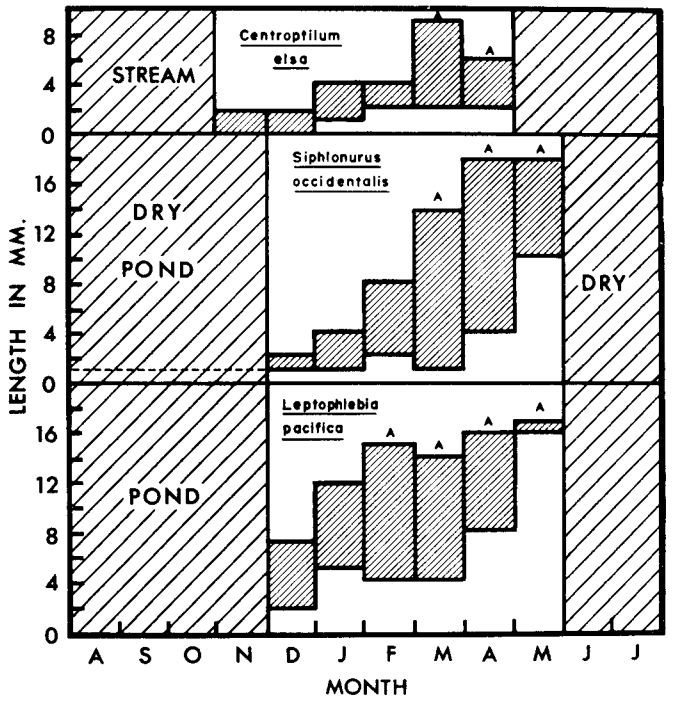

FIGURE 4. Size class distribution of two species in the pool and one species in the stream

which survived the dry period and this is supported by the following facts. Adults of these species have been found only in late winter or spring, and therefore adults originating from other habitats could not have laid the eggs which produced the nymphs collected in December. Secondly, the pond is not connected with permanent water so that migration of nymphs from other areas is not possible. Thus, two types of residents, one of which is opportunistic and the other of which appears well adjusted, are seen in these temporary habitats.

Temporary aquatic habitats are a dependable annual occurrence in the Pacific Coastal region of the Northwestern U.S. These habitats are ideal because water temperatures remain warm enough so that ice forms only rarely, most vertebrate predators such as fish are absent, and food is extremely abundant in the form of decaying vegetation and rich algal growths. This situation is in contrast to inland areas where snow and ice make winter an unfavorable

time for aquatic life. The main problem in temporary ponds is for the aquatic organism to overcome the dry period.

I suggest that a well adapted and characteristic insect fauna has become adjusted to temporary habitats in western Oregon. But the question of how they were able to adjust, a question of fundamental importance, remains unanswered. For example, adults of *Leptophlebia pacifica* (McDUNNOUGH) emerge in the spring, and eggs must be laid at this time. The eggs do not hatch immediately in the field, but rather hatch about six months later after passing through a dry period. This field observation is in contrast to a laboratory observation in which fertilized eggs of *L. pacifica* hatched about one week after being laid. This indicates some flexibility in the behavior of the eggs.

It appears that the question of interest is this : are species such as *L. pacifica* bound by a fixed life cycle to restricted habitats and climatic situations, or does the life cycle of the species, in any given case, simply illustrate a narrow segment of a wide potential range of adjustment inherent in the life cycle ? While it is probable that each species is unique in this respect, we have very little information of this type for the Ephemeroptera. These questions are of interest because, considering the rapid modification of the environment, it is flexibility, or the lack of it, which will determine how long these species will survive.

RÉSUMÉ

L'adaptation au climat maritime illustré par Ephemeroptera

Le climat maritime de la côte pacifique du nord-ouest des États-Unis est caractérisé par des hivers doux, de fortes chutes de pluie de l'automne au printemps et par des étés chauds et secs. Il résulte de cette combinaison de facteurs climatiques de nombreux habitats aquatiques ne connaissant pas le gel et qui subsistent seulement 5 à 7 mois par an avant d'être complètement désséchés chaque été. On trouvera dans cet article une discussion des cycles vitaux des Éphéméroptères trouvés régulièrement dans un cours d'eau et une mare temporaire de la vallée Willamette, Oregon. Le premier type de cycle vital est illustré par deux espèces de rivière, *Ameletus sp.* et *Baetis tricaudatus*. Les espèces ne sont rencontrées dans les cours d'eau que plusieurs mois après que leur assèchement ait pris fin. La présence de ces larves dans des rivières temporaires s'explique par le fait que leurs œufs sont déposés par les adultes vivant dans les rivières du voisinage. Le second type de cycle vital est illustré par *Siphlonurus occidentalis* et *Leptophlebia pacifica* en ce qui concerne la mare, et par *Centroptilum elsa* pour la rivière. Les larves sont présentes et se développent peu de temps (en 2 semaines) après le remplissage de la mare ou de la rivière. Ces larves proviennent probablement d'œufs ou de larves dormantes ayant survécu au cours de la période sèche.

ZUSAMMENFASSUNG

Anpassung an ein Meeresklima illustriert durch Ephemeroptera

Das Meeresklima an der pazifischen Küste der nordwestlichen Vereinigten Staaten ist durch milde Wintertemperaturen, hohe Regenfälle vom Herbst bis Frühling, und durch warme trockene Sommer charakterisiert. Das Resultat dieser Vereinigung von klimatischen

Faktoren sind viele eisfreie Wasserhabitate, welche nur 5-7 Monate pro Jahr existieren und jeden Sommer komplett austrocknen. Dieser Artikel ist eine Diskussion der Lebensläufe von Eintagsfliegen, welche regelmässig in einem zeitweiligen Fluss oder vorübergehenden Weiher im Willamette Tal in Oregon, gefunden werden. Der erste Musterlebenslauf ist von den zwei Stromarten *Ameletus* sp. und *Baetius tricaudatus* illustriert. Diese Arten wurden erst nach einigen Monaten, nachdem er sich mit Wasser füllte, im Strom gefunden. Eier die von Erwachsenen von nahen Dauerströmen abgelegt wurden, mögen diese Nymphen in den zeitweiligen Strömen erklären. Der zweite Musterlebenslauf ist durch *Siphlonurus occidentalis* und *Leptophlebia pacifica* vom Weiher, und *Centroptilum elsa* vom Strom illustriert. Nymphen waren anwesend und gut entwickelt in kurzer Zeit (innerhalb zwei Wochen) nachdem der Weiher oder Strom sich mit Wasser füllte. Diese Nymphen müssen von Eiern oder dormanten Nymphen, die die Trockenperiode überlebten, entsprungen sein.

Discussion

J. Leonard : Do the nymphal stages of *Siphlonurus occidentalis* or *Leptophlebia pacifica* seem to take any longer to reach maturity in permanent waters than they do in these temporary situations ?

D. Lehmkuhl : I have not been able to compare that.

J. Leonard : In other words, you sense that there is a sort of accelerated rate of development of the nymphs in these temporary situations ?

D. Lehmkuhl : I have no information on that now and I really don't want to speculate. *Leptophlebia pacifica* is restricted in range to the Willamette Valley, probably within a radius of 25 miles from Corvallis. I don't know how much the species might be restricted to these habitats within that range.

J. Leonard : Did you, despite the absence of adequate keys for some of the other taxa, attempt to follow the development of some of the other groups, particularly Plecoptera.

D. Lehmkuhl : I did for the stoneflies. Again, I am sure they will have to survive the dry period in the egg stage.

J. Leonard : You don't think that there is any possibility that the eggs might have hatched and early instar nymphs have burrowed to considerable depths in the substrate ?

D. Lehmkuhl : Possibly, although the nature of the soil there would make that very difficult. It is very fine and would become brick-like.

C. Fremling : Have you subjected the eggs to desiccation in this experiment ?

D. Lehmkuhl : This work is based on field data only and I did not have time to do any laboratory work. It would be interesting to study this further.

G. Edmunds : In Utah there are quite a few irrigation ditches or canals which are dry during the period when the fields are unwatered. During that time the canals are completely dried up and there is no water turned into them for distances of 35 to 40 miles. These canals have populations of *Tricorythodes*, *Paraleptophlebia*, *Heptagenia*, *Ephoron*, and *Siphlonurus*. All the eggs of these species overwinter dry. If you go into the laboratory and dry the eggs, they will not hatch. The reason for this is that you are drying them too fast. What you must do is take them into the laboratory and dry them on damp mud substrate so that they gradually dry down, and then they do hatch. For example, in *Ephoron* the eggs completely develop and then, within 10 days of hatching, they go into diapause. To break diapause they

require cooler temperatures. I think this is what is happening in *Leptophlebia pacifica*. The genus *Parameletus* completes it life cycle from egg to adult in 15 to 17 days and spends the rest of its life cycle in the egg.

W. PETERS : I was once very disappointed in relation to egg diapause. I had spent considerable time and money getting to Cerro de Pasco, Peru. At Cerro de Pasco are many species of mayflies named by Dr. NEEDHAM and Dr. MURPHY some years ago. I thought that I might be able to rear some of these species. I reached Cerro de Pasco, looked around me and found no water at all. I was later told that the streams only have water in them for two months each year. So there must be a tremendous mayfly fauna that occurs in these very temporary streams at high elevations in the Andes. Unfortunately I was unable to collect anything at that time because there was no water in any of the streams.