ENVIRONMENTAL FACTORS AFFECTING DISTRIBUTION OF MAYFLY NYMPHS IN DOUGLAS LAKE, MICHIGAN

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Introduction

Most information of an ecological nature dealing with mayflies of lakes is scattered among numerous publications on bottom fauna studies (Muttkowski 1918; Baker 1918; Adamstone 1924; Rawson 1930; Neave 1932, 1934; Berg 1938). In such studies the mayflies are usually treated as an order or as genera and but rarely are specific identifications or specific information given. Also, brief notes on mayfly nymphal distribution which have been made by collectors from incidental observations are often included in taxonomic accounts. A wealth of ecological data is contained in Berner's (1950) publication on Florida mayflies. Ide (1935) has demonstrated clearly the effect of temperature on the logitudinal distribution of mayflies in a stream. Linduska (1942) has shown that the type of bottom in streams is an important factor influencing the local distribution of mayfly nymphs. Up to the present time no intensive ecological study of the mayfly fauna of any one North American lake as a whole has been undertaken. Relatively little is known concerning the environmental factors governing the distribution of immature stages of mayflies within lakes. The present study was made in an effort to ascertain the distribution pattern of all species of mayfly nymphs in Douglas Lake, Cheboygan County, Michigan, and to discover the environmental factors influencing this distribution. The work was conducted during four summers, 1936-1939, supplemented by late-spring and early-fall observations. A description of methods used in this work has been discussed previously (Lyman 1955).

Description of Habitats

Since other authors (Scott 1921; Welch 1928; Eggleton 1931; Moffett 1943) have adequately described limnological characteristics for Douglas Lake, it is unnecessary to repeat a general description of this lake; therefore, only significant habitat details applicable to this study are given.

The littoral region of Douglas Lake (Fig. 1) is primarily sand intermixed with varying amounts of marl depending upon the degree of protection of the particular situation. Prevailing winds blow from a northwesterly direction along the four-mile major axis of the lake. In protected situations such as Maple and Marl bays, marl is more conspicuous while in larger, exposed bays such as North and South Fishtail, the bays between promontories, such as between Robert's and Stony points, or in Nutting's Bay, sand is distinctly predominant and marl is almost absent, especially in the shallower water near the shore. In these bays *Scirpus americanus* occurs close to shore and *S. occidentalis* in the deeper water. West of Fairy Island is a shallow area covered by *Phragmites communis.* Heavy stands of emergent aquatic plants are conspicuously absent from a large proportion of the littoral zone.

In relatively small especially protected situations occurring only in Maple Bay, Marl Bay, Sedge Point, and Hook Point, a fine, organic detritus is present near shore and ecological conditions typical of ponds are approached. Such habitats are of very limited extent in Douglas Lake. The cove of Hook Point and the Sedge Point pools will serve as descriptive examples of this habitat type.

Hook Point cove is well-protected and free from strong wave action. Immediately behind the point is a shallow, organic detritus bottom which grades gradually into a flocculent marl deposit northward along the west shore. Beneath this flocculent marl is fine sand lying upon a coarser sand and pebbles. Few stones occur in this habitat. Farther north along the west shore the marl bottom is replaced abruptly by almost pure sand. Distinctive of the Hook Point habitat is the large quantity of water-soaked logs and sticks deposited there by currents. Such a collection of wood fragments in shallow water is found in no other place in the lake. Higher aquatic plants are relatively scarce in this situation. Among those present are *Nymphaea advena,* just behind the point, and a few scattered plants of *Scirpus americans, S. occidentalis, Potamogeton compressus,* and *Myriophyllum heterophyllum* on the marl bottom.

On Sedge Point are located three beach pools; two of these are closed to the lake but one is still connected to it by a narrow neck of water. The bottoms are covered with organic detritus and plant fragments. The two younger pools do not dry up although the water in the second becomes very shallow by the end of August.

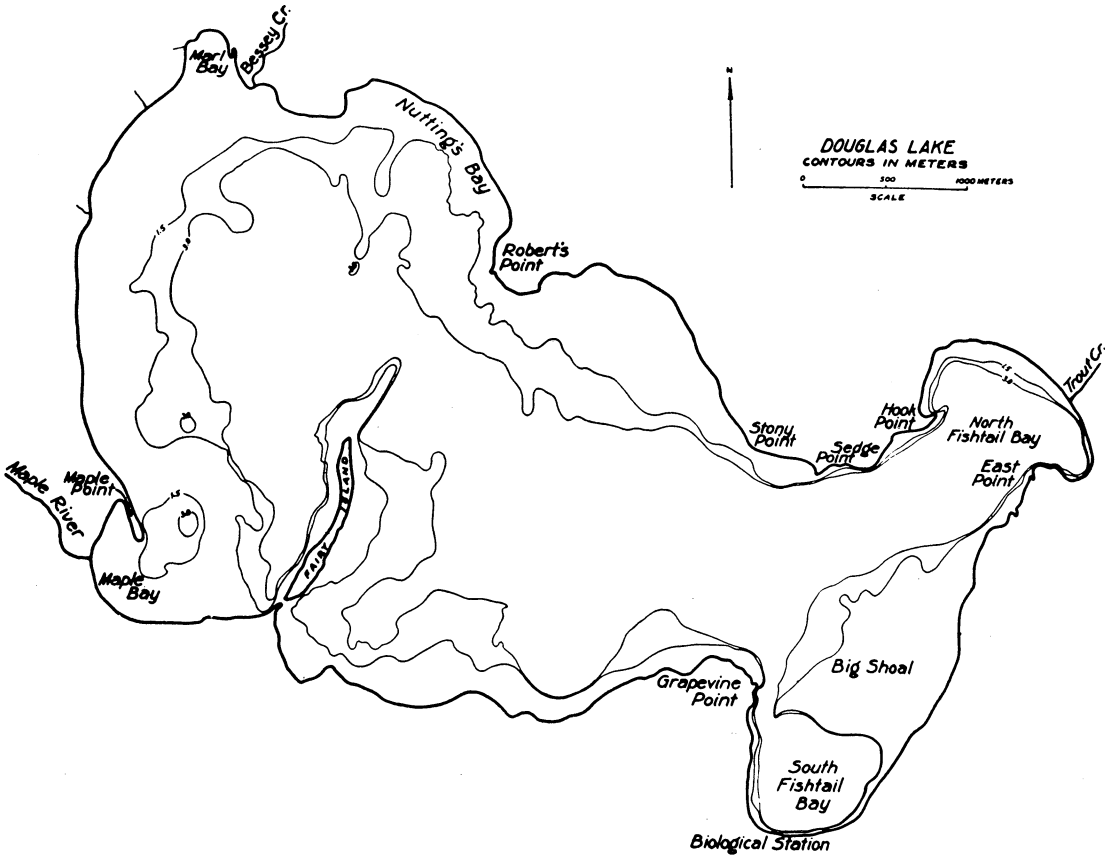

FIG. 1. Map of Douglas Lake, Cheboygan County, Michigan. Contours at 1.5 and 3.0 meters.

The promontories or headlands such as the northeast end of Fairy Island, Grapevine Point, Stony Point, and Robert's Point are gravelly to rocky. For the most part the stones are located in a narrow strip close to shore and do not extend lakeward to the edge of the submerged shelf. These points are all exposed to the sweep of the wind and are subject to strong wave action. On the other hand, those projections such as Maple Point, Hook Point, and East Point, not exposed to strong wave action, are distinctly sandy with few if any stones.

Grapevine Point is exposed to the full force of the prevailing winds and offers a good example of this habitat type. A submerged shelf about 150 meters wide slopes very gradually to a depth of 1.5 meters and then drops off rapidly into deep water. A stony strip about 30 meters wide occurs along the shore while the remainder of the shelf lakeward is loose sand. Near shore the sand is compacted by marl to a depth of 0.5-1.5 centimeters, thus forming a semi-hard crust over the bottom. East of the point proper there are no exposed rocks. Opposite the middle and around the west side of the point are found the larger stones which vary in size from small pebbles to large rocks 15-25 centimeters in diameter. Most of the stones are flatly rounded to oval. Close to the shore line the rocks are clean while those in 0.6-1.0 meter of water are covered on their upper surfaces by a thick coat of encrusting organisms and marl. Some of the rocks are partly embedded but many rest loosely on the substratum. The rocks are scattered more or less uniformly on the bottom and do not closely contact one another over most of the area. In the Robert's Point, Stony Point, and northwest Fairy Island areas the stones are of more uniform size, more numerous, and in close contact with one another, otherwise, these areas are similar to the Grapevine Point habitat.

Factors Influencing Benthic Distribution

Most species of mayfly nymphs in Douglas Lake occupy more or less definite habitats because of the influence of environmental factors which operate in varying degrees within different ecological niches occurring in this lake. In one situation is found a comparatively large number of species while in another, only one species occurs, and in some habitats none may be found. In some cases a single factor can be designated as being the one most influential in causing a particular species to select a definite kind of habitat but in other instances it seems rather to be a number of environmental factors operating simultaneously which lead the nymphs to choose one set of conditions to the exclusion of others. No species is ubiquitous over the entire littoral zone but some approach this condition more than others. The following discussion deals with those environmental factors which cause the various species of mayfly nymphs of Douglas Lake to select a particular set of environmental influences.

Physical character of the bottom

Rocks.—The physical character of the bottom is a factor of no small importance governing the distribution of mayfly nymphs. Its significance in streams has been emphasized by Linduska (1942). In those situations characterized by gravelly and rocky bottoms are found one-third of all the species of mayfly nymphs occurring in the lake. Some of these species, viz., *Stenonema interpunctatum, Heptagenia lucidipennis, Ephemerella bicolor, Baetis phoebus,* and *Cloeon rubropictum,* are found only on rocky bottoms; while others, *Stenonema femoratum, Ephemerella temporalis,* and *Ephemerella lutulenta,* although characteristic of stony bottoms, do occur to some extent in other situations.

All of these species possess a strong, positive thigmotactic response which causes them to seek a hold on rocks as a stable, physical support. Both Wodsedalek (1912) and Berner (1950) have commented on this thigmotactic response in *Stenonema* nymphs. When nymphs of *S. femoratum, S. interpunctatum, Ephemerella temporalis, E. lutulenta,* or *E. bicolor* are placed in a vessel of water without a rock, they tend to form clumps by clinging to one another. However, as soon as a rock is placed in the water, they immediately release their hold on one another and swim to it. The tenacity with which they cling is well-illustrated by the fact that if an attempt is made to detach them from the rock, they will often allow a leg to be torn from the body before releasing their hold. These nymphs have very little swimming ability but they are agile runners which is another reason for their association with rocks. *Stenonema femoratum* and *S. interpunctatum* nymphs seem to prefer to live ventral side uppermost which can readily be accomplished on a rocky bottom (Lyman 1945).

The reactions of *Cloeon rubropictum* and *Baetis phoebus* to rocks are illustrated by placing these nymphs in a dish of water without a rock. They make no attempt to gather in clumps but show a decided restlessness by swimming with rapid spurts here and there and finally become distributed around the periphery of the container. When a stone is introduced into the center of the dish, it barely comes to rest before the nymphs begin swimming toward it from all sides. Even when a rock is held over the dish just out of the water, the nymphs will follow it as it is moved from one end of the dish to the other. These two species are strong and rapid swimmers for short distances. However, they lack the ability to keep up sustained swimming movements for any considerable length of time. Rocks, therefore, offer these nymphs a solid support upon which they can move rapidly without the necessity of sustained swimming efforts. The tenaciousness of all these clinging nymphs is well-shown by the fact that they rarely release their hold when a rock is lifted off the substratum, or even entirely out of the water.

The relative proximity of rocks to one another seems to determine to some degree the distribution of *Heptagenia lucidipennis.* These nymphs are found on Fairy Island, Stony Point, and Robert's Point where rocks occur closer together than on Grapevine Point. This same type of distribution was also found in nearby Burt Lake where similar habitats occur. Indications are that *Stenonema interpunctatum* is also influenced to a lesser degree by the proximity of rocks since these nymphs are found only in distinctly rocky habitats and, unlike *S. femoratum,* they are not found under isolated stones scattered over predominantly sandy areas.

The degree of burial of the rocks in the substratum is important since practically all nymphs which live on rocks choose the under side and do not occur on those that have the lower surface wholly embedded in the bottom.

In the case of *S. interpunctatum* the water depth to which rocks occur is apparently significant for they are more generally found on those rocks in deeper water. In the Stony Point situation where rocks occur only near the shore line very few of these nymphs were ever found yet *S. femoratum* was very common.

The specific gravity of rocks as contrasted to that of wood tends to aid in maintaining the position of rocks on the bottom in the face of strong wave action. Wood, because of its comparatively light weight, is readily eliminated as a possible shelter or stable support for nymphs along a wave-swept shore since it is easily transported by wave action and is usually deposited above the waterline. In a marly or an organic-detritus habitat, rocks are eliminated because they tend to settle and eventually become buried in the deposit.

Sand.—Along the open, sandy beaches practically no mayflies are found in shallow water (0.0-1.5 meters). Sand bottoms are distinctly rejected by mayfly nymphs in preference to other kinds when such nymphs have the opportunity of selecting various bottoms. In the case of clinging forms, sand offers them no means of solid, physical support as it is almost impossible for these nymphs to secure a strong hold on loose sand grains which are readily displaced by the curved claws with each attempt to move. Burrowing forms, such as *Hexagenia limbata,* and probably *Ephemera simulans,* find that a sandy substratum offers too much physical resistance to burrowing for it is is easily demonstrated that clean sand grains tend to settle back into any depression as it is dug by the nymphs (Lyman 1943).

Marl.—The extensive marl-bottom regions of Maple and Marl Bays support few, if any, species of mayfly nymphs. Such a bottom offers no more attraction to clinging forms than does a sand bottom for reasons already stated. Very few burrowing mayflies were found in this type of bottom even though they do have the ability to burrow into it.

Mud.—Mud bottoms are restricted to the sublittoral and profundal regions of Douglas Lake. The only mayflies that inhabit the sublittoral muds are *Hexagenia limbata* and *Hexagenia affiliata.* Mud offers these nymphs a distinctly favorable burrowing medium for which they are adapted both morphologically and physiologically (Lyman 1943; Hunt 1953).

Organic Detritus.—In habitats where organic detritus prevails *Caenis simulans* nymphs are abundant and in some places *Brachycercus lacustris, Ephemerella temporalis, E. lutulenta,* and *Leptophlebia nebulosa* occur in lesser numbers along with them.

On detritus bottoms the sprawling and slow-moving nymphs of *C. simulans* escape detection by partially settling into the surface of the detritus and become almost invisible due to detritus particles which collect on the setae of the body. They are particularly adapted for a detritus environment since the second gill is modified to form a gill-cover which is used for protection and to maintain the gills free of detritus particles (Eastham 1936). Detritus bottoms are rich in microorganisms and organic material which furnishes abundant food for the nymphs. That a detritus substratum rich in organic matter is selected by the nymphs in preference to a more distinctly marl bottom is indicated by the Hook Point, Marl Bay, and Maple Bay situations where marl and detritus bottoms occur side by side, each being more or less distinct from the other. On the detritus bottom are found numerous *C. simulans* nymphs but on the marly bottom a short distance away comparatively few of these nymphs occur.

While *C. simulans* and *E. temporalis* possess the ability to cling to objects, as is evidenced by their association with rocks or the stems of submerged plants, they seem to be limited to those situations where organic debris is prevalent as a constituent of the substratum. Their presence in plant beds is probably due to the organic detritus which collects in these areas.

Wave action

Wave action is one of the principal environmental factors affecting either directly or indirectly the distribution of mayfly nymphs in Douglas Lake. The majority of lake species are inhabitants of the shallow littoral regions. Therefore, they must either seek those situations in which wave action is much reduced or find some means of protecting themselves while living under the rigorous conditions produced by wave action.

Along open sandy beaches, severe wave action results in the sand being shifted from one place to another thus producing molar action and a very dynamic environment with which mayfly nymphs are unable to cope. It is readily conceivable that molar action plays a major part in destroying mayfly eggs which may be deposited on the loose sand of these areas by grinding them to pieces or burying them in such a way as to make it impossible for those nymphs which hatch and have no burrowing ability to reach the surface of the sand.

Mayflies characteristic of lakes do not live in a wave-swept, sandy situation because they are carried by water movements from one place to another, since the sandy substratum offers no means of stable, physical support to which they can cling nor can they maintain their position by swimming. That nymphs are readily carried about by water movements appears to be indicated by the fact that in the spring and autumn some *Caenis simulans* nymphs occur on rocks near the shore line as a result of being carried shoreward from the deeper waters owing to increased wave action during those seasons of the year. Ordinarily nymphs of this species live in ponded situations or at depths below effective wave action.

Experiments were conducted to demonstrate whether mayfly nymphs could live if rocks were provided in an area of sandy bottom subject to very strong wave action but ordinarily containing no rocks. A section of Big Shoal was selected where no rocks were present and from which mayfly nymphs were absent. On May 30 clean rocks collected from land were placed in two piles in about one meter of water on the selected area. No nymphs were found under these rocks on either June 23 or on July 4; however, on August 4 nymphs of *Stenonema femoratum* were found with all sizes present from recently hatched to fully mature. The very small nymphs were most numerous and had probably come from eggs deposited earlier in the summer. On the other hand the mature nymphs had probably been carried in by wave action from another part of the lake and had sought shelter under the only available objects. No other species of nymphs were found on or under the rocks. By August 4 a number of the rocks had already become partially covered by shifting sand and by the following summer the rock piles were almost completely buried and no nymphs could be found. Thus, *S. femoratum* could exist on Big Shoal so long as the rocks were available but disappeared as the rocks became covered by the shifting sands. These nymphs also occurred on isolated rocks in other wave-swept portions of the lake.

The distribution of *Caenis simulans* nymphs at depths of about 1-3 meters around most of the lake seems to be a direct result of the influence of wave action, for in situations where wave action is reduced they occur in shallower water. Under conditions of vigorous wave action in the open portions of the lake *C. simulans* could not exist because of molar action, lack of organic detritus, and water movements. It seems that *C. simulans* has selected a depth below the effective wave-action level (Moffett 1943) and where a fine detritus deposit is also found.

In a habitat such as Hook Point, reduced wave action appears to be one of the principal reasons why *Choroterpes basalis* is common there and absent from a situation like Grapevine Point. This conclusion is also substantiated by observations on other lakes where *C. basalis* is found only in places similar to that prevailing at Hook Point.

In wave-swept areas such as Grapevine Point or Fairy Island, rocks form a stable environment by offering the clinging type of mayfly nymph a means of protecting itself from the force of the waves. Rocks resting on the substratum produce recesses into which the nymphs can retire where molar action and water movements are reduced to a marked degree.

Light

Light is an important environmental factor that plays a major role in influencing the distribution of mayfly nymphs. Both species of *Stenonema* are definitely limited in their distribution to those habitats where rocks are present because they react negatively to light, seeking the under side of rocks during the day and moving to the upper surface only at night (Lyman 1945). *Heptagenia lucidipennis, Leptophlebia nebulosa, Choroterpes basalis, Ephemerella temporalis, E. lutulenta, E. bicolor,* and *Caenis simulans* also appear to be negatively phototactic, since in the natural environment they all select situations where the light intensity is much reduced. It seems that the factor of light alone is sufficient to eliminate these mayflies from open, sandy, or marly areas since these situations offer non-burrowing forms no means of protection from light. *Choroterpes basalis,* for example, seems to show a distinct preference for marl bottoms but does not occur in Marl or Maple Bays. One of the reasons for this fact appears to be the influence of light. At Hook Point and similar habitats in other lakes, *C. basalis* is found only on marly bottoms where wood fragments are present. The under side of wood offers these nymphs a refuge from light during the day. In Marl and Maple Bays practically no wood fragments are found.

Other factors

Emergent plants furnish mayflies, such as *Ephemerella temporalis* and *Caenis simulans,* physical support, shelter and, indirectly, food. In some places these plants aid in reducing the force of wave action and allow finely divided debris to collect on the bottom. *Siphloplecton basale* nymphs were often found in beds of *Scirpus* near the shore where they appeared to congregate for temporary shelter during their shoreward migration just prior to emergence. No species of mayfly nymphs were discovered which were wholly limited to emergent plant zones and those found there appeared to be transients.

The part played by submerged plants as a habitat for mayfly nymphs is probably an important one although little is known concerning it. Krecker (1939) pointed out that in Lake Erie *Myriophyllum spicatum* has the largest population of mayfly nymphs. Since certain species of nymphs were found nowhere else in the lake, it is concluded that they (*Siphloplecton basale, Tricorythodes allectus, Centroptilum fragile,* and *Pseudocloeon dubium*) are undoubtedly limited to the submerged plant zone.

Water level changes markedly affect the distribution of certain species of mayfly nymphs. In the early spring the high water results in the formation of many shore pools into which *Leptophlebia nebulosa, Siphlonurus rapidus,* and in some instances *Ephemerella temporalis* and *E. lutulenta* migrate. As the water level drops during the summer months, many rocks become exposed to the air and are thus eliminated as habitats for those mayflies which normally depend upon them. *Stenonema interpunctatum* which tends to select rocks in deeper water and not those near the shore line probably does not occur at Stony Point for the reason that the drop in water level exposes most of the rocky area leaving but few rocks under water near the shore line.

According to Ide (1935) water temperature is an important factor influencing distribution of mayfly nymphs in a stream. On the contrary, it appears to have but small effect upon the distribution of these insects in a lake since there is a tendency toward temperature uniformity at any given time over the entire littoral region. The only instance in which temperature seemed to be a factor is in the early spring when *Leptophlebia nebulosa* and *Siphlonurus rapidus* migrate into the very shallow water of shore pools. This migration may be a temperature response since the shallow, quiet water of these pools warms faster than does the water of the lake. Neave (1930) has pointed out that in the case of *Blasturus cupidus* (= *Leptophlebia cupida*) the spring "migration is due to an internal instinct." He also stated that the amount and kind of food probably causes the nymphs to seek a new habitat in the spring.

Dissolved oxygen, like temperature, tends toward uniformity at any given time over the entire littoral area and appears to have little if any effect upon distribution of mayfly nymphs. However, in the case of *Hexagenia* nymphs it seems to limit their distribution in Douglas Lake to a maximum depth of about 15 meters. Physicochemical studies on this lake (Welch 1928; Welch and Eggleton 1932, 1935) have shown that beyond this level the amount of dissolved oxygen drops off rapidly. In a recent paper Britt (1955) has shown that *Hexagenia* nymphs in Lake Erie could not survive conditions of low oxygen (0.7 p.p.m.).

Discussion

The mayfly nymphs in Douglas Lake form a definite distribution pattern because of the influence of certain environmental factors that operate simultaneously in each of the more or less distinct habitats. The importance of the interaction of environmental factors should not be overlooked since often the consideration of a single factor alone is not a sufficient criterion to determine the presence or absence of nymphs within a given environment. *Choroterpes basalis,* for example, is restricted to a relatively small area in the vicinity of Hook Point. The principal environmental influences which have led these nymphs to select such a habitat in preference to all others appear to be: (1) a predominantly marl bottom, (2) absence of strong wave action, and (3) presence of wood fragments which afford shelter from light. Grapevine Point offers rocks which afford a shelter from light and which are covered with encrusting organisms and marl that the nymphs eat very readily, yet the presence of strong wave action seems enough to preclude *C. basalis* nymphs from this situation. Marl and Maple Bays have distinct marl bottoms and there is little wave action, but the almost total absence of wood fragments seems sufficient reason for the absence of the nymphs from those areas. In Florida, Berner (1950) found *Choroterpes hubbelli* definitely associated with wood and leaves.

The exclusion of all species of mayfly nymphs from the extensive, shallow, sandy shoal areas (less than one meter depth) of Douglas Lake is due to several factors, and almost any one of them appears to be adequate reason for their absence. This environment presents no means by which non-burrowing forms can obtain shelter from light, wave action, and molar action. Burrowing nymphs find that sand is too difficult a medium for digging. Clinging forms cannot maintain their position on the easily shifted sand grains which afford them no firm physical support. Berner (1950) found mayfly nymphs on sandy lake shoals only when other physical supports such as wood or rocks were present.

Below the level of effective wave action (1-2 meters) on more or less open bottoms adjacent to the shallow, sandy shoal environment is a region where *Caenis simulans* and *Brachycercus lacustris* nymphs occur. While the substratum here is essentially sandy, there are also present varying amounts of organic detritus and flocculent marl that provide these sprawling nymphs with a favorable medium in which to live. The clinging response, while present does not appear to be nearly so strong in these nymphs as in such forms as *Stenonema femoratum, S. interpunctatum, Heptagenia lucidipennis,* and others. This reaction alone accounts for the absence of the latter nymphs. *Caenis simulans* and *Brachycercus lacustris* are both adapted with a modified gill for keeping the gills free from the debris. *Ephemerella* nymphs also have modified gills which probably serve the same function; however, these nymphs are found but rarely in the situation under discussion. The thigmotactic response seems to play its part as a factor in the distribution pattern as displayed by the *Ephemerella* nymphs in rocky situations but *E. temporalis* and *E. lutulenta* were also found in such places as Hook Point and one of the pools on Sedge Point where organic detritus is prominent. In these latter places, however, the nymphs were usually found clinging to such objects as wood fragments or old decaying plant stems and occurred infrequently sprawled in the finely divided detritus on the bottom. Even though these nymphs, like those of *Caenis simulans,* are morphologically adapted for living on an organic detritus bottom, the relative strength of their clinging propensities seems to afford two of them (*E. temporalis* and *E. lutulenta*) a wider range of adaptability but limits the third (*E. bicolor*).

The suitability of the rocky habitats for mayfly nymphs in Douglas Lake is well proven by the relatively large number of species that occur in those situations. The Heptageniinae species of Douglas Lake are particularly adapted to this environment and form the bulk of the mayfly population. They are flattened dorso-ventrally, have a strong, positive, thigmotactic response, possess the ability to move with rapidity over the surface of rocks, are negative to light, and prefer to live ventral side uppermost. The requirements of all these adaptations are met by a rocky habitat. Probably the most important single environmental factor which limits these nymphs to rocks is their strong, negative reaction to light. Wave action appears to be more of an indirect influence since all of these nymphs can live in standing water. *Stenonema femoratum* often occurs in many of the quiet water situations around the lake wherever shelter is available. *Heptagenia lucidipennis* and *Stenonema interpunctatum* are more limited in their distribution than *S. femoratum* since they seem to require situations where the rocks are relatively close to one another. In this respect *H. lucidipennis* reacts more strongly than does *S. interpunctatum* since the former is limited to rocky areas as provided by Fairy Island, Stony Point, and Robert's Point. In contrast to the sandy shoal environments the rocky areas of Douglas Lake are more stabilized. Rocks furnish a solid, physical support. The encrusting organisms which cover the rocks furnish plentiful food. All nymphs characteristic of rocky situations possess a strong clinging response which appears similar in importance to the light reaction.

Outline of Habitat Distribution Pattern as Displayed by Douglas Lake Mayflies

I. Littoral
  A. Beach pools
    1. Temporary
      Siphlonurus rapidus (c)
      Leptophlebia nebulosa (c)
      Ephemerella lutulenta (c)
      Ephemerella temporalis (c)
      Caenis simulans (c)
    2. Permanent
      Ephemerella lutulenta (c)
      Ephemerella temporalis (c)
      Caenis simulans (a)
      Callibaetis ferrugineus (r)
  B. Rocks
    1. Near shore line
      Baetis phoebus
    2. Shallow water
      a. Close together
        Stenonema femoratum (a)
        Stenonema interpunctatum (r)
        Heptagenia lucidipennis (a)
        Ephemerella bicolor (a)
        Ephemerella lutulenta (c)
        Ephemerella temporalis (c)
      b. Scattered
        Stenonema femoratum (c)
        Cloeon rubropictum (s)
  C. Sand
    1. Wave-swept
      Siphloplecton basale (when emerging)
    2. Below effective wave action
      Ephemera simulans (s)
      Hexagenia limbata (r)
      Hexagenia affiliata (?)
      Baetisca obesa (r)
      Brachycercus lacustris (s)
      Caenis simulans (a)
  D. Marl
    1. Wood fragments absent
      Caenis simulans (s)
    2. Wood fragments present
      Stenonema femoratum (c)
      Choroterpes basalis (a)
      Ephemerella lutulenta (c)
      Ephemerella temporalis (c)
      Caenis simulans (s)
  E. Organic detritus
      Leptophlebia nebulosa (c)
      Ephemerella temporalis (c)
      Ephemerella lutulenta (c)
      Caenis simulans (a)
  F. Emergent plant zone
      Siphloplecton basale (when emerging)
      Caenis simulans (s)
      Ephemerella lutulenta (c)
      Ephemerella temporalis (s)
      Ephemerella bicolor (s)

II. Sublittoral
  A. Submerged plant zone
      Siphloplecton basale (?)
      Tricorythodes allectus (?)
      Caenis simulans (c)
      Centroptilum fragile (?)
      Pseudocloeon dubium (?)

B. Mud
Hexagenia limbata (a)
Hexagenia affiliata (?)

III. Profundal (all forms absent)
Symbols: (a) abundant; (c) common; (s) scarce; (r) rare; (?) relative abundance unknown but probably occur in habitat indicated.

Mayfly Productivity of Douglas Lake

While this study involved little attempt at the quantitative approach to mayfly productivity in Douglas Lake, certain conclusions may be reached chiefly from observational data. From the standpoint of both quantity and quality, mayfly productivity in Douglas Lake may be considered low. The principal reason for this is apparent when the relative proportions of those areas which are productive or unproductive of nymphs are contrasted. As has already been pointed out, the wave-swept, sandy shoal regions of Douglas Lake are extensive as compared to those which are rocky or protected from strong wave action. Mayflies occur primarily in the latter situations; consequently, only about 15 per cent of the total area of lake bottom included by the 0- and 3-meter contours supports a mayfly population. It is also significant that the majority of the rocks in the lake are located close to the shore line and many become exposed to the air each year during the period of low water level. The usual drop in water level is about 0.6 meter, and since the slope of bottom in the littoral region is very gradual, a considerable proportion of this area is exposed in late summer. It is very probable that the lowered water level has marked effect upon the population of mayfly nymphs; and if the water level were maintained at a higher point than at present, the mayfly production of the lake as a whole would probably be increased.

The region of Douglas Lake which is most productive of *Hexagenia* is included within the 9 and 15 meter contours and comprises only about 15 per cent of the entire lake bottom. In lakes where the density of *Hexagenia* is high a large proportion of the bottom in deep water is available as a habitat for these nymphs, a condition not true of Douglas Lake. In the latter, about 85 per cent of the lake bottom is unsuitable for *Hexagenia* nymphs because of its sandy character or because of lack of sufficient dissolved oxygen due to thermocline formation in the several individual depressions.

Summary

This investigation is the first intensive study of the mayfly fauna of a North American lake in which the primary purpose was to determine the local distributional pattern of the nymphs together with the environmental factors responsible for it. It was found that the physical character of the bottom, light intensity, and wave action are the principal factors which interact to determine the distributional patterns. The positive thigmotactic response of certain species of nymphs is also an important influence in distribution and accounts for the absence of nymphs from habitats lacking physical support. Temperature and dissolved oxygen have little, if any, effect on nymphal distribution within lakes. However, *Hexagenia* nymphs are limited by oxygen to that portion of the mud bottom above the hypolimnion. Low mayfly productivity in Douglas Lake arises from the fact that only about 15 per cent of the total bottom area is suitable for mayfly populations.

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A STUDY OF A CALANOID COPEPOD POPULATION IN AN ARCTIC LAKE[1]

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Introduction

The purpose of this paper is to describe the cyclical activities of a calanoid copepod, *Limnocalanus johanseni,* in an arctic lake. This lake, called "Imikpuk" by the Eskimos, is a small, shallow, fresh-water body located on the arctic coast of the northernmost tip of Alaska at Point Barrow. The fauna supported by Imikpuk was surprisingly varied. Among the more conspicuous organisms present was the little-known copepod *Limnocalanus johanseni* Marsh; rotifers of the genera *Kellicottia, Synchaeta, Notholca,* and *Keratella; Cyclops scutifer* Sars; and a cladoceran *Daphnia pulex* var. *tenebrosa* Sars, which was conspicuous because of its large size as well as abundance. Occurring in the plankton, but not in excessive numbers, were two species of Anostraca, at least one species of the Notostracan, *Apus,* and occasionally specimens of a second little-known calanoid, *Eurytemora canadensis* Marsh. In one collection only were found two specimens of the calanoids *Diaptomus glacialis* Sars and *Diaptomus alaskaensis* M. S. Wilson.

The field work was done during the summer of 1952 between July 10 and September 27, and the sample counting was done during the fall of the same year. The Arctic Research Laboratory at Point Barrow was the base from which all the field work was done, and its laboratory facilities were adequate to make very frequent determinations of soluble phosphorus, total nitrogen, and chlorophyll, as well as other routine analyses which included oxygen, pH, alkalinity, and the physical measurements of temperature, transparency, and total suspended material (seston). The photosynthetic activity of the lake was also studied during this summer (Comita and Edmondson 1953). Sufficient data were taken so that the heat budget could be computed and seasonal activities of several plankters outlined in addition to those of the copepod being presented at this time. A discussion of these data is in preparation.

During the course of the present work, I have received a great deal of help from many persons to whom I owe a heavy debt of gratitude. Professor W. T. Edmondson has given advice and guidance not only in the planning but also in the execution of the over-all project for which he was principal investigator. Dr. I. L. Wiggins took the April 1953 samples and kindly placed the facilities of the Arctic Research Laboratory at my disposal. John J. Koranda took seven plankton hauls from Imikpuk after it had frozen over in the fall of 1952.

[1] Part of a thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the University of Washington, Seattle, Washington.