

Seasonal Food-Cycle Dynamics in a Senescent Lake*

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“Large fish eats small fish;
Small fish eats water insects;
Water insects eat plants and mud.”

—Chinese proverb.

Introduction

The problem of trophic relationships has long been recognized as a central influence in the field of limnology; few attempts have been made, however, to analyse the quantitative seasonal dynamics of these relationships. The existence of food-chains has been known since the earliest civilizations; the cyclic nature of food-relations, recognized with the earliest development of exact chemistry, was originally clearly stated by Lavoisier (Henderson, 1913). The detailed analysis of trophic relationships has been initiated much more recently, accompanying the development of limnology as a science. A piscian food-chain similar to that of the above apothegm was described in detail by Forbes (1887) in his classical essay, “The Lake as a Microcosm.” The brilliant exposition by Forel (1904) of the general nature of food cycles (dissolved mineral nutrients, autotrophic plants, herbivores, carnivores, bacteria and back to dissolved nutrients) will serve even today as an introductory account of trophic relationships. Subsequent research, until very recently, has been concerned largely with qualitative rather than quantitative aspects of these fundamental community phenomena.

The careful study of food cycles reveals an intricate pattern of trophic predilections and substitutions underlain by certain basic dependencies; food-cycle diagrams attempt to portray these underlying relationships. Insofar as certain members of the food-group units may occasionally vary their diet, particularly toward the predatory ends of the food-chains, all trophic diagrams are somewhat Procrustean.

Various attempts have been made to diagram the general trophic relations in aquatic habitats. The first of these, by Shelford (1913), graphically portrayed the food-chains described by Forbes in 1887. Alsterberg (1924) diagrammed a cycle including nutritive regeneration from benthic ooze by action of the tubificid “sediment-transporters.” The first really comprehensive

* This is the third in a series of papers, “Ecological Studies of a Senescent Lake,” describing various ecological aspects of Cedar Creek Bog, Minnesota. This paper represents a portion of a thesis submitted to the Graduate Faculty of the University of Minnesota in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

diagram of aquatic food cycles was given by Thienemann (1926) in his essay, "Der Nahrungskreislauf im Wasser"; his figure has been modified slightly in the publications of Perfiliev (1929) and Welch (1935). Strøm (1928) published a food-cycle diagram emphasizing the central position of ooze in trophic cycles, as well as the relation of autochthonous to allochthonous nutritives. Rawson (1930) developed a diagram of similar nature, with primary emphasis on the trophic relations of fishes. Wasmund (1930) presented a complex diagram of lake metabolism which emphasizes the relation of allochthonous detritus and dissolved nutrients to stratigraphy and to human influences.

The food-cycle relationships in small senescent lakes, because of such features as relatively uniform depth, general homogeneity of bottom type and absence of violent wave action, tend to be less complicated and more easily studied than those of large lakes. Yet nearly all features of the food-cycle diagram (Fig. 1) resulting from the study of such a lake (Fig. 2) can be applied directly to the earlier eutropic stage of aquatic succession.

Dissolved nutrients, autochthonous and allochthonous, are incorporated into organic substances by producers, of which three types are common in

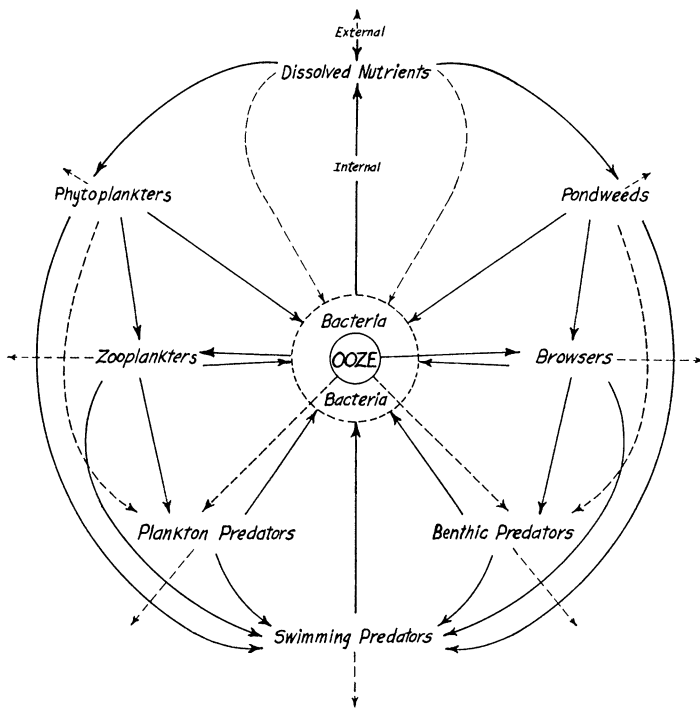


Fig. 1. Food-Cycle Relationships in a Senescent Lake.

lakes: *autotrophic bacteria*, *algae* and *pondweeds*. Each of these may die and decompose by bacterial action into ooze, or may be eaten by some consumer. *Zooplankters* feed as primary consumers upon phytoplankton algae, bacteria and particulate organic matter; they in turn may be eaten by secondary consumers, such as *plankton predators* and small *swimming predators*, or they may die and contribute to the benthic ooze. Plankton predators, as the name implies, feed mostly on zooplankters, although some phytoplankters and some ooze particles also may be consumed. As secondary consumers, they may be eaten in turn by such tertiary consumers as larger swimming predators, they may pupate and leave the aquatic community as adult insects, or they may die and contribute their substance to the ooze by bacterial action.

Pondweeds, synthesizing organic substance from dissolved nutrients, may act as food for many kinds of consumers, or may decompose by bacterial action into ooze. Jacot (1940), to whom the author is indebted for the concept of successively remote consumer groups, considers saprophages as "low primary" consumers. Certain animals feed directly on pondweeds as herbivores (primary consumers); others feed upon the decomposing plant tissue, or nascent ooze. These two groups have overlapping food habits and are most conveniently grouped together in the food cycle diagram. These primary *browsers* are in turn fed upon by secondary consumers, *benthic predators*, and tertiary consumers, *swimming predators*. Secondary consumers may also feed to a certain extent as primary consumers, eating small quantities of green plant tissue and even benthic ooze. Tertiary and quaternary consumers, such as swimming predators, may obtain nutriment from any of the lower consumer groups of the food cycle. Small quantities of green plant materials appear to be eaten by even rather remote predators, although this usually constitutes a very small fraction of the diet. In a general way, the more remote a consumer becomes with respect to the primary sources of food (producers), the more versatile are its food habits. The substance of each group upon death of the organisms contributes to the benthic ooze, from which plant nutritives are again dissolved.

The relationships of consumer food habits to community structure were greatly clarified as a result of the concepts presented by Elton (1927), who stressed the importance of size and of numbers in the animals of a community. Beginning with primary consumers of various sizes, there are as a rule a number of food-chains radiating outwards, in which the predators become successively larger, while the parasites and hyperparasites are progressively smaller than their hosts. Since small primary consumers can increase faster than larger secondary consumers and are so able to support the latter, the animals at the base of a food-chain are relatively abundant while those toward the end are progressively fewer in number. The resulting arrangement of sizes and numbers of animals Elton termed the Pyramid of Numbers. The quantitative dimensions of this Consumer Pyramid depend upon the physiological efficiency of the groups at various levels and the extent to which the consumers at higher levels partake of the food of lower groups.

AREA STUDIED

During the past five years the author has been engaged in an intensive study of Cedar Bog Lake, which represents a late stage of eutrophic senescence (see Fig. 2). The lake originally occupied a rather large ice-block



Fig. 2. Midsummer aspect of Cedar Bog Lake, July 16, 1937.

depression in the Anoka Sand Plain; sedimentation and marginal vegetational invasion, however, have reduced Cedar Bog Lake to less than 1/10 of its original depth and area. The lake at present has a maximum depth of about one meter, an aquatic area of 14,480 square meters, and a "shore line" of 500 meters. The developmental history of the lake is described in the first paper of this series (Lindeman, 1941).

In the following pages we shall discuss first the qualitative food-cycle relationships in the lake, and then attempt to analyse the quantitative seasonal dynamics and the productivity aspects of these relationships.

Qualitative Food-Cycle Relationships

Dissolved nutrients, consisting of those chemical elements considered essential for life (N, P, S, K, Ca, Mg, Fe, Mn, B, Zn, Cu), usually in ionic form, are supplied to the senescent lake from three main sources: (1) drainage and seepage into the lake from the surrounding drainage basin; (2) regeneration from organic ooze by action of heterotrophic bacteria; and (3) excretion of dissolved substances into the water by the aquatic organisms. That the first source may at times be considerable is attested by the fact that, following the spring thaw of 1937, sufficient water drained into

the lake from the surrounding bog to actually double the volume of water in the lake. Unfortunately no data are available as to the amounts of these allochthonous nutrients. A few data on the action of heterotrophic bacteria are discussed on page 650.

Autotrophic bacteria are probably of considerable importance as producers of organic substance in lakes (Henrici, 1939). Since these have not been studied in Cedar Bog Lake, they are mentioned here simply as hypothetical members of the food cycle. Certain colorless flagellates, which are apparently both autotrophic and anaerobic, appear in the lake during winter stagnation (Lindeman, 1942a).

Phytoplankters in the open water of the lake varied considerably, both in quality and quantity, throughout the year. The net phytoplankton consisted largely of dinoflagellates: *Ceratium hirundinella* (O. F. Müller) was present throughout the warmer months of every year, reaching in 1940 a maximum abundance of 6 gm/m² dry weight,* (VII-27-40), while in 1939 (VI-15-39) a tremendous "bloom" weighed more than 10 gm/m²; species of *Peridinium* also occurred, but never reached the abundance of *Ceratium*. Blue-green phytoplankters, such as species of *Anabaena*, *Aphanocapsa*, *Aphanizomenon* and *Oscillatoria*, were common during the summer, but on only one occasion (VIII-15-38), did these forms approach "bloom" frequencies. The diatoms *Melosira* and *Synedra* were conspicuous at times, particularly during late autumn. The green flagellate *Eudorina elegans* Ehr. was common during the summer of 1940.

Nannoplankters (the micro-algae capable of passing through the meshes of a plankton net) are usually far more important to the metabolism of a lake than are the larger plankters. At nearly all seasons, but particularly during spring and late autumn, the weight value of nannoplankters in Cedar Bog Lake far outranked that of the larger phytoplankters. The chief genera involved in this tremendous production, which often exceeded 5 gm/m² dry weight, were *Scenedesmus*, *Westella*, *Micractinium* and *Actinastrum*.

The role of phytoplankton in lake metabolism cannot be over-emphasized. The nannoplankton, of course, is one of the chief sources of food for planktonic rotifers and entomostracans. The larger phytoplankters such as *Ceratium*, *Eudorina*, etc. may also serve as food for the zooplankton. It seems probable that these larger phytoplankters, in addition, serve as food for the plankton predator, *Chaoborus*, as well as for small fishes. In larger eutrophic lakes, and to a lesser extent in Cedar Bog Lake, the phytoplankton is the major source of the benthic ooze upon which the ooze browsers subsist.

The **zooplankters** of Cedar Bog Lake, except during late winter and early spring, consisted largely of rotifers. *Keratella cochlearis* (Gosse) was the most abundant species, increasing in numbers throughout the summer to an autumnal maximum of ca. 2 gm/m² dry weight in 1937. Other genera common during the summer months were *Brachionus havanaensis* Roussetel,

* The weight values of all organisms are expressed as gm/m² of surface area in order to facilitate productivity and efficiency calculations.

Polyarthra trigla Ehr. and *Synchaeta* spp. *Filinia longiseta* (Ehr.) seemed most tolerant of inimical winter conditions, surviving long periods of anaerobiosis, and appearing as the most common rotifer in winter and early spring. Many other genera inhabited the pondweed zone of the lake, but these "pseudoplankters" have not been especially studied. Species of the copepod *Diaptomus* were common only during the late autumn and winter of 1938-39 and 1939-40, reaching a maximum frequency during January of ca. 0.5 gm/m² dry weight.

These zooplankters are primary consumers, feeding indiscriminately upon nanoplankters and suspended organic particles less than 10 μ in diameter (Naumann, 1923; Myers, 1941). The suspended excrement of zooplankters may be readily attacked by aerobic bacteria to release considerable amounts of dissolved nutrients. The bodies of dead zooplankters likewise may be attacked by aerobic bacteria as they settle toward the bottom. The substance of dead plankters furnishes nutriment for the many benthic ooze browsers; it is finally attacked by benthic bacteria, which further dissolve the softer tissues to release nutrient salts. More resistant structures such as jaws and loricae of rotifers, spines and ephippia of cladocerans, etc., may persist as semi-fossils buried deep in the ooze. The living zooplankters, particularly the copepods, fall prey to larvae of *Chaoborus* and to small fishes; rotifers, being smaller in size, are less frequently eaten by these forms.

Plankton predators in the open water of the lake consist largely of the "phantom larvae" of *Chaoborus punctipennis* (Say), which at times are tremendously abundant. These larvae are primarily predatory, feeding on zooplankters (Frankenberg, 1915; Eggleton, 1931) and small benthic organisms (Muttkowski, 1918). Study of the food relations in Cedar Bog Lake strongly suggests that *Chaoborus* larvae feed in part upon *Ceratium* and rotifers, and also upon benthic ciliates and ostracods. Plankton predators, in turn, are much preyed upon by small fishes. The synthesized organic substance of this species may be entirely lost to the metabolism of the lake by emergence of the adult midges. Dead larvae are usually quickly reconverted to dissolved nutrients by bacterial action.

The appellation plankton predator is also applied (with some hesitation) to the back-swimming bugs, *Plea striola* Fieber, *Buenoa margaritacea* Bueno and nymphs of *Notonecta* species, all of which occur among the pondweeds. These bugs subsist primarily upon the "pseudoplankton" entomostracans (Hungerford, 1919). Their relative scarcity and small size forces them to a minor role in the food cycle of most lakes.

The pondweeds, as primary producers of organic substance, are relatively more important in Cedar Bog Lake than in deeper, larger lakes. During two of the four years studied, the pondweeds (used here in the broadest sense of the term) produced more organic substance than did the phytoplankton. *Najas flexilis* (Willd.), together with *Potamogeton zosteriformis* Fernald and *P. panormitanus* Biv., was so abundant (except during 1938) as to form a submerged "meadow" covering more than half of the entire lake bottom.

Ceratophyllum demersum L. is usually interspersed with *Najas* in the shallower water near the lake margin. This pondweed "meadow" forms an abundant source of food for a great variety of browsing animals, as well as a locus of attachment for many sessile plants and animals. Several different food groups are thus dependent upon the submerged pondweeds. In late autumn the pondweeds die and partly decompose, forming a thick nutritive layer of nascent ooze over a considerable part of the lake bottom. The decomposition of this ooze accounts to a considerable extent for the annual depletion of oxygen beneath the winter ice.

The epiphytes attached to the submerged pondweeds, including many kinds and varieties of bacteria, diatoms, green and blue-green algae, form an increasingly heavy coating over the pondweeds as summer progresses. Most conspicuous of these is *Gloeotrichia pisum* (Ag.); this species grows so rapidly that by midsummer the leaves and stems of *Potamogeton zosteriformis*, the species first affected, are thickly encased with the hemispherical thalli. During this period the dry weight of the epiphyte is considerably greater than that of the supporting pondweed. The trichomes of *Gloeotrichia*, incompletely decomposed on the lake bottom, are found in great numbers in the sediments of the lake.

Filamentous algae such as species of *Spirogyra* and *Oedogonium* are commonly associated with the pondweeds. During early summer these algae form dense masses which blanket the water surface near the margins. Certain colonial flagellates such as *Pandorina morum* Bory and *Eudorina elegans* Ehr. seemed to be more common among the pondweeds than in the open water zone.

The microfauna associated with the pondweeds includes many sessile, creeping and free-swimming herbivores. Rotifers, including such genera as *Diurella*, *Lecane*, *Euchlanis*, *Trichocerca* and *Platyias*, were abundant; entomostracans, including such cladoceran genera as *Pleuroxus* and *Chydorus*, and such ostracod genera as *Cypria* were usually common. These organisms, feeding on seston and to a lesser extent upon the nearby epiphytes, are preyed upon by certain carnivorous species of *Cyclops* (Naumann, 1923); both micro-predator and micro-prey are subject to intense predation by small fishes and other swimming predators.

The macrofauna, which portrays an almost infinite variety of food habits, has been classified according to "primary" dietary habits into browsers, benthic predators, plankton predators and swimming predators. The term **browser** is here roughly defined as an herbivorous or saprophagous animal which feeds primarily on its substrate. The distinction between plant browsers and ooze browsers does not appear to be justified; many species which are primarily herbivorous during the summer are saprophagous during the winter; others appear to feed indiscriminately upon both living and dead plant material.

Many **browsers** are associated primarily with living pondweeds. Prominent among these are several genera of pond snails, *Helisoma*, *Planorbula*,

Menetus, *Gyraulus*, *Physa* and *Ammicola*; these usually are found on living pondweeds, but also feed on epiphytes, ooze and even decomposing animal tissue (Wesenberg-Lund, 1939), depending upon predilection and availability. Although some specific food-differences have been observed, these genera are essentially similar in relation to the general food cycle. The common amphipod *Hyalella azteca* (Sauss.), which is primarily a browser on pondweed epiphytes (Jackson, 1912), occupies a food-cycle position essentially similar to that of the snails. A small species of the oligochaete *Nais*, possessing pigmented eye-spots, was often abundant among the pondweeds; according to Wesenberg-Lund (1939), *Nais* feeds primarily on epiphytic plants and certain members of the associated microfauna.

Several types of immature insects browse on the pondweeds and pondweed epiphytes. Such chironomid larvae as species of *Endochironomus*, *Tanytarsus* and *Cricotopus* (cf. Moore, 1915, p. 284) become particularly abundant at certain times of the year. Certain mayfly naiads of the subfamily *Baetinae* are often observed creeping and apparently browsing upon the pondweeds. Caddisfly larvae of such genera as *Phryganea*, *Limnophilus* and *Platyphylax* are found associated with the pondweeds; these larvae feed upon green plant tissue (cf. *ibid.*), although they may also eat ooze, depending upon which source of food is most convenient (Lloyd, 1921).

Browsers particularly abundant in *Spirogyra* masses include larvae of the ceratopogonid genera *Stilobezzia* and *Dasyhelea*, and species of the crawling water beetles, *Haliphus* and *Peltodytes*. The former were found only among *Spirogyra* masses, on which they feed, while the latter were also found among pondweeds and sometimes in the ooze. According to Hickman (1931) *Spirogyra* is the principal food of the larvae of these beetles, while the adults forage upon a wider variety of vegetation.

Browsers common during the summer months on both the pondweeds and the benthic ooze include naiads of the mayfly genus *Caenis*, larvae of the soldierfly genus *Odontomyia* and tadpoles of the leopard frog, *Rana pipiens* Schreber. *Caenis*, which is usually abundant in the pondweed zone of Cedar Bog Lake, is characteristic of the upper sublittoral zone of larger eutrophic lakes, as a "Pflanzendetritus bevorzugendes Tier" (Lundbeck, 1926, p. 168). The larvae of *Odontomyia*, often numerous among pondweeds near the lake margin, feed on pondweed epiphytes, entomostracans and nascent ooze (Malloch, 1917). Frog tadpoles, usually common near the lake margin, feed on filamentous algae and various constituents of the benthic ooze (cf. Morgan, 1930).

A group of browsers more strictly associated with the ooze in the pondweed zone consists of the water-boatmen (*Corixidae*), the adult water scavenger beetles (*Hydrophilidae*) and the deerfly (*Chrysops*) larvae. The *Corixidae*, which are at times very numerous in the lush *Najas* "meadow" of Cedar Bog Lake, are primarily ooze browsers, sweeping the flocculent surface ooze into their mouths by means of their fore tarsi (Hungerford, 1919). These

small bugs are much parasitized by larval water mites, and are extensively preyed upon by various carnivorous insects. Hydrophilid beetles are represented in the lake by *Tropisternus*, *Enochrus* and *Berosus*, as well as other genera of smaller size. The adults of these beetles are primarily ooze browsers, but also eat dead animal tissue (Richmond, 1920). The larvae of *Berosus* are sluggish browsers (Wilson, 1923), in contrast to the (predatory) larvae of the other genera. *Chrysops* larvae, which occur rather commonly in the marginal ooze, are also (Johannsen, 1935) primarily ooze browsers.

The true ooze browsers of eutrophic lakes consist largely of midge larvae belonging to the genus *Chironomus*. In the marginal and pondweed areas of Cedar Bog Lake, *Chironomus lobiferus* Say is the most important species, living in crevices of sticks, inside the stems of aquatic plants, or in the absence of these, in reinforced U-shaped tubes in the ooze. The primary species in the more tenuous planktogenic ooze in the middle of the lake are *Chironomus plumosus* L. and *Chironomus decorus* Johannsen, which also live in reinforced tubes. The food of these three species is essentially similar, consisting largely of settled plankton, ooze-film organisms and flocculent particles of planktogenic ooze (cf. Richardson, 1921; Leathers, 1922).

Because of their abundance *Chironomus* larvae play an important role in the "intermediary metabolism" of the lake. Much of the benthic ooze passes at least once through their digestive tracts, as indicated by innumerable fecal balls in the unconsolidated deposits. The flow of water through the deep tubular burrows, set up by undulatory (respiratory?) movements of the larvae, serves to permit oxidation of the ooze to considerable depths by the action of aerobic bacteria, thus furnishing large amounts of released nutrient ions to the water above. *Chironomus* larvae are able to withstand extended periods of anaerobic conditions (Lindeman, 1942a). The seasonal distribution of the above species in Cedar Bog Lake is considered in detail in another paper (Lindeman, 1942b). They harbor considerable numbers of the large parasitic nematode, *Hydromermis* sp; by serving as a source of food for benthic and swimming predators, *Chironomus* larvae form an important link in the food cycle of the lake.

Less numerous ooze browsers in Cedar Bog Lake are the finger-nail clams, species of *Pisidium* and *Musculium*. The former were collected in the deeper areas during 1937 and 1938; numbers of the latter were found in marginal collections during 1939 and 1940. The slender worm leech, *Helobdella nepheloidea* (Graf), common in the marginal areas during 1937 and 1938, is also primarily an ooze browser (cf. J. P. Moore, 1912).

Microscopic ooze browsers, because of their periodic abundance, may often be as important to the food-cycle economy of the lake as are the macro-browsers. During the late autumn of 1939, for example, a tremendous fauna of *Chaoborus* is believed to have been maintained largely by the great masses of micro-browsers present at that time. The great majority of these browsers consists of ciliates, primarily *Frontonia leucas* Ehr. and *Loxodes rostrum* (O. F. M.). With the exception of a few protozoan and rotiferan predators, most

of these organisms are ooze browsers, feeding on tiny particles of ooze and probably obtaining much of their nutritive requirement from the benthic bacteria. Besides the ciliates are found such gastrotrichans as *Lepidoderma rhomboides* (Stokes) and several species of *Chaetonotus*, many small free-living nematodes, *Ilyocryptus* and smaller benthic cladoceran genera, the copepod genus *Canthocamptus*, and the ostracod genera *Candona* and *Cypria*. All of these organisms are primarily ooze browsers (cf. Wesenberg-Lund, 1939), and form a very interesting and taxonomically complex fauna. Unfortunately no attempt was made to evaluate the role of micro-browsers in the food-cycle dynamics of the lake. This was due partly to the difficulties of counting such organisms in freshly taken ooze and partly to the belief that larger browsers, such as chironomid larvae, did not discriminate between the surface ooze and its contained microbiota. It now appears, however, that at least certain predators, such as *Chaoborus*, carefully discriminate between ooze and microfauna.

The **sediment-transporters** deserve particular mention, although the results of their ooze-browsing activities are not conspicuous in Cedar Bog Lake. The tubificid oligochaetes, *Limnodrilus* and *Tubifex*, live in tubes with their anterior ends deep in the ooze and their posterior ends waving about in the water just above. Alsterberg (1922) was the first to demonstrate that these worms suck in particles from the lower ends of their tubes and defecate the undigested remains at the ooze surface; he later (1924) described the trophic significance of their role as sediment-transporters in a paper which has been widely quoted. Wesenberg-Lund (1939), however, declares that it still remains to be demonstrated that the scraping together of particles from the ooze surface may not equally serve as a source of nutrient. Observations on tubificids in aquaria by the present author indicate that sediment-transportation does occur, and that with large populations of these worms, its effects may be considerable.

In summarizing the status of the many diversified browsers in the food cycle of Cedar Bog Lake, it should be re-emphasized that these organisms constitute the most important link between the synthesized organic matter produced by autotrophic plants and the higher predators of greatest economic importance to man. Within the broad limitations imposed by differential respiratory adaptations, the practical fish productivity of a lake seems to be directly correlated with the abundance of browsers.

The **benthic predator** sector of the food cycle contains several groups of secondary consumers related only in their predatory dependence on the browsers and the general inability to swim. Several types of predatory techniques are employed, varying from pursuit to ambush and allurement. The effect upon the prey may vary from engulfment to bloodsucking and temporary or permanent parasitism.

The most important creeping predators in the central portion of the lake are midge larvae. *Chironomus* (*Cryptochironomus*) *stylifera* Johannsen represents a carnivorous larval group of an otherwise herbivorous genus. The larvae of *Procladius culiciformis* (L.), *Tanytus stellatus* Coq., *Pentaneura*

sp., and *Anatopynia dyari* (Coq.) of the predatory (cf. Johannsen, 1937) subfamily *Tanypodinae* are also sporadically common. Predatory (cf. Thomson, 1937) vermiform larvae of the *Palpomyia*-group of *Ceratopogonidae* are usually very abundant in the central part of the lake. Since these predatory larvae appear to feed primarily on browsing chironomid larvae, a large predatory population may greatly reduce the numbers of browsers. These predators are in turn subject, together with the remaining browsers, to extensive predation by the larger swimming predators.

The creeping predators of the pondweed beds consist primarily of leeches. The snail leeches, *Helobdella stagnalis* (L.), *Helobdella fusca* (Castle) and *Glossiphonia complanata* (L.), sporadically abundant in the lake, creep along the ooze surface and among the pondweeds; they feed by sucking the internal tissues from such snails, worms, insect larvae and other sluggish forms as cannot elude them (cf. Moore, 1912). As the name "snail leeches" implies, snails form the chief component of their diet. The turtle leeches, *Placobdella rugosa* (Verrill) and *Placobdella parasitica* (Say), appear to be alternately predatory and parasitic. They are often found as ectoparasites on the painted and snapping turtles, respectively, but they seem unable to swim and spend their free-living periods on the marginal bottom or among the pondweeds. Their predatory food habits (cf. Moore, 1912) are essentially the same as those of the snail leeches. The turtle leeches are thus seen to occupy at different times two quite different sectors of the food cycle. Since turtles are usually uncommon in the lake, these leeches are grouped with the snail leeches. Small leeches are extensively preyed upon by fishes and other swimming predators.

More sedentary benthic predators are the naiads or dragonflies and damselflies, which are often numerous in the marginal areas of the lake. The damselfly naiads are usually found in the tangled masses of pondweeds, where they prey upon such browsers as chironomid larvae and mayfly naiads, as well as upon entomostracans (Garman, 1917). The dragonfly naiads can be found half-buried in the ooze or supported on bits of aquatic vegetation; they lie in wait for the approach of smaller animals, which are impaled on the labial hooks by a quick thrust of the labium and drawn toward the crushing mandibles. Because of their size dragonfly naiads are the most "dominant" of the benthic predators; they are immune from the small fishes inhabiting the lake, and only the large swimming leeches are able to prey upon them.

A specialized group of small animals which are both predators and parasites are the water mites or *Hydracarina*. Considerable numbers of these animals are found in the pondweed beds; a species of *Limnesia* is found rather consistently in the ooze of the open water zone, and is able to withstand considerable periods of anaerobiosis. The larvae are ectoparasites on various aquatic insects; the adults feed as swimming predators on entomostracans and small insect larvae, although because of their small size they are preyed upon in turn by small fishes.

Before discussing the role of swimming predators in Cedar Bog Lake, we shall veer from our course to mention an obvious "side-chain" to the aquatic food cycle — the *neuston*, or surface-film organisms. The *neuston* has consid-

erable claim to being considered as a separate community in its own right. Autotrophic bacteria, unicellular algae and abundant masses of *Lemna* and *Spirodela*, covering the surface in quiet-water areas, act as the producers for the community; the animal consumers include both browsers and predators. The associated organisms of a *Lemna* community are charmingly described by Scotland (1934) in her short paper, "The Animals of the *Lemna* Association."

Animals extending beyond the limited areas of the "*Lemna* association" consist of certain protozoans and entomostracans suspended from the under side of the surface film; *Microvelia* species which feed on these (Hungerford, 1919), are present during the summer in considerable numbers. The larger predators, which "skate about" on the surface film and feed on terrestrial animals fallen into the water from the margin or the air above, include such genera as the water strider *Gerris*, the whirligig-beetle *Dineutes*, and the semi-aquatic spider *Dolomedes*. All of these forms may at times become rather abundant on the surface of the lake. All members of this surface-film community are subject to the action of swimming predators from below, which tends to incorporate the organic substance of this community into the larger food cycle of the lake.

The most conspicuous swimming predators in quantitative collections from the pondweed and marginal areas consist of the larger aquatic insects. Among these must be included the adult back-swimmer, *Notonecta* sp. (Hungerford, 1919), although the nymphal stages feed primarily as plankton predators. The adult *Notonecta* is a fierce predator, quite capable of attacking small fishes and other animals larger than itself. Other highly carnivorous animals in the pondweed areas are the water-tigers and the predacious diving beetles, larvae and adults, respectively, of the family *Dytiscidae*. The water-tigers have an amazingly insatiable appetite, possessing hollow piercing mandibles which enable them to suck the juices from their victims without loosening their initial hold. Mayfly and damselfly naiads, chironomid and smaller beetle larvae are choice prey for these creatures, but no aquatic animal may consider itself safe from the larger water-tigers—snails, tadpoles, frogs and even fishes all fall before their onslaughts (Wilson, 1923). The larvae of *Tropisternus* and other aquatic *Hydrophilidae* are similarly carnivorous. The adult *Dytiscidae*, represented in the lake by such genera as *Hydaticus*, *Coptotomus*, *Desmopachria* and *Rhantus*, are agile swimmers and strictly carnivorous. According to their size they eat dragonfly, damselfly and mayfly naiads, as well as aquatic hemipterans, chironomid larvae and snails (Wilson, 1923). All of these beetles must be considered as swimming predators.

A group of more sluggish swimming predators, definitely restricted to the dense pondweed masses near the lake margin, are represented by large bugs, including species of *Ranatra*, *Nepa*, *Lethocerus* and *Belostoma*. The former two, known as water-scorpions because of their long caudal breathing-tubes, spend most of their time in the tangles of *Najas* and *Ceratophyllum* waiting motionless for some unwary creature to come within reach; when this happens the raptorial fore legs quickly snatch the prey, and the nutritive fluids are

sucked from its body (Hungerford, 1919). *Lethocerus* and *Belostoma* are fierce predators, able to kill and devour even such large organisms as minnows and frogs (Needham, 1918), although their usual diet consists of smaller forms. No organisms in the lake except the turtles and muskrats are safe from these bugs. These four genera, together with the predatory beetles, compete for "animal dominance" in the marginal areas, since the small fishes present in the lake seem unable to prey upon them effectively. This "dominance" must, however, be shared with the swimming predatory leeches, which also function as the "end of the food-chain" in this part of the lake.

Another important group of swimming predators is composed of the swimming leeches, *Erpobdella punctata* (Leidy) and *Macrobdella decora* (Say), which are numerous during those years when fishes are few in numbers. These leeches are good swimmers and, although occasionally acting as scavengers, ordinarily prey upon worms and aquatic insects (Moore, 1912). *Erpobdella*, the more common genus, even attack small fishes and frogs; large quantities of ooze are often swallowed, but this is believed to be an unimportant factor in its diet. *Macrobdella*, the well-known blood-sucker, prefers to feed upon the blood of vertebrates plus whatever invertebrate forms it can capture. Frog eggs are often eaten, and the writer has observed the consumption of *Pimephales* eggs by this leech. Because of the versatility in food habits of these leeches, enabling them to fit into several carnivorous food-groups according to predilection and availability of food, it seems certain that they should be grouped with the fishes as very important swimming predators.

The major swimming predators of Cedar Bog Lake, the fishes, are of extreme importance in the food-cycle dynamics of the lake. During the course of this investigation four species, all small and of the type known as "forage fishes," were found in the lake: *Pimephales promelas* Raf., *Umbra limi* (Kirtl.), *Eucalia inconstans* (Kirtl.) and *Apomotis cyanellus* (Raf.). All of these species typically are found in small sluggish streams with marshy bottoms. Cedar Creek, into which the lake sporadically drains, is definitely of this type. The lake outlet follows a vague surface course through the bog forest, where tree roots and hummocks combine to conceal any continuous channel. Presumably the fishes are able to perceive a current, and since the maximum flow coincides with the spring spawning season, they must manage to follow its mile-long course by wriggling from pool to pool until they arrive at the lake itself.

The difficulties involved when one attempts to place an organism into a rigid "niche" of an arbitrary food cycle are particularly apparent in the case of certain fishes. The food habits appear to vary in different habitats; it may be that fishes have individual food preferences at different times, occasionally varying their usual diet (of chironomid larvae, for example, with pondweed fragments), just as terrestrial carnivores occasionally modify their usual diet with bits of grass.

The fat-headed minnow, *Pimephales promelas*, is a hardy species, very resistant to asphyxiation; it is not surprising to find it the most abundant fish

in the lake. The food of 3 young specimens 12-15 mm. in length was found to consist of mixed phytoplankton and zooplankton, the latter consisting of protozoans, rotifers and nauplii, but no adult copepods nor cladocerans. The food of 8 specimens 28-38 mm. in length was found to consist of filamentous algae and larger zooplankters. Two individuals 35-40 mm. in length were starved for a week and then placed in an aquarium containing submarginal Cedar Bog Lake ooze, to which a small mass of *Spirogyra* (abundant in the lake at that time) had been added, so that the resulting food conditions were believed to correspond to those existing in the lake. Two days later the fishes were removed and their food determined. No ooze was taken by the minnows in spite of their proximity to it; the food was almost wholly of animal origin and consisted of chironomid larvae, bryozoans (*Plumatella*), *Plea* and chironomid adults. A very small amount of algae (ca. 5%) was eaten, consisting of *Spirogyra* and *Oscillatoria*. From these food-habit data it was concluded that *Pimephales* changes its food preference with growth. The young individuals seem to be general plankton predators, while the adults, although they never quite renounce their vegetarianism, may be considered as swimming predators.

The five-spined stickleback, *Eucalia inconstans*, although never abundant, was found in the lake during three of the five years studied. This species, which has a short intestine typical of carnivores, was reported by Forbes and Richardson (1920), based on five specimens, to feed on filamentous algae, entomostracans and chironomid larvae, the algae making up 50% of the food. Two specimens from Cedar Bog Lake were found to have fed almost entirely on copepods and ostracods, as well as on a few smaller zooplankters. Thus these individuals seem to prey upon the microbenthic ooze-surface organisms as do such other plankton predators as *Chaoborus* larvae. Since *Eucalia* is also known to eat *Chaoborus* and chironomid larvae, it must be considered as a swimming predator.

The mud minnow, *Umbra limi*, the most mud-loving of our piscian fauna, was found very regularly in the lake; during 1938 it was the only species found. *Umbra* is reported by Forbes and Richardson (1920) to be largely vegetarian, with animals making up about one-fourth of its food. A study of 8 individuals from Cedar Bog Lake showed that more than 90% of the food taken was of animal origin. Chironomid larvae, corixids, small adult beetles, collembolans, water mites and many entomostracans made up most of its food. Because of the definitely carnivorous diet of the specimens examined, the author has no hesitation in considering *Umbra* as a swimming predator.

The green sunfish, *Apomotis cyanellus*, was rare in the lake, and present only during 1939 and 1940. Although this species is typical of small soft-bottomed streams, it seems rather surprising that it could have accomplished the "hedge-hopping" presumed necessary to traverse the bog forest area from Cedar Creek to the lake. This species, in common with other *Centrarchidae*, is definitely predatory. Young individuals feed on entomostracans; older ones on insects, small crustaceans and other fishes. It readily falls into the category of a swimming predator.

It should be emphasized that the fish population of Cedar Bog Lake is quite different from that of larger eutrophic lakes. In larger lakes the larger carnivorous fishes are able to prey on the smaller "forage fishes" as well as on any other of the subservient groups of the food-chain. In Cedar Bog Lake the devastating anaerobic period during winter stagnation necessitates new immigration each spring, so that the offspring of such large carnivorous fishes as might reach the lake cannot attain more than the first year of growth. As a result the fishes must share honors as "dominant animals" with the swimming leeches and those larger swimming insects which the fishes are unable to eat. The swimming predators of Cedar Bog Lake are thus seen to be secondary consumers rather than tertiary consumers as are the dominant fishes of larger lakes.

Although **air-breathing tetrapods** are not, strictly speaking, a part of the senescent lake community, many of them are intimately dependent on it for food. The leopard frog, *Rana pipiens* Schreber, is often common near the margin, preying upon snails, Hyalellae, worms and aquatic insects (Dickerson, 1906), which comprise substantial portions of its diet. The painted turtle, *Chrysemys picta bellii* (Gray), of which several individuals can usually be seen in the lake, makes up about $\frac{2}{3}$ of its diet from pondweeds. The remaining third is made up chiefly of aquatic insects, but also includes snails, Hyalellae, leeches and fishes (Lagler, 1940). Numerous ducks feed on such aquatic plants as may be found during the migration periods, and usually one or two pairs of teals nest on the lake during the summer. Kingfishers and bitterns, birds which feed on the aquatic fauna, have been occasionally observed, but are not believed to exert much influence on the food cycle of the lake as whole. During 1939 several pairs of muskrats (*Ondatra*) immigrated to the lake, and presumably consumed a considerable amount of aquatic vegetation (cf. Enders, 1932); these muskrats perished during the winter and have not since been replaced. The tetrapod predators are not numerous in Cedar Bog Lake and, from the point of view of the lake as a whole, do not seriously affect the purely aquatic aspect of the lake's ecology.

Heterotrophic bacteria are the primary agents, apart from the excretion of dissolved substances by higher organisms, in the regeneration of dissolved nutrients within a lake. Very few data have been published on this aspect of food-cycle dynamics, so that a few preliminary notes from Cedar Bog Lake material are noteworthy. A series of cultures of benthic ooze (XII-8-40), at three concentrations of ooze in standard culture water (cf. "Standard Methods for the Examination of Water and Sewage," 1936) at 20° C. for 5 days, showed an oxygen consumption of 4.7 mg/l of O₂ per 50 mg dry ooze. This represents the activity of aerobic bacteria. The activity of anaerobes in ooze from the same place (XI-15-39) is suggested by data taken from another manuscript (Lindeman, 1942a). Quantities of ooze representing approximately 30 times the concentration above were placed in blackened culture jars and kept under anaerobic conditions at constant temperatures of 0°, 5° and 10° C. for a maximum of 120 days. The increase in bicarbonate alkalinity was recalculated as increase in CO₂ (mg/l of CO₂) per 50 mg dry ooze

for direct comparison with the aerobic data given above. The recalculated values are:

	30 days	60 days	90 days	120 days
0°	.12	.31	.37	.42
5°	.09	.20	.21	.40
10°	.18	.32	.44	.51

Although such data may be criticized on several bases, these figures suggest that aerobic bacteria are many times as effective as anaerobes in regeneration of benthic nutrients; the accumulation of organic deposits in the profundal areas of eutrophic lakes also indicates that such is the case.

Regeneration of dissolved nutrients, at least in part, is absolutely essential to the functioning of any nutritive cycle. A certain amount of essential nutrient substance potentially may leave the lake from any sector of the primary food cycle. Drainage through the lake outlets during periods of high water may remove dissolved nutrients, phytoplankton and zooplankton. Emergence of adult stages of aquatic insects may remove living animal tissue from the browser, plankton predator, ooze predator and swimming predator food groups. Predation by tetrapods may permanently remove organic substance from the pondweed, browser and any or all of the predator groups mentioned above. Perhaps the most important loss of substance to the food cycle in this lake is by sedimentation on the lake bottom. Compensating for these losses, however, is the influx of a certain amount of dissolved nutrients from the surrounding drainage basin. Aside from these losses and additions, the aquatic food cycle is self-contained, again decomposing that organic substance to which it has given rise, and in a large measure regenerating from the organic ooze the nutrient salts essential for further photosynthesis.

In brief recapitulation of trophic relationships, the autotrophic plants are the producers of organic substance in the lake; numerous animal groups play intricate, interrelated roles as primary, secondary and even tertiary consumers of this organic substance; heterotrophic bacteria act as decomposers of organic substance and, from another point of view, as regenerators of essential plant nutrients. Thus the food cycle revolves.

Quantitative Seasonal Dynamics

The study of seasonal changes in the metabolism of lakes requires comprehensive analyses of processes both directly and indirectly related to the food cycle. In the present study on the senescent Cedar Bog Lake, the author makes no claim for such comprehensive treatment. An attempt has been made, however, to determine simultaneous seasonal values for certain environmental conditions as well as for the biological populations.

The seasonal dynamics was studied by means of periodic surveys, covering the period from December 21, 1936, to March 28, 1941. Nearly 50 such survey trips were made, during which more than 40 series of plankton and water-chemistry samples, and 30 series of bottom samplings (338 Birge-Ekman dredge collections) were obtained. While most stress was placed on the fluctuations in bottom fauna, quantitative estimates of various other food groups and environmental conditions were made at the time of each survey.

Since fluctuations in certain of the environmental "factors" are reflected in the coincident biomass, it seems advisable to present the seasonal analysis of (1) water level variations correlated with climate and (2) fluctuations in chemical conditions, before considering the quantitative biological dynamics.

WATER-LEVEL VARIATIONS CORRELATED WITH CLIMATE

The surface level has been so directly correlated with profound changes in the ecology of the lake that an accurate account of its fluctuations, together with those of the causative climatic factors, is highly desirable. The available data on mean monthly temperature, mean annual precipitation and mean monthly precipitation from nearby weather stations, as well as the surface level of Cedar Bog Lake, depth of winter ice and depth of free water in the center of the lake, are recorded in Fig. 3.

The mean annual duration of ice, shown as shaded blocks in the figure, was estimated from personal observations: in this region ice usually forms on small shallow lakes in mid-November and lasts until about April 1. Deviations from this arbitrary norm may be seen by the way in which the curve of mean monthly temperature intersects the block representing mean annual duration of ice. Thus, the spring of 1938 was abnormally warm, as was also the late autumn of 1939. The air temperature curve was plotted from the mean monthly values at Cambridge, Minnesota, about 15 miles north of Cedar Bog Lake.

Mean monthly variations in aqueous precipitation at Cambridge, Minnesota, are indicated by the solid line representing "precipitation." Extreme deviations from the mean annual curve (based on the 37-year records of precipitation at Milaca, Minnesota, about 35 miles from the lake) were found at all seasons of the year. It should be noted that in general the greatest amount of precipitation occurs during the warmest part of the year.

Measurements of water level fluctuations in the lake are indicated by small circles along the curve representing surface level. The records for 1936 were established by survey from the upland (Buell, 1941), while the intervening fluctuations for 1936 were estimated, as shown by the broken line. All levels with lettered vertical ordinates indicate the maximum depths of water and of ice on successive dates when bottom-fauna collections were made. Undulations in the curve reflect indirect evidence that the lake had accordingly varied during the intervals between visits.

Comparison of the surface level curve with the mean monthly precipitation curve indicates a definite relationship; in spite of marked irregularities in precipitation, differential seasonal evaporation and the damming effects of the surrounding peat, a simple correlation coefficient of .409 was obtained for the two curves. The summer of 1936 was extremely dry, with the result that the lake level dropped more than one-half meter, exposing considerable sub-marginal ooze; vernal precipitation in 1937 greatly raised the lake level, serotinal drouth caused a decline, and autumnal precipitation produced another rise.

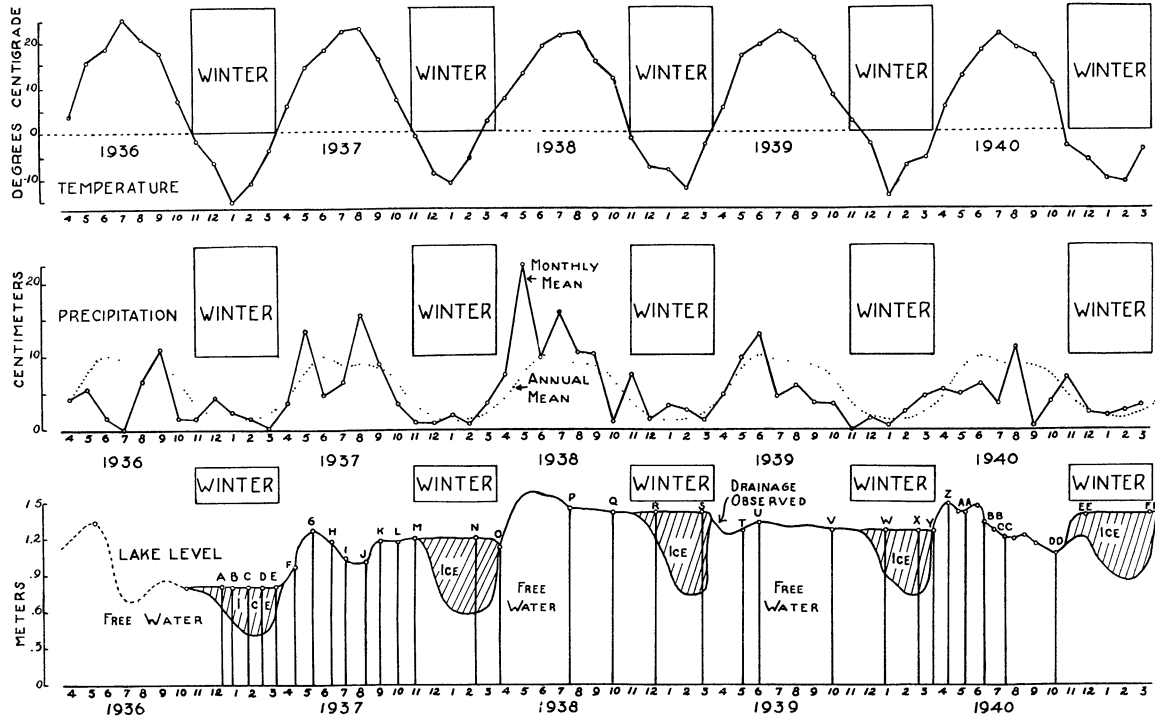


Fig. 3. Correlation of temperature and precipitation with the water level of Cedar Bog Lake.

Heavy precipitation throughout 1938 produced very high levels with theoretical drainage, although none could be observed on July 30. Buell (1941) has shown that the level of the entire bog forest fluctuates directly with precipitation, and that the forest is, in a manner of speaking, floating! Thus perhaps the lake outlet area floated up to a level at which surface water did not *flow*, but rather slowly *seeped* into the Cedar Creek drainage from adjoining portions of the bog. A similar damming effect of peat on lake drainage was noted by Lewis and Cocke (1929).

A peculiar phenomenon was observed in the spring of 1939; although precipitation was normal and melting snow should have greatly raised the water level, just the opposite event occurred, and the level *dropped* some decimeters. Fortunately for our records, Dr. W. H. Crone observed in early April that a considerable drainage stream "6 inches deep and quite wide" was flowing from the southwest portion of the lake across the bog forest toward Cedar Creek. The lake was almost free of ice at that time but the forest peat, at depths of about 1 to 4 decimeters, was still frozen. The hypothesis is proposed that the surface waters of the lake and surrounding mat quickly drained in response to warm weather before the forest peat could thaw out sufficiently to float up and impede the drainage.

The data summarized in Fig. 3 thus indicate that the water level of Cedar Bog Lake is determined primarily by the aqueous precipitation. The surrounding forest peat seems to exert a damming effect upon drainage from the lake.

SEASONAL FLUCTUATIONS IN CHEMICAL CONDITIONS

The chemistry of the water is so intimately related to the metabolic food cycle of the lake that seasonal fluctuations in dissolved substances often can be used to evaluate the intensity of biological processes. Field analyses of carbon dioxide, total alkalinity, pH and dissolved oxygen (according to the techniques described in "Standard Methods for the Examination of Water and Sewage," 8th ed.) were made during each survey visit to the lake, as shown in Fig. 4. It should be emphasized that the indicated lines in Fig. 4 merely show changes for consecutive survey dates and hence give no indication of the duration of a particular type of chemical conditions.

Dissolved oxygen in the center of the lake varied from 150% saturation on sunny midsummer afternoons to 0% in late winter. The exact duration of this winter oxygen-free period was determined only for the winter of 1939-40, when anaerobic conditions prevailed for 50 days (cf. Lindeman, 1942a). Reciprocal correlations between the summer concentrations of dissolved oxygen and of hydrogen ions, carbon dioxide acidity and total alkalinity (Fig. 4) are rather striking.

Carbon dioxide, produced largely from the decomposition of organic substances by bacteria and by respiration, combines readily with the salts of calcium and magnesium to be temporarily "stored" as bicarbonate dissolved

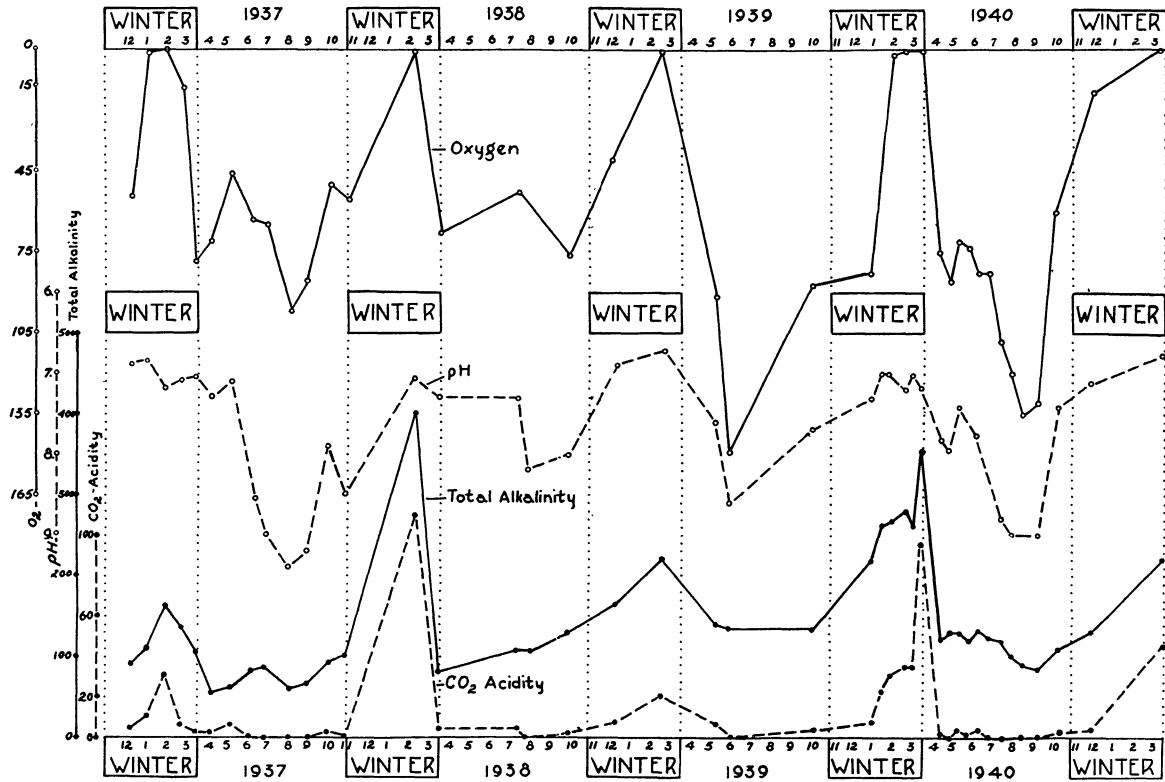


Fig. 4. Seasonal variations in dissolved oxygen, ph, total alkalinity and carbon dioxide in Cedar Bog Lake.

in the water, or more permanently stored as mon carbonate (marl) in the benthic ooze. Tests on the benthic ooze (IX-1-40) indicated a total alkalinity "reserve" of marl representing more than 1 gram per liter (as CaCO_3). The hydrogen ion concentration is largely a reflection of the equilibrium ratios existing between dissolved carbon dioxide and bicarbonate or between bicarbonate and mon carbonate, together with small amounts of other ionized substances. During winter stagnation the more soluble bicarbonate increases (as does carbon dioxide), so that the total alkalinity is raised three- or four-fold over its summer minimum. To obtain such extremes the light necessary for photosynthesis must be effectively shut out by snow or granular ice. In midsummer carbon dioxide is "extracted" from the bicarbonate by the plants for photosynthesis, mon carbonate is precipitated from the warm lake water, the pH may rise as high as 9.4, and total alkalinity of the water is greatly reduced. Under such conditions the water is often supersaturated with oxygen, a product of photosynthesis.

The amount of carbonates and bicarbonates in a lake is limited, not by the ever-present carbon dioxide, but by the supply of calcium, magnesium and manganese. Total alkalinity is thus an index of these dissolved alkaline-earth metals. Analyses of the lake water for various seasons of the year indicated that the calcium content varied from 31 to 92 mg/l, while the magnesium content varied from 7 to 17 mg/l; manganese, present in relatively minute quantities, is included with the above magnesium values. Adding these together gives alkaline earth values ranging from 38 to 107 mg/l, figures which correlate very well with the total alkalinity values for corresponding dates, expressed in terms of the metals rather than as CaCO_3 . Such concentrations of these metals, rather high for lakes in general, are due to leaching from the porous lime-containing soils of the surrounding region.

Iron, dissolved and suspended, is very abundant in the lake water. During winter stagnation ferrous salts are dissolved in considerable quantities; an analysis of water taken March 4, 1939, showed an iron content of 18.20 mg/l, as contrasted with a summer content of 0.2 mg/l. Reductive processes, initiated after the dissolved oxygen has been depleted, convert much benthic and suspended ferric iron to the ferrous state, which is very soluble in the carbon dioxide-laden, oxygenless water (Hutchinson, 1941). Samples collected after the onset of winter stagnation are bluish-black in color, reminding one of very dilute ink. If such samples are exposed to the air, the color of the water gradually changes to a brilliant ochre hue, while transparency becomes so greatly reduced (from ca. 50 to ca. 600 U.S.G.S. units) that one cannot see through it for more than a few centimeters. The ferrous ions are converted to insoluble ferric compounds (Einsele, 1936), which precipitate and are perhaps adsorbed upon some of the abundant dissolved organic substances to form the ochre-colored colloids. Since ferric phosphate may be precipitated in this manner, Hutchinson (1941) has emphasized that this process may play an important role in inhibiting the regeneration of phosphates from the benthic ooze.

BIOLOGICAL FOOD-CYCLE DYNAMICS

Quantitative seasonal studies on lake biology have seldom emphasized the inter-relationships of various sectors of the primary food cycle. Such studies have been limited largely to the study of plankton or bottom fauna as a single unit without attempting either (1) to correlate the seasonal changes of the organisms studied with simultaneous changes in sectors of the food cycle other than water chemistry, or (2) to differentiate predators from prey. A partial exception to the first of these generalizations is represented by the correlations on Lake Mendota of Juday (1940), which, however, are not based on simultaneously collected data. A partial exception to the second generalization is represented by the analyses of Deevey (1942) of the bottom fauna of Linsley Pond, Connecticut.

The bottom biota of Cedar Bog Lake was sampled by means of the conventional Birge-Ekman dredge (15 x 15 cm.), modified to the tenuous ooze of Cedar Bog Lake by soldering a copper screen (40 meshes per inch, the same mesh size used for sifting) to the top of the dredge chamber. The sampler thus actually encompassed a vertical column from the surface of the water to a depth of at least 20 cm. in the bottom ooze. The samples were usually sifted in a wire-bottomed sieve immediately after collection, to remove all particles less than 0.5 mm. in diameter. The remaining coarse debris, including the biota, was placed in a glass jar, labeled, and preserved for examination in the laboratory. During the early part of this work 4 samples were collected in the open water zone, 4 in the pondweed zone, and 8 in the marginal zone. During 1940, 5 samples were taken from the open water and 5 from the pondweed zone, each sample being kept separate to permit statistical treatment of distributional data. During the winter months the marginal areas were frozen solid, so that samplings could be made only in the deeper zones.

Laboratory analysis of the bottom samples required the careful separation of organisms from the coarse detritus. This proved to be a laborious and time-consuming task, particularly in the marginal samples, because of the abundance of detritus on the lake bottom. The sorted organisms were identified, measured, counted and weighed. The weighing technique for each sample consisted of placing all the organisms of a single species in a small bolting-silk bag, centrifuging them in the bag for 3 minutes at 800 rpm to remove surface moisture, and then weighing them on a sensitive torsion balance. The resultant *moist* (centrifuged) weight is used as the basis, unless otherwise specified, of all weights mentioned in this paper. Conversion factors to dry weight for certain organisms are as follows:

Hydaticus	3.7	Caenis	5.6
Tropisternus	4.8	Chironomus	5.0-6.0
Palpomyia	5.3	Chaoborus	12.0-16.0
Hyaella	5.5		

It will be seen from these values that organisms possessing the greatest amount of chitin (*Hydaticus* and *Tropisternus* adults) are given less weight value than those possessing the least chitin (*Chaoborus*). This is as it should be, for chitin is quite indigestible. From the trophic point of view, since dry weight values for insects as food are quite misleading, the moist weight values are believed to be based upon a more useful standard. The centrifuging technique has the added advantages of rapidity of measurement and of non-injury to the specimens, which may then be retained for other studies.

Field collections of net plankton were made by pouring approximately 100 liters of water through a No. 25 bolting-silk net; these samples, taken from three areas of the lake, were immediately preserved with formalin. Usually at the same time, quart samples of water from each station were preserved for the evaluation of nannoplankton.

Laboratory analysis of the net plankton consisted of comparing its quality and quantity (settled volume) with similar plankton samples from sources other than Cedar Bog Lake. The plankton of these other samples had been measured for quality and volume of settled organisms; then these were centrifuged for 3 minutes at 800 rpm, to remove surface moisture, and weighed on a sensitive torsion balance. From a series of such analyses conducted on miscellaneous samples of diverse species composition, factors were obtained for interpolating the settled volume of Cedar Bog Lake plankton, of known composition, into the appropriate centrifuged weights per unit volume. Although this round-about procedure was doubtless less accurate than centrifuged weights obtained directly from the quantitative plankton samples, the potential errors involved were deemed insignificant in comparison with the seasonal variation found. More important, this technique avoided the destruction of quantitative seasonal samples so valuable for future taxonomic and cyclomorphic studies. In small lakes containing abundant macrophytes, plankton often varied considerably in quantity from one part of the lake to another, requiring considerable subjective discrimination in estimating "true" values. Furthermore, the net samples often contain considerable floating debris. During microscopic analysis the percentage and quality of zooplankton, net phytoplankton and debris were estimated for each sample, and calculated in terms of moist weight. Analysis of the nannoplankton samples showed that while practically all of the zooplankton was retained by the net, often more than 90% of the phytoplankton consisted of minute nannoplankters which were not retained. The calculated populations of both nannoplankters and net phytoplankters are shown in Tables 1 and 2.

TABLE 1.—Food-Group Populations in Cedar Bog Lake, as gm/m², moist weight.

Series	Date	Swimming Pre- dators	Benthic Pre- dators	Browsers	Plankton Pre- dators	Zoo- plank- ton	Net Phyto- plank- ton	Nanno- plank- ton	Pond- weeds
A	XII-21-36*	4.60	50.20	0.03	0.00	0.02	1.0	0.0
B	I-18-37*	1.00	2.06	19.03	0.35	0.00	0.00	0.0	0.0
C	II-14-37*	2.85	35.64	0.70	0.00	0.00	0.0	0.0
D	III-8-37*	8.39	1.96	51.02	0.25	0.00	0.01	0.01	0.0
E	III-29-37*	4.36	3.03	52.90	0.58	0.01	0.04	0.01	0.0
F	IV-26-37	0.38	1.81	23.14	0.61	0.03	0.06	1.0	0.0
G	V-25-37	0.28	1.08	18.68	0.15	0.70	0.00	3.0	6.0
H	VI-26-37	0.81	1.26	3.38	0.01	0.10	0.10	1.9	150.0
I	VII-16-37	1.81	0.63	1.94	0.15	0.58	0.20	3.8	800.0
J	VIII-20-37	2.59	0.41	2.08	0.31	1.10	0.37	1800.0
K	IX-15-37	2.58	0.35	1.35	0.56	10.18	0.73	19.3	600.0
L	X-17-37	3.29	0.15	1.32	0.64	6.00	0.00	9.0	3.0
M	XI-13-37	3.63	0.15	1.03	0.31	2.52	0.03	15.0	0.0
N	II-26-38	0.01	0.05	0.54	0.27	0.00	0.00	0.0	0.0
O	IV-3-38	0.69	0.25	1.18	0.76	0.29	0.01	0.04	0.0
P	VII-30-38	0.07	0.02	1.55	0.37	0.69	1.38	0.6	250.0
Pa	VIII-15-38	2.16	19.40	0.6	300.0
Q	X-16-38	0.58	1.64	4.24	7.25	1.64	0.55	19.5	2.0
R	XII-22-38	±0.65	1.99	1.45	3.36	1.75	0.21	21.8	0.0
S	III-4-39	0.01	1.00	3.54	3.32	0.01	0.00	0.01	0.0
T	V-23-39	0.15	0.38	1.11	2.94	4.04	1.16	4.0	75.0
U	VI-15-39	0.11	0.30	0.84	1.80	2.45	46.55	0.5	200.0
Ua	IX-1-39	1000.0
V	X-15-39	2.63	0.71	3.56	26.27	1.22	0.16	6.8	3.0
W	I-13-40	2.50	0.44	14.82	22.95	2.00	0.43	7.5	0.0
Wa	I-31-40	2.12	0.00	3.0	0.0
Wb	II-7-40	1.17	0.07	0.03	0.0
X	III-3-40	0.00	0.77	16.93	±25.00	0.31	0.00	0.0	0.0
Y	III-30-40	0.01	0.00	0.0	0.0
Z	IV-28-40	0.48	0.79	7.91	18.76	1.21	0.01	10.0	1.0
Za	V-11-40	1.13	0.01
AA	V-26-40	0.13	0.90	2.69	22.05	2.59	0.11	2.4	50.0
AAa	VI-9-40	1.54	1.23
BB	VI-24-40	0.30	0.89	12.97	8.65	0.57	0.95	1.0	400.0
BBa	VII-7-40	0.71	2.73
CC	VII-27-40	1.20	1.09	16.86	0.97	1.20	23.70	0.3	1500.0
CCa	VIII-12-40	0.51	0.70	1800.0
CCb	IX-1-40	0.29	1.45	1.5	2000.0
CCc	IX-22-40	1.49	0.62	2.4
DD	X-20-40	3.00	1.54	1.96	3.02	0.26	0.06	5.0
EE	XII-8-40	3.25	3.60	1.50	3.70	0.40	9.00	3.0	0.0
FF	III-28-41	0.00	0.67	0.20	3.78	0.00	0.00	0.0	0.0

* Samplings inadequate, only 4 Ekmans taken on each date.

TABLE 2.—Food-Group Populations in Cedar Bog Lake, as cal/cm².

Series	Date	Swimming Pre- dators	Benthic Pre- dators	Browsers	Plankton Pre- dators	Zoo- plank- ton	Net Phyto- plank- ton	Nanno- plank- ton	Pond- weeds
A	XII-21-36*	0.46	4.18	0.00	0.00	0.00	0.06	0.00
B	I-18-37*	0.12	0.21	1.58	0.02	0.00	0.00	0.00	0.00
C	II-14-37*	0.28	2.97	0.03	0.00	0.00	0.00	0.00
D	III-8-37*	1.01	0.20	4.25	0.01	0.00	0.00	0.00	0.00
E	III-29-37*	0.52	0.30	4.32	0.03	0.00	0.01	0.00	0.00
F	IV-26-37	0.05	0.18	1.93	0.03	0.01	0.01	0.07	0.00
G	V-25-37	0.03	0.11	1.56	0.01	0.10	0.00	0.19	0.21
H	VI-26-37	0.10	0.13	0.28	0.00	0.01	0.01	0.12	5.25
I	VII-16-37	0.22	0.06	0.16	0.01	0.09	0.01	0.25	28.00
J	VIII-20-37	0.31	0.04	0.17	0.01	0.16	0.02	63.00
K	IX-15-37	0.31	0.03	0.12	0.02	1.48	0.05	1.25	21.00
L	X-17-37	0.40	0.02	0.12	0.03	0.87	0.00	0.59	0.10
M	XI-13-37	0.43	0.02	0.08	0.01	0.37	0.00	0.97	0.00
N	II-26-38	0.00	0.01	0.04	0.00	0.00	0.00	0.00	0.00
O	IV-3-38	0.08	0.03	0.10	0.03	0.04	0.00	0.00	0.00
P	VII-30-38	0.01	0.00	0.13	0.02	0.10	0.08	0.04	8.75
Pa	VIII-15-38	0.31	1.22	0.04	10.50
Q	X-16-38	0.07	0.16	0.35	0.32	0.24	0.03	1.27	0.06
R	XII-22-38	±0.08	0.20	0.12	0.15	0.25	0.01	1.41	0.00
S	III-4-39	0.00	0.10	0.30	0.15	0.00	0.00	0.00	0.00
T	V-23-39	0.02	0.04	0.09	0.13	0.59	0.07	0.26	2.62
U	VI-15-39	0.01	0.03	0.07	0.08	0.37	2.94	0.03	7.00
Ua	IX-1-39	35.00
V	X-15-39	0.32	0.07	0.30	1.15	0.18	0.01	0.44	0.10
W	I-13-40	0.30	0.04	1.23	1.01	0.29	0.02	0.49	0.00
Wa	I-31-40	0.31	0.00	0.20	0.00
Wb	II-7-40	0.17	0.01	0.00	0.00
X	III-3-40	0.00	0.08	1.41	±1.10	0.04	0.00	0.00	0.00
Y	III-30-40	0.00	0.00	0.00	0.00
Z	IV-28-40	0.06	0.08	0.66	0.82	0.18	0.00	0.65	0.03
Za	V-11-40	0.16	0.00
AA	V-26-40	0.02	0.09	0.22	0.97	0.37	0.01	0.16	1.75
AAa	VI-9-40	0.22	0.07
BB	VI-24-40	0.04	0.09	1.08	0.38	0.08	0.06	0.06	14.00
BBa	VII-7-40	0.10	0.17
CC	VII-27-40	0.14	0.11	1.40	0.04	0.17	1.50	0.02	52.50
CCa	VIII-12-40	0.07	0.04	63.00
CCb	IX-1-40	0.04	0.09	0.10	70.00
CCc	IX-22-40	0.22	0.04	0.16
DD	X-20-40	0.36	0.15	0.16	0.14	0.03	0.01	0.17
EE	XII-8-40	0.39	0.36	0.12	0.16	0.06	0.57	0.20	0.00
FF	III-28-41	0.00	0.07	0.02	0.16	0.00	0.00	0.00	0.00

* Benthic samplings inadequate; only 4 Ekmans taken on each date.

Seasonal fluctuations and inter-relationships of the primary food groups were analyzed in the following manner. Each species or genus was grouped according to food habits, as previously described, into the appropriate unit of the primary food cycle of the lake (Fig. 1). The resulting values, together with those obtained for the plankton, permitted the assemblage of seasonal weights for the following groups: (1) browsers, (2) benthic predators, (3) plankton predators, (4) zooplankters and (5) phytoplankters. Data for (6) pondweeds were based largely on estimates for the season, and include the weight of the epiphytic alga, *Gloeoetrichia*. Fair estimates of (7) swimming predators were also obtained, since each year's fish production could be observed following suffocation during winter stagnation. The remaining units of the food cycle, unfortunately, were not similarly evaluated: no persistent attempt was made to analyze dissolved nutrients, bacterial activity or the annual increment of benthic ooze. The seasonal values for the seven food groups listed above are shown as gm/m², moist weight, in Table 1, and as calories/cm² in Table 2.

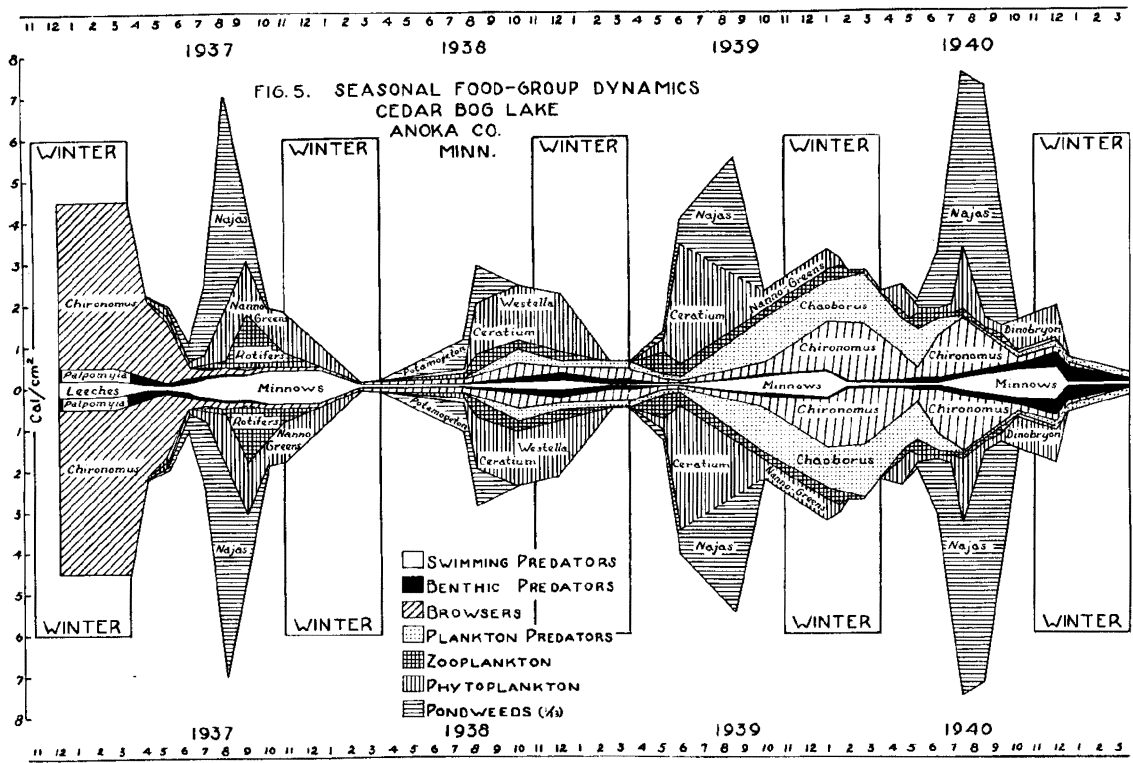
The conversion of weight values to calorific values is highly desirable for evaluating the relative nutritive content of various food groups. Thanks to the chemical analyses of many types of aquatic organisms by Birge and Juday (1922), the generally accepted bomb-calorimetry values for carbohydrate (4100 calories per gram), protein (5650 calories per gram) and fat (9450 calories per gram), as used by Juday (1940), can be utilized for the conversion. This method has certain inherent errors, since the organic composition of organisms changes with growth and nutrition, and since the bomb-calorimeter values do not indicate the extent of utilization of the food by the consuming organisms. It is, however, the most satisfactory method known for dealing with food conversions. The generalized factors for the conversion of food-group populations values from grams per square meter (dry weights and centrifuged weights) to calories per square centimeter are as indicated in Table 3.

TABLE 3.—Factors for the conversion of food-group weight values (gm/m²) to food values (cal/cm²).

<i>Food-Group</i>	<i>From Dry Weight</i>	<i>From Moist Weight</i>
Nannoplankton2610	.0652
Net Phytoplankton2525	.0631
Pondweeds3500	.0350
Zooplankton5800	.1450
Plankton Predators5330	.0440
Browsers5000	.0833
Benthic Predators5000	.1000
Swimming Predators6000	.1200

A more graphic presentation of the seasonal relationships of these food-group values is shown in Fig. 5, in which the calorific values of each group*

* Pondweed values are diagrammed as only 1/13 of the actual values to keep them within the confines of the chart.



are plotted successively in both directions from a central axis to emphasize the relationships of the groups to each other. The figure may be visualized as a sort of "sagittal section" through a cylindrical diagram. The duration of winter ice cover is indicated by the blocked areas labeled "ice."

Interpretation of the changing relationships of these food groups requires the careful consideration of simultaneous changes in water chemistry and climatic conditions, particularly the water level of the lake. The corresponding seasonal changes in climate, lake level and water chemistry are shown in Figs. 3 and 4.

The seasonal surveys were begun in the fall of 1936, following a summer of excessive drouth. The lake level was then lower than at any subsequent time during the period of this survey. No fishes were present in the lake during 1936, presumably because adults had been unable to immigrate during the preceding spring. The swimming predators were composed very largely of leeches, *Erpobdella punctata* being very abundant. *Palpomyia* larvae predominated among the benthic predators. Ooze browsers, composed very largely of *Chironomus lobiferus* larvae, were enormously abundant; pondweed beds had apparently covered most of the lake bottom during the summer, so that this pondweed-associated species could extend its range over the entire lake bottom. Plankton and plankton predators were very scanty during the winter.

Accompanying the spring thaw and heavy vernal precipitation of 1937 was a tremendous influx of water, actually doubling the volume of water in the lake. Some drainage must also have occurred through the bog forest peat west of the lake, as adults of *Pimephales*, *Eucalia* and *Umbra* were able to immigrate from Cedar Creek. Emergence of *Palpomyia* adults greatly reduced the benthic predators during early summer, although considerable numbers of creeping leeches were present. Emergence of *Chironomus* adults similarly reduced the browsers, although a tremendous May population of *Tanytarsus* tended to compensate this effect on the chart (Fig. 5). Plankton predators (*Chaoborus*) remained very scanty throughout this year. A slight bloom of the dinoflagellate *Ceratium* in May was followed later in the summer by a tremendous bloom of nannoplankters, primarily *Scenedesmus*, accompanied by a corresponding increase in the planktonic rotifers, particularly *Keratella*. As summer progressed an immense mass of *Najas* developed in the pondweed zone, estimated to average nearly 500 plants per square meter; these pondweeds became increasingly covered with epiphytic *Gloeo-trichia* as the plants reached vegetative maturity.

Myriads of immature *Pimephales*, offspring of the spring immigrants, became increasingly predacious as summer progressed. Correspondingly, though perhaps not relatedly, the population of insect larvae changed completely from that of the preceding year. Almost no larvae of *Chironomus lobiferus* and *Palpomyia* could be found; *Chironomus plumosus* larvae were completely replaced by those of the smaller species, *Chironomus decorus*. During the winter following 1937 anaerobiosis was severe and prolonged, killing all of the fishes, the plankters and much of the benthos. On Feb. 26, species of the

following genera of organisms were still alive: *Chironomus* (*decorus* and *lobiferus*), *Procladius*, *Palpomyia*, *Chaoborus*, *Limnesia*, *Cypria* (?) and *Tubifex*.

In the spring of 1938, although the water level became very high, there was little surface drainage through the bog forest, probably due to differential thawing of the lake and the bog forest peat. Consequently, little new immigration of fishes occurred, so that, since the previous year's crop had all suffocated during the winter, the swimming predators consisted mostly of leeches. *Macrobdella* and *Erpobdella* were the most abundant swimming predators during 1938. The lake community had remarkably changed from its appearance in 1937. The tremendous *Najas* meadows of the former season were almost entirely gone, their photosynthetic function being only fractionally replaced by a sparse stand of *Potamogeton zosteriformis*. Total production of organic substance in the lake was thus strikingly reduced. During the early summer, predators, browsers and plankton remained at a low ebb. Between July 30 and August 15, however, a fifteen-fold increase in *Ceratium* transformed the entire aspect of the lake; whereas the water had previously appeared dark and blackish, it became "pea-soup green" from the contained dinoflagellates. The rotifer fauna also increased during this period, though not so phenomenally as the *Ceratium*.

Autumnal collections in 1938 indicated increasing populations of swimming predators (leeches), benthic predators (*Palpomyia*) and miscellaneous browsers, as well as a tremendous increase in the plankton predator, *Chaoborus*. While no experimental proof is at hand, it seems quite probable that the increased dinoflagellate supply aided in the population rise of this plankton predator. As the phytoplankton changed from *Ceratium* into the fall nanoplankton blooms of *Westella* and *Scenedesmus* (which was this year unaccompanied by a rotifer maximum), the *Chaoborus* population declined. Although populations disappeared rather abruptly with the onset of winter anaerobiosis, *Chaoborus* was able to maintain itself (on benthic ciliates?) until spring.

In the spring of 1939, as mentioned in the previous discussion of water levels, a small but definite stream of water was observed flowing through the bog forest from the lake toward Cedar Creek. A considerable number of adult minnows, and a few green sunfishes, were thus able to reach the bog lake. A distinct spring maximum of nanoplankters and zooplankters (*Keratella*) was noted (for the first time in the course of this survey) in May. Between May 23 and June 15 occurred another phenomenal (nearly fifty-fold) increase in *Ceratium*, which gave the water an even more striking "pea-soup" appearance than it had during the previous summer. It is further noteworthy that the "bloom" occurred fully two months earlier than in the previous year. Another striking difference from the previous summer was the reappearance of extensive *Najas* beds in the pondweed zone, although these were estimated to be only about $\frac{2}{3}$ as abundant as during 1937.

By autumn the immense *Ceratium* population had declined to near extinc-

tion, but an equally immense predatory *Chaoborus* population suggested at least one reason for its decline. Nannoplankters (*Scenedesmus* and *Westella*) attained an autumnal maximum which during this year was again unaccompanied by a rise in planktonic rotifers, these latter possibly also influenced by the *Chaoborus* hordes. Great numbers of *Chironomus* larvae appeared in October, this time with *plumosus* predominating, accompanied by great numbers of *decorus* and *lobiferus*; all grew very rapidly during the early winter. These, together with the *Chaoborus* larvae, showed a high survival of the 50 days of winter anaerobiosis. Surprisingly enough, the fishes, whose predatory capacities were increasing throughout the summer and autumn, seemed quite unable to keep these tremendous larval populations under control.

The effects of winter anaerobiosis during this winter were very carefully studied and compared with anaerobic simulation cultures kept at controlled temperatures. Although the details of this study appear in another paper (Lindeman, 1942a), the benthic larvae were found able, with considerable mortality to be sure, to survive at least 120 days of continuous anaerobiosis at 0° and 5° C., but could scarcely survive this duration at 10°. Comparisons made with changes in the lake fauna during its 50 days of anaerobiosis indicated that the natural populations in the lake declined more rapidly than did those in the simulation cultures.

In the spring of 1940, although surface drainage could not be observed, the lake level was very high and adult fishes were again able to immigrate to the lake. Emergence of *Chironomus decorus*, followed later by *lobiferus* and *plumosus*, greatly reduced the early summer population of browsers. A spring nannoplankton bloom of *Trachelomonas*, *Fragilaria* and *Euglena* was belatedly followed by an increase in rotifers. The large population of overwintered *Chaoborus* larvae was slightly augmented by a new brood in May, but gradually declined to a small minimum in late July.

The 1940 bloom of *Ceratium*, less conspicuous than in the two preceding years, occurred in July. Self-evident on the seasonal chart is the prolific summer crop of *Najas*, fully as abundant as that of 1937, and equally beset in midsummer with masses of epiphytic *Gloeotrichia*. The autumnal nannoplankton bloom of 1940, unaccompanied by a zooplankton bloom, was composed almost exclusively of *Dinobryon*. During midsummer a second generation of *Chironomus plumosus* reached an impressive maximum, but autumnal and winter samplings indicated that its offspring, confronted by a large population of predatory *Palpomyia*, and a large fish population in early winter, followed by an extended anaerobic period, did not survive. The winter population of *Chaoborus*, although only about $\frac{1}{5}$ as great as the year before, was somewhat more impressive.

These rather extensive data suggest that sweeping conclusions as to the quantitative interaction of food groups under natural conditions should be made with caution. At the beginning of these surveys it was optimistically expected that the food groups would show seasonal periodicity somewhat comparable from one year to the next, and that although species-substitution might occur

within a food group, the "balance of nature" would rapidly re-establish an equilibrium between the food groups. Such is certainly not the case, at least in the senescent lake. While the relationships of nannoplankton to rotifers, and those of net plankton to *Chaoborus*, have been noted as suggesting predator-prey dynamics, gross productivity (utilization of dissolved nutrients), browsers and predators varied tremendously and independently.

The well-known annual variations in terrestrial communities are usually ascribed to climatic changes. Marked variations in the benthic invertebrates of coastal waters are believed to be partly due to physical conditions during the transition from the pelagic to the benthic stage in the life histories of the organisms (Blegvad, 1925). Eight-fold variations in the numbers of *Chironomus* larvae in a large eutrophic lake (Grosser Plöner See) between 1923 and 1925 were reported by Lundbeck (1926), for which he advanced no explanation. On the other hand, the extended studies of Lake Mendota, Wisconsin, covering a period of many years (Juday, 1940), failed to show such variations.

The annual variations in Cedar Bog Lake can be partly attributable to such indirect climatic effects as water level, duration of winter anaerobiosis, water temperature, climatic conditions during the mating season (for aquatic insects), drainage, etc. Certain unknown trophic relationships, such as growth rate in relation to temperature, disease and parasitism, may also be involved, but it is believed unlikely that browser populations were in any way limited by lack of food. For the predators, of course, such a generalization cannot be made.

In summary, the above quantitative analysis of seasonal food-cycle dynamics over a four-year period suggest the following conclusions: (1) an abundance of green plants as producers does not necessarily indicate an abundance of animals as consumers; (2) remarkable annual variations occur in all food groups of a natural population; (3) apparent predator-prey relationships often prevail between *Chaoborus* larvae and net plankters; and (4) climatic factors, resulting in water level changes, winter anaerobiosis, etc., play an important role in the annual productivity of Cedar Bog Lake.

Biological Productivity

Productivity is a rather loosely used term which indicates the general rate of production of any or every food group in a lake; depending upon how much of the food cycle is to be emphasized, one may speak of gross (or biological) productivity, plankton productivity, zooplankton productivity, bottom-fauna productivity, fish productivity, etc. The amount of substance produced per year, an arbitrary time unit, is known as the annual production, and is a convenient basis for expressing productivity. The quantity usually measured in routine surveys is biomass or "standing crop," a quantity which at best only partially reflects the productivity. The rates of production and consumption of food continually change throughout the year; diversified aquatic producers, including pondweeds, phytoplankton algae and autotrophic

bacteria, possess differential rates of growth, reproduction and completion of life cycle. Juday (1940) estimates that "the average turnover in the organic matter of the mean standing crop of plankton takes place about every two weeks throughout the year." The pondweeds usually develop but one generation per year, while the bacteria may divide several times per day. The year is generally the most useful time unit for expressing productivity.

The production per year includes only a single crop of pondweeds and pondweed epiphytes, but many "crops" of phytoplankters, which have been synthesized, partly consumed, decomposed and resynthesized several times from parts of the same original supply of essential nutrients. In stratified lakes dying phytoplankters during the summer months settle largely undecomposed into the hypolimnion, where a considerable portion of the released nutrients are not again available for synthesis until the fall overturn; these redissolved nutrients are then available, of course, for the large autumnal and vernal pulses of nanoplankton. Thus it is hardly fair to compare the total annual production of phytoplankton with the annual production of pondweeds. Recognition of this inherent error in the given method for evaluating total annual production of a lake is essential for the comparison of productivity between lakes.

The processes responsible for the productivity of any food group are extremely complex and very incompletely understood. Determinations of quantitative values for the annual production of certain groups are fraught with many uncertainties and arbitrary assumptions. In the present inadequate status of our knowledge, it may be argued by some that quantitative estimates of food-group productivity are futile until more definite information has been acquired. In response to which, the author can only plead that for the purpose of tentatively testing certain widely accepted "principles" based largely on theory and qualitative observations, rough approximations of quantitative trophic values are better than none.

The gross production of Cedar Bog Lake can be expressed in terms of the total annual production of pondweeds and of phytoplankton. The maximum or mature standing crop of pondweeds (including pondweed epiphytes) is taken as equivalent to the annual production. The phytoplankton is rather arbitrarily considered to complete a life cycle every week during the summer months (May-September) and every two weeks during the remainder of the year (cf. Juday, 1940). The annual phytoplankton production thus represents the sum of the weekly and biweekly "standing crops" indicated in Fig. 5 (p. 662). The zooplankton is arbitrarily considered to complete a life cycle every two weeks throughout the year. The plankton predators (*Chaoborus* larvae) are believed to develop three generations per year, while both the browsers (chiefly midge larvae) and the benthic predators (chiefly *Palpomyia* larvae) are believed to average about two generations per year in this lake (Lindeman, 1942b). The swimming predators are assumed to develop an average of one generation per year. The annual production of each of these food groups, calculated in approximately the same manner as Juday's (1940) data, is presented in Table 4.

TABLE 4.—Annual Production of Food Groups in Cedar Bog Lake, as cal/cm².

	1937	1938	1939	1940	Mean	S.E.
Nannoplankters	19.6	20.4	16.7	9.9	16.7 ± 2.2	
Net phytoplankters	1.5	9.8	18.9	6.3	9.1 ± 3.7	
Pondweeds	63.0	10.5	35.0	70.0	44.6 ± 9.7	
Zooplankters	8.5	5.3	7.4	3.2	6.1 ± 1.2	
Plankton Predators	0.1	0.3	1.9	0.9	0.8 ± 0.4	
Browsers	1.0	0.3	1.0	1.0	0.8 ± 0.2	
Benthic Predators	0.1	0.2	0.1	0.4	0.2 ± 0.07	
Swimming Predators	0.5	0.1	0.4	0.4	0.3 ± 0.13	
Total Producers	84.1	40.7	70.6	85.9	70.3 ± 10.14	
Primary Consumers	9.5	5.6	8.4	4.2	7.0 ± 1.07	
Secondary Consumers	0.7	0.6	2.4	1.7	1.3 ± 0.43	
Total Consumers	10.2	6.2	10.8	5.9	8.3 ± 1.22	

The extreme annual variation observed in the seasonal food-group diagram (Fig. 5, p. 662) is also very apparent in these annual productivity values. Nannoplankters are the least variable of the food groups, while the plankton predators are the most variable. When the producers, primary consumers and secondary consumers are totaled separately, the annual productivity is more constant. This decrease in variability suggests a certain amount of "compensation," or transfer of function from one food group to another, within these larger categories.

The efficiency of food conversion from one consumer group to another may be evaluated by comparing the amount of food ingested with the resultant amount of growth. This experimental method, which has been applied to very few organisms, gives conversion factors varying according to stage of development, environmental conditions, etc. The growth efficiency of fishes under laboratory conditions is reported as 43.5% (Moore, 1941), 30% (Detwiler, 1930) and 13% (Dawes, 1931). Under field conditions the reported efficiency ratios of fishes, as would be expected, are much lower: 6% (Bajkov, 1932) and 5.5% (Peterson, 1918). Lundbeck (1926) calculated a rough conversion ratio of 13-14% for *Chironomus* larvae. Juday (1940) has used 20% as an arbitrary physiological efficiency ratio for all animals. The theoretical aspects of apparent and true food-group efficiencies for Cedar Bog Lake will be discussed in detail in a forthcoming paper.

The relative productivities of food groups under natural conditions reflect the physiological efficiency ratios only when food is the sole limiting factor in natural populations. Since food is seldom the only limiting factor, the production-ratios between food groups under natural conditions provide at best only crude indices of actual efficiency. As was previously mentioned, food groups are rather arbitrarily delimited: all the organisms of one group need not be completely dependent upon the food group with which that group is compared; a certain excess of food must always remain unconsumed, in conformity with the principle of Le Chatelier; furthermore, in such a broad unit as predators, for example, may exist many internal predator-prey relationships. Efficiency ratios based on natural populations should not, therefore, be taken too literally. Table 5, which gives various food group ratios for Cedar Bog

TABLE 5.—Percentage Ratios of Food Groups in Cedar Bog Lake, calculated from data of Table 4.

	1937	1938	1939	1940	Mean*
Zooplankters/Nannoplankters	43.4	25.6	43.4	32.3	37.0
Plankton Predators/Zooplankters	1.2	5.5	25.6	28.8	13.4
Plankton Predators/Net Plankters	1.0	2.0	7.2	9.4	5.6
Benthic Predators/Browsers	10.0	67.6	10.0	40.0	25.0
Browsers/Producers	1.2	7.4	1.4	1.2	1.1
Benthic Predators/Producers	0.1	0.5	0.1	0.6	0.3
Swimming Predators/Producers	0.7	0.3	0.6	0.6	0.5
Primary Consumers/Producers	11.3	13.8	11.9	4.9	9.6
Secondary Consumers/Producers	0.8	1.1	3.4	2.0	1.8
Secondary Consumers/Primary Consumers	6.7	10.8	28.6	40.0	18.5

* The figures in this column represent the ratios between the mean values given in Table 4, rather than the means of the ratios shown in this table.

Lake, shows such extreme annual variation that the mean ratios must be interpreted with considerable regard for their deviations.

The very high ratio between nannoplankters and zooplankters is understandable in view of the ability of zooplankters to feed upon floating organic particles as well as nannoplankters. The ratio of *Chaoborus* larvae (plankton predators) to net plankters appears to remain low; re-examination of Fig. 5 p. 662), however, indicates that during certain seasons the ratio is much higher. The ratio between benthic predators and browsers for 1938 and 1940 appears to indicate a sub-minimal food supply for the former; it is quite probable that food-substitution (browsing?) may have considerably alleviated such a condition.

The relation between consumer and producer groups is very interesting. Both browsers and zooplankters are here considered as primary consumers, neglecting for the sake of simplicity the intermediate action of bacteria on those foods consumed as ooze. During three of the four years studied, the annual ratio of primary consumers to producers was 11.3-13.8%, values remarkably similar to that given by Lundbeck (1926) for the theoretical efficiency of *Chironomus* larvae. The major component of this primary consumer group, however, consists of zooplankters which at least after death may be consumed by the ooze browsers. The considerably lower ratio of browsers to producers (1.1%) gives an indication of the relative efficiency of "saprophy" in Cedar Bog Lake.

The ratio of secondary to primary consumers gives a mean value of 18.5%, approximately the value (20%) assumed for the physiological efficiency of all animals by Juday. It will be observed that during 1939 and 1940, the ratio was well above this mean; during these years, however, the predator population consisted to a large degree of *Chaoborus* larvae, which, as we have already mentioned, appear to have been at least partly herbivorous. The well known ability of predators to vary their food habits under force of circumstance makes most hazardous the determination of "starvation thresholds" from

natural productivity data. Such data do have value, however, both in indicating the variations found between related food groups and in broadly defining the dimensions of the Eltonian Pyramid for the particular community concerned.

ACKNOWLEDGMENTS

The author wishes to express grateful acknowledgments to the many persons who have aided at various times in the furtherance of this study. Dr. Samuel Eddy, at whose suggestion this problem was undertaken, has given most valuable counsel and encouragement. The author is indebted to Drs. Chancey Juday, G. E. Hutchinson, E. S. Deevey, Jr., and A. C. Hodson for comments and helpful criticisms of the manuscript. Drs. John B. Moyle and G. W. Prescott kindly verified identification of the pondweeds and certain phytoplankters, respectively. Several colleagues have assisted at various times in the field work, especially Dr. W. C. Moore, Dr. C. B. Reif, Mr. J. N. Wilson, Mr. L. E. Hiner and Mrs. J. B. Moyle. To Dr. and Mrs. A. D. Corneia and Dr. and Mrs. W. H. Crone, owners of tracts adjacent to the lake, the author is grateful for hearty cooperation and generous hospitality. Most important acknowledgment, however, is due my wife, Eleanor Hall Lindeman, who has cooperated during the entire course of this study with painstaking field work, with tedious laboratory manipulations, and with the preparation of this manuscript, all with stimulating comradeship and kindred zeal.

Summary

1. Cedar Bog Lake, which has been the subject of a four-year study in dynamic ecology, represents a late stage of eutrophic senescence.
2. A generalized diagram of food-cycle relationships is presented: the autotrophic plants, free-floating and attached, are the producers of organic substance; numerous animal groups play intricate, inter-related roles as primary, secondary, tertiary, etc., consumers of this organic substance; heterotrophic bacteria act as decomposers of organic substance and, from another point of view, as regenerators of essential plant nutrients, which again contribute to the synthesis of organic substance.
3. The biotic inter-relationships of the various consumer groups, particularly the browsers, benthic predators and swimming predators, are discussed in some detail.
4. The quantitative seasonal distribution of food groups showed remarkable variation from year to year. These annual variations seemed to be correlated at least in part with marked fluctuations in water level and in chemical composition of the water. Prolonged winter anaerobiosis often completely destroyed the swimming predators and decimated the numbers in other food groups.
5. Climatic variations, resulting in water level changes, winter anaerobiosis, etc., played an important role in the annual productivity of this senescent lake.
6. Limited predator-prey dynamics were suggested in the population ratio of zooplankters to nannoplankters and of *Chaoborus* larvae to net plankters

(Fig. 5). Plankton predators were relatively the most variable of the food groups with respect to annual production, while nannoplankters were relatively the least variable.

7. The mean annual ratios of producers to primary consumers to secondary consumers (including the small swimming predators found in the lake) were: 70.3:7.0:1.3 cal/cm². Annual variation was relatively greatest for the secondary consumers and least for the producers.

8. The relative annual production of the food groups, as might be anticipated on theoretical grounds, indicates an efficiency of food conversion much lower than the probable physiological efficiency ratios of the species. Only occasionally did the factor of food supply appear to limit the production of a food group.

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