SYMPOSIUM ON ECOLOGY OF THE CLADOCERA

[*Editor's Note.* At the 86th Annual Meeting of the American Microscopical Society, held in Bloomington, Indiana, a "Symposium on the Ecology of the Cladocera" was presented over a period of three days, 24–26 August 1970. Under the able leadership of Dr. David G. Frey, Vice-President and Program Officer of the Society, all four sessions of the symposium were well attended and judged to be highly successful by audience and participants alike. We are pleased to publish here, following a short introduction by Dr. Frey, abstracts of the 18 papers presented at the symposium. In some respects these preliminary reports or reviews of specific research projects are more than "typical abstracts," and we have allowed the authors considerable liberty—with respect to length, inclusion of selected references, etc., etc. Readers interested in more details, in information as to probable location of related full reports, etc. should send such inquiries directly to the symposium speakers, whose addresses are included in full with their abstracts.]

Recent years have seen great expansion in our knowledge of the Cladocera—their overall role in limnetic and littoral communities, their functional morphology especially with respect to food getting, the dynamics of filter feeding, greater precision in their taxonomic discrimination and zoogeography, possible environmental controls in the alteration of parthenogenesis and gamogenesis and especially the influence of photoperiod, the significance of cyclomorphosis, the role of predation in controlling the species composition and size distribution of communities, new looks at diel migration and its significance, new insight into the origin of the Cladocera and trends in their evolution, response of cladoceran communities to seasonal and long-term environmental changes including those resulting from man's activities, etc.

An organizational meeting of persons concerned with Cladocera who were attending the 16th Congress of the International Association of Limnology in Warsaw, Poland, in 1965, disclosed great activity and interest in these organisms and a desire to coordinate research programs. The present symposium, which represents the first major sequel to that Congress, brought together some of the active scientists in the field, including a number of persons from abroad, both among participants and audience. Greater participation from abroad would have been welcome, but regretfully no funds were available to make this a truly international symposium.

To help remedy this deficiency, the participants were encouraged to submit expanded abstracts of their papers, with citations to a few major references if much of the work reported on had already been published. The abstracts are arranged in the same order as listed in the program to preserve any coherence in subject-matter grouping. The first four were presented on the afternoon of 24 August; five through eight on the morning, and nine through thirteen on the afternoon, of 25 August; and fourteen through eighteen on the morning of 26 August. The chairmen of the sessions were David G. Frey (Indiana University), Richard A. Parker (Washington State University), Kenneth B. Armitage (University of Kansas), and John P. Harding (British Museum of Natural History), respectively. The Program Chairman and the American Microscopical Society wish to thank all participants and a faithful audience for a highly interesting series of meetings.

—David G. Frey

GRAZING RATE OF CLADOCERA

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In order to gain insight into the relationship between phytoplankton and zooplankton, and to evaluate the role of different particles in the nutrition of zooplankton, we need information on the feeding behavior and rate of these animals. Either the differential cell-count or the radioactive tracer technique gives a good measure of feeding rate, provided it is applied with suitable precautions.

Laboratory studies have shown that the feeding rate of Cladocera is a function of concentration of food, size of animal, temperature, physiological condition of the animals, and occasionally of the species of alga provided as food. Cladocerans appear to gather small particles (1–5 μ) more efficiently than calanoids, and also have higher average filtering rates.

Filtering rates of Cladocera under natural conditions are frequently much lower than predicted by laboratory studies. At times, this is because the food supply is above the incipient limiting level.

A method of measuring the natural grazing rate of the entire zooplankton community on particles between 1 and 12 μ in diameter has been developed by J. F. Haney. He showed that the average grazing coefficients (fraction of cells consumed per day) in a eutrophic lake ranged from 0.05 in winter to 0.8 in summer with brief periods as high as 3. In this lake Cladocera were the dominant grazers with *Daphnia* species responsible for 90% of the grazing pressure, except in mid-summer when *Ceriodaphnia* was abundant. Comparisons between grazing coefficients and published values for renewal coefficients of algae in lakes of different trophic status suggested that, except during brief periods of intensive grazing, the summer biomass of nannoplankton is not appreciably reduced by zooplankton. However, it was suggested that grazing by zooplankton might be responsible for the decreasing ratio of nannoplankton biomass to net phytoplankton biomass observed in series of lakes ranging from extreme oligotrophy to extreme eutrophy.

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ENERGY RELATIONS IN CLADOCERAN POPULATIONS

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Presently, the most profitable descriptions of fresh-water ecosystem structure and function are formulated in terms of energy transformation and nutrient cycling. Budget components (Fig. 1) are required for natural populations. Primary attention has been focused on assimilation (literature efficiency values ranging

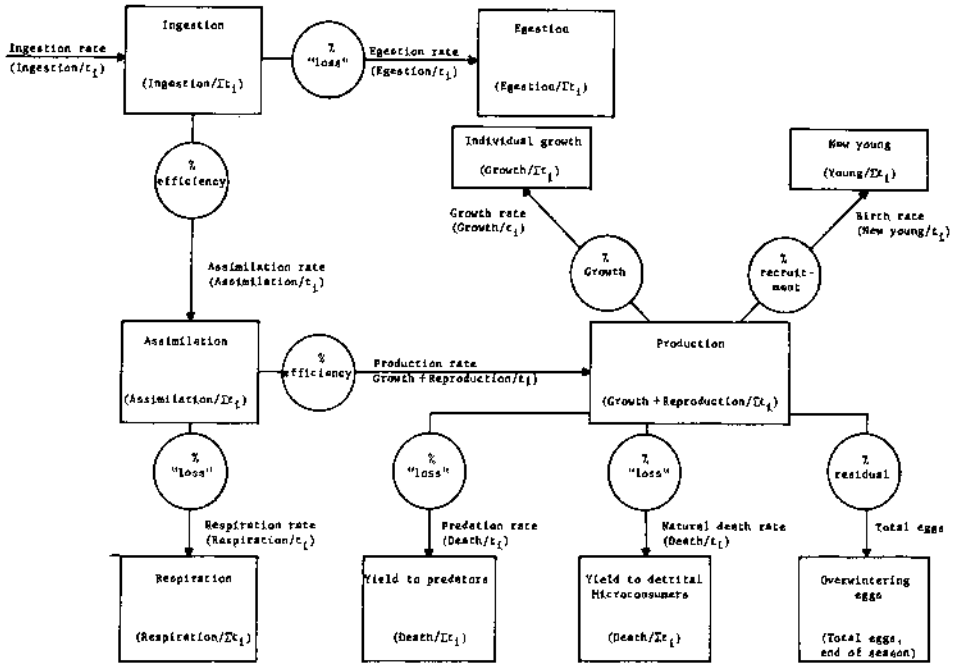

FIG. 1. Energy budget components for a cladoceran population. Rates are for time intervals t; compartments are the rates summed for the entire season. Efficiencies and proportions are calculated as %.

from 20–90%) or the production component of assimilation (literature values ranging from 10–70%). Assimilation and production efficiency estimates depend on the accuracy with which the respectively much larger components, ingestion and respiration, are measured.

In our studies of cladoceran energetics, particularly *Leptodora kindtii*, primary effort was directed toward respiration and production measurements. When both were measured with great care, respiration was 90% of assimilation over two seasons. It proved extremely important to partition natural populations into young and mature (egg-bearing) individuals and by sex when males appeared, since these segments were distinctly different physiologically, behaviorally, and ecologically.

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FUNCTIONAL MORPHOLOGY AND NICHE SPECIFICITY IN CHYDORID AND MACROTHRICID CLADOCERANS

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Considering the very obvious structural diversity exhibited by anomopod cladocerans, ecologists have shown an amazing disregard for functional morphology when seeking to define those features which restrict individual species to particular niches. At the purely mechanical level anomopods are extremely complex machines; and, as many of these machines are very different, they might be expected to operate in different ways—as indeed they do.

One would hardly expect a man-made machine designed to sift particles from mud to be efficient at scraping material from surfaces to which they are firmly attached, at tearing and manipulating large chunks of fibrous, plastic-coated material, or at sieving minute particles from suspension; yet in ignoring the construction of anomopods, ecologists have evidently entertained such expectations. On the other hand they have devoted much time to the study of factors, the variation of which, while easily measured, is often of scant significance to the animal. The latter approach is rather like trying to decide why a bulldozer is employed in different places and performs different functions from a pneumatic drill by studying the grade of lubricating oil that is used by each. Just as many machines can tolerate a variety of lubricating oils, so can many anomopods tolerate considerable variation of factors such as temperature, pH, and the content of various salts in the water. That such variables play a part in determining the geographical and ecological distribution of anomopods is not denied—some species are confined to the tropics, others are arctic, and the presence or absence of plants frequented by certain species may be determined by physical and chemical factors—but in many cases what is more important is the presence of material on which the machinery can be used. Apparatus that is designed for sweeping particles from the leaves of plants may in some cases be used in appropriate situations almost anywhere in the world, but is useless for life on rocky, sandy, or muddy bottoms. For example, the many complex and interrelated morphological specializations of the chydorid *Graptoleberis testudinaria* enable it to feed as it glides, snail-like, over the surfaces of leaves, in climates as different as those of Greenland and tropical Africa, yet are such as to preclude it from performing these feats on the mud surface from which the plant protrudes. Another extremely clear-cut case of morphologically determined niche-specificity is that of species of *Anchistropus* whose whole anatomy is directed towards life on hydra, for protection against the nematocysts of which they show numerous specializations, and from whose body they tear their food.

Even closely related species may differ in ways which enable them to perform very different feats and thereby occupy different niches. *Alonella exigua* and *A. excisa* provide an example of this. *A. exigua* has morphological specializations that enable it to crawl inverted beneath floating leaves and thus occupy a niche that is inaccessible to its near relative *A. excisa*, which lacks these specializations and hence this ability. Similar examples are provided by the genus *Chydorus*.

Some of the specializations recently elucidated have been such as to permit not only the demonstration of precise niches but to show that the animals that occupy them have hitherto been assigned to the wrong genus. Thus *Disparalona rostrata*, which is specialized for filtering particles by a method which is prob-

ably unique within the Chydoridae, has no place in the genera *Rhynchotalona* or *Alonella* to which it has at different times been assigned. Likewise *Pseudochydorus globosus*, which is specialized for the seizure and manipulation of the dead bodies of other small crustaceans, shows only convergent similarity to the genus *Chydorus* to which it is only distantly related.

Similar correlations are emerging for macrothricids on which work is now proceeding.

Intriguing problems remain. For example, while the functional morphology and ecology of many species of *Alona* are gradually becoming known, in many cases it is still difficult to define with any precision the niches of particular species. The difficulty is compounded by the taxonomic problems that still remain, and this group provides ideal material for coordinated studies on taxonomy, functional morphology, ecology, and geographical distribution. Problems of a different kind are presented by a species like *Chydorus sphaericus*, which is extremely widespread and is capable of exploiting a wide range of environmental conditions. In the case of *Alona*, it seems that a particular body form has proved eminently suitable for life in a variety of rather similar situations. Here adaptive radiation (as indicated by the large number of species in the genus) has evidently taken place in subtle ways whose significance may be less easy to elucidate than that of some of the extremely complex specializations exhibited by members of the smaller, and not infrequently monotypic, genera.

NICHE SPECIFICITY OF LITTORAL CLADOCERA: HABITAT

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Encouraged by earlier findings in Minnesota (Quade, 1969), the relationship of littoral Cladocera abundance and community composition to sediment, depth, and aquatic plants was examined in Northeast Indiana.

Collections of Cladocera taken from the sediment along ten transects within the littoral zone in a single lake demonstrated an inverse relation between abundance of Cladocera and the diversity and biomass of plants. Samples from the 0–2 m depth zone accounted for 54% of the animals collected, those from 2–6.5 m accounted for only 14%, and samples from 6.5–9 m depth for 31%. The shallow zone in the ten transects was represented by *Chara*, *Nymphaea odorata*, and *Nuphar variegatum*; the middle zone was characterized by a diverse floral assemblage of *Potamogetons*, *Vallisneria americana*, *Elodea canadensis*, *Myriophyllum exalbescens*, and *Naias flexilis*; the deep zone was characterized by *Nitella*, *Ceratophyllum demersum*, and open areas. *Chydorus sphaericus* was dominant in the sediments of the first zone, while *Alonella excisa* and *Ceriodaphnia quadrangularis* were dominant in the middle and deep zones, respectively. Those transects with a border of *Nuphar* and *Nymphaea* and a deep *Ceratophyllum* zone had the highest counts. Within these transects there is little plant substrate, supporting the contention that Cladocera are in the sediment habitat as a substitute for a more preferred plant habitat.

To determine whether or not there was a corresponding plant-sediment relationship, an examination was made of proximate chemistry and grain size along an annual transect. Plants lived in the winter down to two-thirds their summer depth distribution although they showed a decline from 14 species to 4. The

lack of heavy snow cover and relatively thin ice accounts for the capacity of plants to maintain themselves year-round. On an annual basis in time and space the proximate chemistry within the 0.5–7 m depth zone showed a remarkable similarity, as did the grain-size distribution from 0.3–7 m. This was the zone of continuous annual plant occurrence. Regardless of the plant species the associated sediment within these zones showed no differences in proximate chemistry and grain size distributions over the year.

Bagged plant collections of constant area made during July, the month of maximum plant biomass and diversity, were examined to determine the relation of cladoceran abundance to plant dry weight and to depth. As much as a five-fold increase in dry weight of a plant species did not cause an increase in cladoceran abundance. An application of Jaccard's "Coefficient of Community," as well as "Percent Similarity" demonstrated that not only total abundance but also community similarity was not directly related to depth either inter-specifically or intra-specifically with regard to the flora and its associated Cladocera populations.

Very close similarity was seen in the plant preference of individual cladoceran species to the results found in Minnesota. As in Minnesota, the Indiana collections showed that the highest number of Cladocera species were found on *Ceratophyllum demersum* followed by *Chara* and the broad-leaved Potamogetons.

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THE EVOLUTIONARY EFFECTS OF PREDATION

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The evolutionary effects of predation on planktonic Cladocera can only be inferred from the nature of the predation to which the species are now subject. This statement assumes that the long-sustained predation has had approximately the same characteristics as that now observable. Most species of fresh-water planktivorous fish appear to select only certain categories of zooplankters, Cladocera being favorite prey. Within categories, size is the critical determinant of predator interest (Brooks, 1968).

This paper considers only the polymorphisms of *Daphnia* and *Ceriodaphnia* to predation. It suggests that dimorphism (to use the simplest case) is an adaptation to a persistent pattern of the intensity of predation, with one morph having greater survival value in situations with little predation, the other in situations with intense predation. For the relationship between anti-predation adaptions and feeding efficiency in Cladocera, consult Brooks & Dodson (1965).

The predation patterns can be spatial or temporal. The dimorphism that persists where the intensity of predation has a spatial pattern is less complex than that associated with a temporal (seasonal) pattern. Two instances of dimorphic Cladocera in tropical lakes have been clearly related to spatial patterns of predation. The ecology of *Daphnia lumholzi* in Lake Albert of equatorial Africa has been studied by Green (1967), that of *Ceriodaphnia cornuta* by Zaret (1969).

One morph of *D. lumholzi* has a large spine on the anterior margin of its head, a lateral on each fornix. The un-spined morph is larger and more robust at the onset of nature than is the spined. In the extensive central portion of the lake the larger, un-spined morph predominates, the spined morph being extremely rare. The smaller, spined morph is much the more abundant inshore, wherever the water is less than 20 m deep. The only planktivorous fish of Lake Albert preying significantly upon *Daphnia* is the characin, *Alestes baremose*, and it occurs only in water shallower than 20 m. Stomach contents demonstrated that *Alestes* selects the much rarer un-spined individuals from the mixture of morphs in the inshore waters, only very rarely taking the much commoner but slightly smaller spined morph.

The "horned" morph of *Ceriodaphnia cornuta* in Gatun Lake, Panama, resembles a minature spined *D. lumholzi*, but is only about a third the length (ca. 0.35 mm at maturity). Zaret showed that the unhorned morph is the same size at the onset of maturity, but has a much larger compound eye making this morph more visible to the vertebrate eye. In Gatun Lake, predation on *Ceriodaphnia* by a small atherinid fish is much more intense inshore, where the horned morph is the more abundant. Zaret is continuing his study of this dimorphism.

In lakes of the north temperate zone many species of *Daphnia* exhibit remarkable seasonal difference in shape and in the size of the visible body at the onset of maturity. The mid-summer morphs are visibly smaller at maturity and they possess large, streamlined transparent outgrowths of the head, the helmet. The intensity of fish predation in most temperate lakes is highest at just this time (high temperatures, long twilights, and many young fishes). It has been suggested (Brooks, 1965) that the size–shape differences are environmentally determined. The smaller, helmetted *Daphnia* are subject to less predator interest at least through the first few mature instars.

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PREDATOR–PREY RELATIONSHIPS BETWEEN YELLOW PERCH AND *DAPHNIA* IN A LARGE TEMPERATE LAKE

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A four year study of *Daphnia galeata* and *D. pulex* population dynamics in Oneida Lake, N. Y., reveals a consistent summer population decline. Whereas egg production also declined in summer, the net reproductive rate of the populations based on observed egg ratios and laboratory survival estimates at com-

parable temperatures never dropped below 1.0. Population size structure was skewed towards the young even though population densities declined in summer, suggesting a high adult mortality. *Daphnia* were never observed to be infected with fungal parasites, nor were corpses ever encountered among the thousands of individuals collected alive each summer.

A series of near-natural life table experiments were performed during the *Daphnia* decline to test various possible sources of mortality including increased water temperature, lack of food, or toxic bluegreen algae. Large adult (old) *Daphnia* from Oneida Lake were observed at three densities over two seven-day periods in one-half liter jars. Natural lake water was replaced daily. Survival was equivalent to optimal laboratory growth conditions. These adults produced eggs all of which developed to egg-producing adults within seven to ten days depending upon temperature. Again the net reproductive rate exceeded 1.0. These experiments would seem to eliminate the above suggested sources of mortality as valid hypotheses capable of accounting for the declining *Daphnia* populations.

Fish predation is implied from both the field data and life table studies as a likely factor causing the *Daphnia* decline. Extensive fisheries investigations on Oneida Lake by Dr. J. Forney, Cornell University, reveal yellow perch as the dominant fish. An obligate planktivore in early life, older perch appear to feed extensively on *Daphnia* in early summer. Stomach analyses reveal that large numbers of *Daphnia* are consumed by perch. Observations of temporal feeding activity, stomach evacuation rates, demersal stage perch densities, and number of consumed prey, carried out by Dr. Rich Noble, Cornell University, when coupled with the author's fish consumption data indicate that fish predation may be sufficient to explain the *rates* of *Daphnia* decline during the summer. This is the first known case where a dynamic, quantitative evaluation of the impact of fish predation on zooplankton has been applied.

Summer primiparous adult *Daphnia retrocurva* showed the greatest reduction in body length when compared to June individuals. This species never disappeared during the summer. *Daphnia galeata mendotae* revealed a similar tendency but of a reduced magnitude. *Daphnia pulex* remained the same size and was the first species to disappear in the summer. Perch show strong size selectivity of prey which would account for the above sequence.

MEASUREMENTS OF ZOOPLANKTON PRODUCTION COMPATIBLE WITH ECOSYSTEM ANALYSIS

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A quality aquatic environment for our burgeoning population requires a reduction in the rate of cultural eutrophication. This may be accomplished either by reducing the amount of plant nutrients reaching our waters or by cropping the nuisance algae at a greater rate. The evaluation of aquatic communities subjected to such drastic manipulations as nutrient reduction must rely both upon a more complete understanding of resource allocation and spatial and temporal niche stratification within these communities, as well as upon the develop-

ment of new techniques permitting rapid in situ estimates of secondary production.

Recent studies of the limnetic zooplankton of Lake Michigan have provided striking evidence that potential competition is reduced more through habitat selection than resource allocation. We now realize that the vertical migrations of the Cladocera provide for temporal niche stratification, eliminating the enigma concerning the adaptive significance of these movements (Lane & McNaught, 1970). Several niche parameters have been measured for herbivores and carnivores through application of Levins' (1968) theory of the niche. Hopefully, such measures will have a predictive value, for trophic relationships have long been a problem in aquatic ecology.

Actuarial techniques have provided the most efficient measure of secondary production for the field ecologist, as demonstrated by Hall (1964) and others. Instantaneous birth rates of the limnetic Cladocera are closely related to the availability of food (Costa, 1967). But classic egg-ratio methods (Edmondson, 1965) are laborious and could be profitably replaced by methods for estimating birth rates in situ and in real-time. High-frequency sonar can be used to estimate the standing crop of zooplankton, as animal biomass is proportional to backscattering strength (McNaught, 1968). The use of a multi-frequency sounder should enable us to make estimates of biomass within five size classes, as this device is age-group selective (McNaught, 1969). Perfection of multi-frequency sounding will provide us with the capability of making estimates of birth and death rates of the limnetic Cladocera rapidly and over large expanses of water. Thus, for the first time we expect to be able to assess the effect of stimulatory or inhibitory perturbations upon the production of Cladocera.

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A PROBABILISTIC APPROACH TO THE DYNAMICS OF NATURAL POPULATIONS OF THE CHYDORIDAE

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This study had three objectives: description of annual changes in abundance and reproductive structure of natural chydorid populations, use of laboratory data to estimate rates of natural population processes, and probabilistic analysis from the basis of a simple birth rate model.

Chydorid populations were sampled in the littoral of Lawrence Lake, Barry Co., Michigan. The chydorids were counted and classified in six reproductive categories. Four species dominated: *Chydorus sphaericus*, *Acroperus harpae*, *Camptocercus* sp. cf. *rectirostris*, and *Graptoleberis testudinaria*. Populations of *Acroperus*, *Camptocercus*, and *Graptoleberis* appeared in April, stayed low during the summer, peaked in August, September, or October, and then dropped rapidly, disappearing in December. Populations of *C. sphaericus* peaked in March, dropped sharply to a low summer level, rose during the fall, and remained high through the winter. Young individuals formed 40–60% of all populations through most of the year. Ephippial females and males dominated the populations of *Camptocercus*, *Acroperus*, and *Graptoleberis* before their winter disappearance. Males and ephippial females of *C. sphaericus* appeared briefly in small numbers during early December.

Simple population models can give insight into processes of change. The familiar "egg-ratio method—one such model—is well adapted for field studies of chydorids. Its use requires knowing water temperatures and development times of chydorid eggs at these temperatures. Littoral temperature was monitored continuously with a recording thermistor. Egg development times for the four species were found in the laboratory at eight temperatures between 4 and 27 C. The rates of birth (b), observed change (r), and mortality (d) were calculated with slight changes in the usual way. Preliminary results show *C. sphaericus* with stable predicted birth rates, rising from low levels in late fall and spring to a plateau in July and August. The observed rates of change (r) were relatively stable and low from November through April, with negative values as the populations declined in May and October. During the summer months, (r) fluctuated violently from (+) to (−).

Given a population's size and reproductive potential, one may ask two probabilistic questions of importance: what is the most expected size at some later time, and what is the probability of the size actually observed at that later time. From the data collected above, one knows the time between samplings (t), the egg development time (D) during that interval, the number of eggs (E) in the population at the initial observation, and the increase (X) in the population size. If (t) is short so that no initially immature female will reproduce during the interval, and if one assumes that (E) is constant during (t), then when (t) equals (D), (X) will equal (E). If one also assumes a random, uniform distribution of egg ages, then (t/D) is the probability that a given egg will hatch at time (t), with (t) less than (D). The probability of finding (X) out of (E) eggs hatching at (t) out of (D) time can be found with the standard binomial distribution formula:

$$P(X; E, t/D) = (E/X)\ (t/D)^X\ (1 - t/D)^{E-X}.$$

When (t) is larger than (D), some straight-forward arithmetic is needed to find (t) and (X). For *C. sphaericus* the probabilities of the observed increases are relatively large from late fall to early spring, and during the summer are mostly zero, because of decrease or insufficient increase in population size.

SEASONAL POPULATIONS, PREDATION, AND DIVERSITY IN THE CHYDORID TAXOCENE

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Seasonal changes in species abundances of chydorid Cladocera were analyzed to determine if abundance of individual species changed as species diversity of the fauna increased. Total populations living in the littoral sediments of Lake Lacawac, Pennsylvania, at three sites were found to increase in the spring after the ice went out. Three species, *Chydorus piger*, *Rhynchotalona falcata*, and *Chydorus sphaericus* were dominant, depending on the area of study. These three species decreased precipitously in the late spring with no concordant increase by other species, as would be expected when competitive exclusion occurs. The chydorid populations again increased in the late summer, but then three species of *Alona*: *A. affinis*, *A. intermedia*, and *A. rustica*, were dominant, with several other species subdominant (the spring populations were almost without subdominants). Diversity increased in the late spring as the populations declined and decreased slightly in the late summer with the fall population maximum.

After testing different hypotheses, it was concluded that predation by benthic invertebrates, particularly tanypodine midges, was the major factor causing the late spring population crash of chydorids living in the sediments. The populations increased in the late summer as the midges pupated or were in turn prey of fish.

The increase in diversity coincided with the population decline and thus demonstrates that predation, as Brooks and Paine have suggested, can be a major regulator of species diversity. However, this effect is only short term for after the predators leave the system, prey populations increase quickly and diversity is reduced.

PHOTOPERIODISM AND DIAPAUSE IN *DAPHNIA*: A STRATEGY FOR ALL SEASONS

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Development in the *Daphnia* embryo may be continuous or interrupted with a diapause in an early stage. In *D. pulex* Leydig the reproductive switch leading to the diapause expresses itself in a variety of seasonal cycles. In the dicycle the population may enter the embryonic diapause in the long day-lengths of late

spring and the short day-lengths of autumn. Although the day-length stimulus may control both onset and termination (Stross, 1969b, 1970; Stross & Hill, 1968), other stimuli and genotypic differences are required to explain the variety of seasonal patterns in the field.

Day-length or photoperiod may be shown to be the master stimulus. In the laboratory, cultures of three commonly recognized seasonal patterns respond to an inductively short photoperiod. Removed from lakes at 42°–45° N, the critical photoperiod is 13 hours of light per day. The embryonic stage of the mother is the most sensitive to the photoperiod stimulus. Latitudinal adjustment in critical photoperiod is shown by comparison with a related species, *D. middendorffiana*, which at 71° N has a critical photoperiod of 22 hours of light per day at constant temperature (Stross, 1969a).

Environmental control of the variety of seasonal patterns of diapause expressed by *D. pulex* involve both a facultative response to photoperiod and a temperature determined sensitivity to the photoperiod stimulus. The so-called acyclic strains where an embryonic diapause is omitted definitely require a second or mediating stimulus in conjunction with an inductively short photoperiod. In short day-lengths, the incidence of diapausing embryos is directly proportional to the density of culture.

The range in sensitivity to the density mediating stimulus is large. In a clone of an acyclic strain, threshold density may be approximately 175 individuals per liter. In a clone of a dicyclic strain, only diapausing embryos are produced at the minimum test density of 50 individuals per liter. The involvement of a density related stimulus in the dicycle may be demonstrated, however.

Expression of the dicycle involves temperature and a density stimulus, both of which influence photoperiod control of diapause. At 12 C one female per container (50 per liter) is sufficient to provide a standard response curve to photoperiod (Stross, 1969b). At 19 C, one female per container results in only non-diapausing embryos being produced. However, when the density is increased to two or more, most of the embryos enter diapause in long day-lengths and virtually all do so in short day-lengths.

A temperature influence may also be observed in the arctic where a daily oscillation in temperature could override the continuous light of the arctic summer resulting in a reproductive shift in the field that would not be predicted on the basis of experiments in the laboratory at a constant temperature (Stross, 1969a).

The facultative nature of photoperiod control is also observed in studies of diapause termination (Stross, 1970). Embryonic development in the *Daphnia* embryo may be reactivated following exposure to a single long-day photoperiod or its skeleton equivalent. When elevated CO_2 tensions are employed to sensitize the embryo, the photoperiod control disappears. The interaction of CO_2 and light provide an opportunity for deducing basic features of photoperiodic control in *Daphnia*, however.

The diapause interval in *Daphnia*, as with other arthropods, contains both photo-refractory and photo-sensitive phases. Variation is observed in duration and environmental control of the refractory phase in various strains of *D. pulex*. All embryos collected from the field require low temperature and for different intervals, depending on cyclic type and latitude of collections.

Most of the study has been devoted to a supply house strain in which the refractory phase of diapause may be completed without a temperature depression. In this strain, four stages or states of refractoriness may be identified with manipulation of O_2 and CO_2 tensions prior to and with exposure to light.

The obligatory light requirement for reactivating embryonic development

may be present in most but not all strains of *Daphnia pulex*. The light requiring response is believed to be a part of the photoperiodic mechanism. In one strain there is evidence for two, not one, photo-inducible phases in each 24-hour rhythm. One of the light-sensitive phases requires light, the second may accept an alternative stimulus such as an elevated tension of carbon dioxide (Stross, 1970). Additional functions may be attributed to CO_2 when it assists in reactivation.

The subversion of the photoperiod dictum in some strains of *Daphnia* permits a deployment of ecological strategies that must be largely surmised with current knowledge. Apparently the complexity observed in the response to photoperiod represents adjustments to escape rather than to adopt day-length as the master stimulus. It may be more productive to ask how escape has been achieved rather than doubt the potential responsiveness of all Cladocera to photoperiod.

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NONPHOTOPERIODIC LIGHT RESPONSE OF *DAPHNIA*

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While light quality and quantity and darkness are known to affect some aspects of cladoceran biology, no known investigation has been concerned with a comprehensive study of light effects. Data reported on are for *Daphnia pulex*. Although obtained in the laboratory, they have significant implications for field populations and for studies done in the laboratory where field conditions are approximated. Since *D. pulex* is found in a wide range of aquatic habitats, light may be an important factor affecting its distribution and population dynamics.

The effects were studied of eight light intensities and darkness, polarized light, and four wavelength ranges on individual growth, molting, survival, oxygen consumption and filtering rate as a function of body size and acclimation, reproduction and energy budgets.

Light and darkness did not affect molting rate or survival. Growth was inhibited at 28 ft-c. The animals were largest in the dark but were not necessarily much larger than those raised in the light. Differences among regression coefficients and adjusted means for oxygen consumption and filtering rate varied with acclimation and size of the organism. The reproduction curves under 0, 7, and 14 ft-c did not decline rapidly after the initial peak. Under 3.5, 28, and 55 ft-c there were never prominent peaks. Populations 3.5 and 28 had the least young per brood. Populations 55 and 110 released more undeveloped young and nonviable eggs, and populations 3.5 and 14 released the least. Abortion rate was highest under 55 and 110 ft-c. The growth efficiency of pre-adults exceeded 50% under intensities less than 28 ft-c. The net efficiency of growth and reproduction

of adults exceeded 74% at intensities below 28 ft-c, being greatest under 1.7 and 14 ft-c. The ratio of respiration to growth and reproduction was less than 35% below 28 ft-c and was least under 1.7 ft-c. Because the efficiencies of growth and reproduction are highest and efficiencies of respiration are lowest under 1.7 and 14 ft-c, it is tempting to speculate on the adaptive significance of vertical migration where the organisms may move between two optimum zones of light intensity.

The effects of polarized light were generally inseparable from the effects of light intensity.

Growth was retarded under red wavelengths, and molting rate was accelerated under green wavelengths. Mortality rate was high under green wavelengths and under a portion of the visible spectrum. Generally, there were no effects of wavelength among the regression coefficients and adjusted means obtained for metabolism and filtering rate of acclimated and unacclimated animals; however, acclimation to their respective light conditions did result in some differences among regression coefficients and adjusted means. Reproduction peaked two to four days later than it did under the light intensities, and reproduction under violet and green wavelengths did not decline rapidly after the peak. Population red took longer to release the first brood. Population blue had the most young per brood. Wavelength did not affect abortion rate and production of nonviable eggs. The net efficiency of growth of preadults was lowest under the green wavelengths. Except for red wavelengths, the net efficiency of growth and reproduction exceeded 79%, and the ratio of respiration to growth and reproduction was 25% or less.

While the data presented are preliminary, they do indicate that light may be a very important factor in population success, and they also suggest that light should be more controlled in laboratory experiments.

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PLASTICITY OF CLADOCERAN VISUAL SYSTEMS TO ENVIRONMENTAL CHANGES[1]

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The limnetic Cladocera are especially responsive to light, both to changes in wavelength and total flux. Their vertical migrations, which result in temporal and spatial niche stratification (Lane & McNaught, 1970), are controlled exogenously by changes in intensity (McNaught & Hasler, 1964; Ringelberg, 1964) and the angular distribution of incident light (Ringelberg, 1964). Previous behavioral investigations (Heberdey, 1948; Smith & Baylor, 1953) had indicated the presence and possible function of a system for trichromatic vision. However, the sensi-

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tivity, plasticity and ecological significance of these visual systems had not been studied photochemically.

The photic environments of three species of Cladocera were determined in the field by first measuring their vertical distribution, and secondly the quality of light at corresponding depths. The collecting sites were selected to provide narrow photic environments in either the red or blue, as well as broad photic environments from blue through blue red. Difference spectra for these same species living in a number of selected photic environments were determined in the laboratory by modifying classical methods of extraction for use with these small crustaceans.

Photochemically the visual pigments of the Cladocera are very similar. Most species have four visual pigments, maximally sensitive at about 370, 430, 560, and 670 mm. Such spectral clustering may be explained by hypothesizing four discrete opsins (Dartnall, 1965). All pigments except those of *Eubosmina* are based on retinal$_2$. Different species of the genus *Daphnia* can be separated on the basis of the absorption maxima of their visual pigments.

Ecologically these four pigments, sensitive to ultraviolet, blue, yellow, and red light, all occur in cladocerans collected from broad photic environments. In looking at variations in sensitivity, we realized that eutrophication leads to more reddish photic environments, whereas oligotrophic lakes have extremely narrow blue photic environments at great depth. In the most extreme cases, *Daphnia* from very bluish environments have lost their red receptor. Typically, *Daphnia* living in both bluish and reddish environments exhibited a shift in the absorption maxima of the pigments towards the red when living in eutrophic lakes. Differences were significant at the 95% level.

When *Daphnia schodleri* was grown under blue light, the red-sensitive pigment was not produced after a period of 44 days. When the same cultures were then returned to white light, production of this pigment reached former levels after 90 days. Thus this cladoceran showed considerable plasticity in a rapidly changing photic environment.

We conclude that the Cladocera are capable of rapidly adapting to changes in their photic environment, and that such changes are inevitable during eutrophication. Such plasticity is required in their visual systems, since vision is basic to undertaking vertical migrations, which in turn are involved in the important adaptive strategies and niche relationships of these crustaceans.

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PIGMENTS IN CLADOCERA

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The cladoceran pigments that have been studied in greatest detail are the hemoglobins (Fox, 1955) and carotenoids (Green, 1966). Hemoglobin is known from most genera of fresh-water Cladocera, except *Leptodora*. The amount of hemoglobin in the blood varies inversely with the oxygen content of the habitat. There are specific and clonal differences in ability to synthesize hemoglobin in response to oxygen deficit. The amount of hemoglobin in the blood of a female cladoceran also varies during the course of an intermoult cycle, as the pigment is passed into the eggs. Hemoglobin can be broken down in the fat cells (Green, 1955), but this process does not produce bile pigments. The only bile pigment known in the Cladocera is the biliverdin in the eye of *Polyphemus pediculus* (Green, 1961).

The carotenoids in Cladocera are derived from those present in the food. The plant pigments are oxidized to form canthaxanthin and astaxanthin. Carotenoids are found in many different cladoceran tissues, and are passed into the eggs. An intermoult cycle in fat cells and blood can be demonstrated, and there are seasonal cycles of pigmentation in some tissues. The amount of carotenoid stored in the tissues varies with the amount of light received by the cladoceran, both within one species under experimental conditions and between species under field conditions. For instance, *Sida crystallina* living in the shade of aquatic plants contains much less carotenoid than *Scapholeberis mucronata* which swims at the surface in open water.

Cladocera may also be colored by infection with pigmented bacteria. *Spirobacillus cienkowskii* has been found infecting several species of Cladocera, and the final stages of infection lead to a brilliant red coloration of the host. The pigment is a carotenoid produced by the bacteria (Green, 1959).

Other pigments known from Cladocera are the ommochromes in the eyes, and a tanned protein which appears in patches at abnormally high pH values in the habitat. The dark pigments of *Scapholeberis* have not been studied, but their distribution suggests that they have a protective function against sunlight. A similar explanation is offered for the dark carapace pigmentation of *Chydorus sphaericus* at high altitudes and *Daphnia middendorffiana* at high latitudes.

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GENETIC STABILITY IN THE CLADOCERA

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The gamogenetic cycle of chydorid Cladocera has been induced and completed in the laboratory by proper manipulation of photoperiod (Shan & Frey, 1968; Shan, 1969, 1970). Interpopulational crosses between allopatric stocks of *Pleuroxus denticulatus* from Florida and Minnesota and sympatric stocks of *Pleuroxus procurvus* and *P. denticulatus* from Minnesota have been induced by the pairing method and mixing method, respectively. The pairing method was carried out in small depression slides containing filtered lake water and small pieces of algal mat as food. One ephippial female and one male were placed together in such a depression. The mixing method involved a mixed population of two closely related but morphologically distinct species, which was started by placing one parthenogenetic female of each species in the same chamber.

Of the 11 hybrid progeny from the crosses of allopatric *P. denticulatus* stocks, none lived beyond the third instar, and none exhibited any gonadal development. Hence, they were parthenogenetically sterile. Reciprocal crosses were attempted, but none succeeded.

One inter-species hybrid was obtained from the mixed cultures of sympatric *Pleuroxus* species from Minnesota. The female that developed from the ephippial egg developed a population by parthenogenesis, which was intermediate between the two parental populations with respect to the morphology of the rostrum and the number of denticles on the posterior margin of the carapace. The hybrid population demonstrated no tendency to recover the two parental types over a number of parthenogenetic generations, demonstrating that gene segregation does not occur during diploid parthenogenesis in these cladocerans, even though it has been claimed by Bacci et al. (1961) to occur via endomeiosis in a population of *Daphnia pulex*. The hybrid population produced both gamogenetic females and males, which were used in crossing experiments in all possible combinations. The gamogenetic females could copulate freely with hybrid males and males of the two parental species but did not produce any viable ephippial eggs. Copulation between hybrid males and gamogenetic females of the parental species likewise did not result in any ephippial eggs, suggesting that the males are sterile. This result agrees with Agar's (1920) experiment on hybridization between *Daphnia obtusa* and *Daphnia pulex*.

Interspecific hybridization between closely related species of Cladocera probably does occur in nature, but quite likely, at least in the chydorids, the hybrid is gamogenetically, or even parthenogenetically, sterile, and hence there can be no exchange of genetic material.

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THE CRUSTACEAN PLANKTON COMMUNITIES OF LAKES

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Sixty-two species of pelagic crustaceans were found in the summer plankton communities of seven Great Lakes and 257 smaller North American lakes, distributed from the Arctic Islands through the Canadian Shield and British Columbia to the Colorado Mountain and Plains. The species list comprises 29 species of cladocerans, 25 calanoids, and eight cyclopoids. The number of species in the communities of Great Lakes, ranging from five in Great Bear Lake to 23 in Lake Huron, was positively correlated with the depth of the lake and with the epilimnic water temperature. In these communities there were only two to four dominant species, i.e., those reaching more than 10% of the total number of individuals. The number of dominant species in a lake was unrelated to the total number of species in the lake. In the northern Great Bear and Great Slave Lakes, these dominant species were: *Limnocalanus macrurus* and *Diaptomus sicilis* and/or *D. ashlandi*. In lakes Winnipeg, Superior, and Huron *Diaptomus sicilis* and/or *D. ashlandi*, *Cyclops bicuspidatus thomasi* and/or *Cyclops vernalis* were the dominant species. In lakes Ontario and Erie, the dominants were *Cyclops bicuspidatus thomasi* and/or *Cyclops vernalis*, *Daphnia retrocurva* and/or *Bosmina longirostris*. From north to south a trend was apparent in the diminishing significance of calanoids and in the increasing role of cyclopoids and cladocerans. Based on a high percentage of species in common plus the same dominant species, the following lakes had the highest community similarity: Great Bear and Eastern Great Slave; Western Great Slave and Winnipeg; Superior and Huron; Huron, Erie, and Ontario.

The number of species in smaller lakes of a single lake region, ranging from one in high Arctic lakes to 32 in Manitoban lakes, increased proportionally to the length of the growing season (number of days with air temperature above 6 C). About 30 seems to be an asymptotic number of species of pelagic crustaceans in any one region. Based on Jaccard's community coefficient, which expresses the percentage of shared species by two lake regions, the Manitoban and Southern Ontario lakes showed the highest similarity, while British Columbia lakes had a very low similarity with all lakes east of the Rocky Mountains. Lakes of the MacKenzie Delta were more similar to Central Canadian Shield lakes than to lakes on the Arctic Islands. Within a single lake region, the number of species increased with the depth and area of the lakes. Both very low and very high concentrations of dissolved solids limited the number of species. Communities had one to five species as dominants, the most frequent numbers being two to three. Usually only one species within a genus was a dominant; however, situations were encountered, especially in deeper lakes, where two dominants of the same genus co-occurred.

With increasing eutrophication, changes at various levels of zooplankton organization could be seen. In Polish lakes a much bigger *Daphnia cucullata* was found in mesotrophic lakes than in oligotrophic and eutrophic ones. Various subspecies of *Bosmina coregoni* were characteristic of lakes with different trophic conditions. In the range from oligotrophic to eutrophic lakes, these subspecies can be arranged as follows: *B. c. longispina*, *gibbera*, *crassicornis*, *kessleri*, *coregoni*, and *thersites*. At the community level three principal changes occurred with change in trophy: disappearence of some species, appearance of others, and changes in the relative abundances of species.

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THE AMERICAN SPECIES OF *EUBOSMINA* SELIGO

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As most recent workers have recognized, the two "species" of *Bosmina* (*B. longirostris*, *B. coregoni*) listed by Brooks in the new edition of Ward & Whipple are the types of two clearly separable genera, *Bosmina* Baird and *Eubosmina* Seligo. *Bosmina longirostris* (O. F. Müller), nearly cosmopolitan, may be monotypic, but needs much more study before its numerous forms can be ranked. *Eubosmina* is represented in the Americas by at least four species, of which two, *E. coregoni* (Baird) and *E. longispina* (Leydid), are Holarctic, while two, *E. hagmanni* (Stingelin) and *E. tubicen* (Brehm), appear to be strictly neotropical. *E. coregoni* which lacks a mucro, has rarely been reported from North America, but now appears to be common in the Great Lakes. *E. longispina* with ventral incisures on the mucro, is familiar as a late- and post-glacial fossil in eastern U.S. and is the common bosminid today in northern New England and eastern Canada. The two American endemics, with dorsal incisures on the mucro, occur widely from Argentina to southern Canada, and can be extremely difficult to separate unless males are present. In typical summer populations, however, the female rostrum shows positive allometry in *E. hagmanni*, but negative allometry in *E. tubicen*; the mucro shows zero or weakly negative allometry in *E. hagmanni* but positive allometry in *E. tubicen*. One or both species were known to Birge, who recognized their distinctness from *E. longispina*, but applied the invalid name *B. obtusirostris* Sars; the "*B. hagmanni americana*" of Aurich was almost certainly *E. tubicen*. In no known locality do these two species occur together, but in a few New England and Canadian lakes, where *E. longispina* is present, populations that otherwise resemble *E. tubicen* show negative allometry of the mucro; these animals may constitute a fifth species, but males have not yet been found.

All American species of *Eubosmina* tend to be larger than *B. longirostris*, at least in winter. In a high proportion of lakes whose late-glacial history has been studied, *B. longirostris* either replaced or persisted long after one of the larger species, usuallly *E. longispina*. Of several possible explanations, the most interesting would be size-selective predation. In Rogers Lake, Connecticut, where *E. tubicen* and *E. longispina* both disappeared, leaving *B. longirostris* as the sole bosminid, there is circumstantial evidence that *Chaoborus* may have been the responsible predator.

EVOLUTIONARY TRENDS AND ADAPTATIONS OF CLADOCERA

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Permian and Jurassic daphniids and a Permian chydorid (*Propleuroxus freyi* Smirnov, 1970) are described from Transbailalia. Quaternary Cladocera have been studied from the sediments of East European lakes. In the latter, time differences are mainly changes in ratios of present-day species. In the search for "living fossils" seven endemic species (five in the new genus *Kozhowia* Vasil'yeva & Smirnov, 1969) have been found in Lake Baikal.

Quantitative distributional data have been published for present-day littoral Cladocera faunas of Lake Baikal (Vasil'yeva & Smirnov, 1969) and of the Cherepovets Reservoir on the Volga River. For some USSR inland water bodies numerical data on zooplankton have been collected for more than 20 years. These long series of data are being prepared for publication in the context of the International Biological Programme.

Attempts to review major groups of the Cladocera on a world-wide basis should be continued, the first such revision being that by Goulden (1968) on the Moinidae. The revision of Chydoridae of the world (Smirnov, in press) shows the number of species to be about 171.

Evolutionary trends leading to a decrease in size, and to the oligomerization of homologous structures are pointed out. The structure of the limbs of chydorids have been studied in detail. The data confirm the subfamilies described by Frey (1967) and contribute to the more precise delimitation of genera and species.

Thoracic limbs II–VI of Cladocera Anomopoda present an example of the plasticity of a metameric organ having the same basic structure. Homologous groups of setae can be identified and attempts have been made to elucidate their functions. Different morpho-functional types within the Chydoridae are defined on the basis of the structure and functional interrelations of the limbs.

The Chydoridae have constituted the main group studied, but the Macrothricidae (Baird, 1843) and Moinidae (Goulden, 1968) are now being added to the study program.

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ZOOGEOGRAPHY AND EVOLUTION

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Because of the ease of passive distribution by means of resting eggs and because a single female can initiate a new population, species of Cladocera are usually considered to have broad geographic ranges, encompassing at least major

portions of continents and often being intercontinental. This concept is partly illusory, because names proposed originally for populations occurring in Europe have often been applied rather carelessly to morphologically similar populations elsewhere without the necessary documentation to show that they do in fact belong to the same morphospecies. Males are essential in any such comparisons, but because reproduction is normally by parthenogenesis, males generally are lacking from collections unless specifically sought at appropriate times of the year or induced in laboratory cultures by manipulation of environmental conditions. For these reasons, literature records for many species are virtually useless in working out patterns of global distribution.

The broad outlines of the geographic distribution of chydorids are largely inadequately documented impressions at present. The species at high northern latitudes tend to be Holarctic in distribution, with little apparent morphological differentiation between North American and Eurasian populations. The species in middle northern latitudes likewise are mainly Holarctic in distribution, although there tends to be morphological differentiation at the subspecies level (e.g., *Alona rustica*), and there is at least one interesting pair of cognate species (*Anchistropus*) probably deriving from a longer period of genetic separation. In this region also there is a considerable number of species confined to one continent or the other, or even confined to a portion of a continent, as New England or Western Europe.

The Tropics are completely different, in that many of the species here are circumtropical. These push northward into the low or middle latitudes of both continents, especially North America. Only in South America is there any appreciable number of tropical species with restricted distributions.

In middle and high southern latitudes the species characteristic of middle northern latitudes tend to be dominant, sometimes as disjunct populations. And, as at comparable latitudes in the Northern Hemisphere, some species are restricted to single continents.

Endemic species and species flocks can occur in water bodies that have been in existence since the Tertiary, such as the chydorid genus *Kozhowia* in Lake Baikal (Vasil'yeva & Smirnov, 1969) and the flock of polyphemids in the Ponto-Caspian Basin (Mordukhay-Boltovskoy, 1965).

Evidence is accumulating from experimental crosses that even on a single continent a species tends to be broken down into smaller geographic populations with different ecologies although similar morphology. We also know that *Pleuroxus denticulatus* in North America consists of a pair of essentially allopatric cryptic species, almost identical morphologically but incompatible genetically (Shan & Frey, 1968).

In some taxa, such as *Daphnia* and *Bosmina*, introgression may well occur. On the other hand, in *Moina*, where more than one species commonly occur in the same water body and are gamogenetic at the same time, interspecies crosses do not occur. Goulden (1968) believes that the texture of the ephippial surface and the presence of one versus two egg locules enable a male to recognize the proper female tactilely by means of his highly modified antennules. This is only one of many possible isolating mechanisms among closely related sympatric species. Among the chydorids, males in a mixed population of *Pleuroxus denticulatus* and *P. procurvus* attempted to copulate with females of both species and even with other males of both species. The one hybrid female that resulted could reproduce parthenogenetically but not gamogenetically, demonstrating an effective genetic barrier against introgression (Shan, this symposium).

The Cladocera are old. Prior to Smirnov's report of a daphniid and a chydorid from the Permian of the Soviet Union, the oldest records were ephippia of *Daphnia*

and *Moina* from the Tertiary. Various lines of evidence suggest that, at least for the non-planktonic species and except for the short-term (?) adaptations of local populations to local conditions, much of the evolution and adaptive radiation within various groups of the Cladocera occurred long ago, most likely pre-Quaternary. In Europe the chydorids have been stable morphologically and ecologically since at least the last interglacial age.

Patterns of distribution and evolutionary trends have been described in detail for the Moinidae (Goulden, 1968) and the North American *Daphnia* (Brooks, 1957). From morphological evidence Frey (1967), Fryer (1968), and Smirnov (1969) have speculated about evolution in the Chydoridae.

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DETROIT SYMPOSIUM A SUCCESS

At the First National Biological Congress, held at Cobo Hall in Detroit, Michigan, 7–10 November 1970, under the joint sponsorship of the American Institute of Biological Sciences and the Federation of American Societies for Experimental Biology, one of the many symposia was arranged by the American Microscopical Society. Under the chairmanship of our Secretary, Dr. David T. Clark, AMS presented an interesting and well attended symposium entitled "Advances in Science Through Microscopy." Speakers (all members of the Society) and topics at the meeting, which was held from 2–5 p.m. on Sunday 8 November, were as follows:

Dr. Oscar W. Richards—"Microscopy: Yesterday and Tomorrow"

Dr. Peter H. Bartels—"Cell Recognition from Computer Analysis of Images"

Dr. Lewis E. Lipkin—"The Microscope as an Input to Artificial Intelligence Systems"

In spite of the competition from dozens of the other symposia going on concurrently in Cobo Hall, ours may be judged to have been highly successful, based on the good number in attendance and the audience reaction to the speakers and their papers as noticeable particularly in the discussion following the presentation of the three well delivered illustrated talks.