A THEORETICAL AND EMPIRICAL CONSIDERATION

OF TROPHIC DYNAMICS

IN SOME KANSAS FARM PONDS

by

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I. Introduction

The Problem.   The extension of the grassland biome into eastern Kansas is
the tallgrass prairie.   Scattered about the prairie are farm ponds, small
artificial impoundments created by damming the drainages of intermittent
streams.   Just as there are differences between these two ecosystems, the
prairie and the pond, there are variations within each.   Between any two
ponds, for example, the composition of fish populations can vary, or the
abundance of aquatic plants or invertebrates.   My question, and the subject
of interest here is, why are there these differences?   There seem to be
two general types of answers.

The first group of answers incorporates an "extrinsic" theme of
causality.   Proximate physical factors are important: pond size (area, depth
or perimeter), the quality and quantity of nutrient input, pH, micronutrients,
turbidity and so forth.   The second group involves an "intrinsic" theme:
the biological nature of a community determines the patterns manifested by
that community.   For example, Paine's (1966, 1974) starfish studies demonstrate
the effect of a "keystone" predator in maintaining a more diverse prey
community.

Clearly, both factors operate and interact in varying proportions,
although in at least some cases extreme seasonality may never allow biological
factors (competition, predation) the time to influence the community
(Hutchinson 1961).

The purpose here is to test, in an aquatic system, the predictions of
a model which incorporates the extrinsic variable of nutrient input (measured
by primary production) and the intrinsic variable of predator-prey relations.
Fretwell (MS) has developed the model from basic graphical predation theory
(Rosenzweig and MacArthur 1963) and Rosenzweig's (1971) paradox of enrichment.
I first present a summary of the model with its predictions, and then the

experimental design of the study.

The Model. With more energy entering a community, an increase in the abundance of the populations comprising that community may be exepcted. Where, for example, vegetation is sparse or seasonally unavailable, the density of herbivores may be low. But when the vegetation increases, the herbivores may flourish and, in turn, support a carnivore. Thus, as a first approximation, food chain length can increase as primary production increases and the internal arrangement of the system changes as predators are added to the system.

Consider a system of n trophic levels, each acting like a single species, where level n_i feeds exclusively on level n_{i-1}. Level n_o is autotrophic (P) and levels n_i, i > 0, are the consumers (Ci). Let the relationship between levels n_i and n_{i-1} be specified by graphical predation theory (Rosenzweig and MacArthur 1963). This system of n-1 predator-prey pairs will be analyzed under the conditions of enrichment, the case of n=2 being Rosenzweig's (1971).

Assume the following: (1) enrichment leads to infinitesimally small increases in the carrying capacity of P, resulting in increased P production with both rate and standing crop components, (2) once level n_i reaches some threshold density a new level, n_{i+1}, can enter the system and act as a top predator, (3) evolutionary effects are negligible, (4) all predator isoclines are vertical (no predator squabbling or sociality), and (5) the prey isoclines may or may not be the humped curves characteristic of an Allee-effect species (Rosenzweig 1971, 1973a), but if they are humped, a higher predator (n_{i+1}) enters before the lower (n_i) reaches a density at the peak of the n_{i-1} prey isocline. This last simplifying assumption excludes potentially unstable interactions.

The actual (or realized) equilibrium density of any level, n_i, is

K_{ij}, when there are j levels in the system. If all predators above n_i were removed from the system, the equilibrium density of level n_i would increase to K_{ij}^*, simply referred to as the carrying capacity of the ith level. The threshold density of the ith level which is going to begin to support a higher level, k (k > i), is called the transitional density, or K_{ik}'.

Figure 1a shows a two-level predator-prey system similar to Rosenzweig's (1971). With enrichment, the humped victim isocline becomes larger and the rightmost intercept, K^*, increases towards the right. Any further increases in victim density beyond K_{11}^*, which in this case equals K_{12}' and K_{11}, will lead to increases in the predator density. The changes in density are graphed against victim carrying capacity (Figure 1b) and show that the initial increase in victim density ceases when the predator enters the system, due to the vertical predator isocline.

By extending the logic to n = 4, Figure 2 may be drawn. The isoclines are entirely similar to Figure 1 and because the predator isoclines are vertical, once any Ci enters the system and begins to increase, its prey's density remains the same. For example, when there are three levels in the system (Figure 2b), the C2 increase with enrichment, the C1 remain the same, but the P increase once more.

The assumption that all predator isoclines are vertical is simplifying. If any of the predators are partially self-limited (if they squabble or are territorial), their isoclines slope up to the right (Figure 3a). If the predators help each other (sociality, packs), the isoclines slope up to the left (Figure 4a). In the first case the plateaus of Figure 2b disappear (Figure 3b) and in the second there are actually dips in the equilibrium density of, say, the producing level as production increases (Figure 4b). Gilpin (1975) notes the various forms of the predator isocline and provides their equations which are not critical to the arguments here.

The Predictions. In all three cases of the predator isoclines (Figures 2b, 3b, 4b), the C1 and C3 levels increase when the producers are between K_{13}^* and K_{14}^*; that is, between a 3 and 4 link system. P and C2 density are constant when the vertical predator isoclines are assumed, but increase when predator interference is assumed. If the assumption is predator-assistance, then the P and C2 densities decrease with enrichment between the third and fourth link. So depending on the form of the predator isocline, three different predictions are possible.

Since there is no reason to suppose either interference or assistance (assumption 4, above), the trends in Figure 2b will be used to form the following ecosystem hypothesis: as primary production increases in a 3-4 link system, the densities of the primary producers and secondary consumers will remain constant while the densities of the primary and tertiary consumers will increase. This is the major prediction to be tested, but there is another.

Irrespective of the predicted density patterns, the producing and secondary consuming levels do become exposed to more predation in the model. The organisms in those levels should possess, at higher nutrient levels near the fourth link, adaptations indicative of more predation. Particular responses can not be predicted, but the following might be expected:

(1) within the secondary consumer level, species more resistent to predation might occur; body size or shape could change, although how is not clear; and behavioral changes such as spatial or temporal displacement of activity to avoid predators might be found;

(2) within the producer level, a reduction in standing crop (if production were not increasing) or direct evidence of increased grazing could be found, as well as higher growth rates which might compensate for grazing losses.

The Field Test. This study will test the predictions from the ecosystem hypothesis in farm ponds, artificial impoundments used for watering cattle. A strict test of the predictions would require artificial enrichment of a pond, but among these ponds, a range of natural differences in nutrient input (or other factors leading to greater energy flow through the producers) is expected. Therefore, the condition of enrichment from the model is fulfilled by comparing ponds. The level of enrichment, or the richness of each pond is operationally defined as total gross primary productivity.

Data will be gathered to:

(1) measure the physical characteristics of the ponds,

(2) estimate total and planktonic primary production, then by the difference, macrophytic or littoral production,

(3) estimate the standing crops of the major trophic level populations based on the macrophyte-epiphyte complex, and

(4) measure the body sizes of benthic invertebrates.

II. MATERIALS AND METHODS

The Field Site and Morphometry. Six farm ponds on a grazed pasture site, the Simpson Hereford Ranch, about 9 miles east-southeast of Junction City, Kansas were the study site (Figure 5). The general ranch area, part of the Kansas Flint Hills, is described by Robel et al. (1970). These are permanent ponds formed by dams, and water level does fluctuate seasonally.

Each pond was surveyed by drawing approximate outlines and accurately measuring distances between perimeter features (bends, cowpaths, trees) with a 25 meter tape. Depth contours were determined by lowering a weighted marked line from a small boat and recording depth and position relative to shore. Transects were followed whenever possible. Maps were sketched and a planimeter used to estimate the area.

The average, or mean depth, was computed as $\bar{D} = \sum\limits_{i=1}^{n} d_i \left(\frac{a_i}{A}\right)$; where n is the number of contour intervals, d_i is the mean depth of the ith contour interval (the minimum plus maximum interval depth divided by two), a_i is the doughnut-shaped area over the ith contour interval and A is the total surface area at sampling time.

The ponds were named by a one letter-one number convention. Ponds on the north side of the dirt road bisecting the ranch begin N and those on the south side begin S. A number is added which reflects the order in which I found them in an early spring traverse.

Primary Production. Diurnal oxygen curves (Odum 1956, Owens 1969) were generated for each pond with 25 consecutive hourly samples. Each sample taken by a Kemmerer bottle at 0.3 meters depth over the deepest point (called the sampling station) was titrated in duplicate by the azide modification of the Winkler technique (APHA 1965). Ponds were sampled at various times, two (N1 and S1) were repeated and similar weather conditions prevailed; i.e.

bright, sunny days.

An open 9-liter carboy was suspended at the sampling station for concurrent diurnal oxygen estimates of phytoplankton production. Hourly samples were withdrawn by siphoning water through a rubber tube connected to a two-holed stopper on a 300 ml. BOD bottle. This tube extended to the bottom of the bottle while a shorter rubber tube exited _via_ the second hold and ran to the experimenter's mouth. There, suction could be applied and a sample taken.

Diurnal curves were eye-drawn and planimetery gave results in ppm O_2 for the day (photosynthesis minus respiration plus or minus diffusion) and the night (respiration plus or minus diffusion).

Diffusion was corrected by the following relationship: $D_i = k(SD_i)$; where D_i is the amount of oxygen diffused and SD_i is the saturation deficit for the ith hour. SD is computed as the mean hourly oxygen concentration (ppm) minus the saturation value of oxygen for that hour's temperature. The constant k is assumed to be linear and equal to 0.1 (Odum 1956). Actual data points, not estimates from the curve, were used in calculating SD. These corrected values were converted into hourly rates and a photosynthetic quotient of 1.2 used to change dissolved oxygen values into CO_2.

Macrophyte standing crop was sampled at the approximate height of the growing season in mid-August. A square-meter frame was placed at 2 sites chosen randomly from a map of the ponds; all the vegetation beneath that frame was cut away with shears and placed into plastic bags. These bags were returned to the lab, the plants washed, the remaining animals removed and the plants hung to drip excess water (Penfound 1956). A wet weight was then taken, the vegetation subsampled and dried in an oven at $105^{\circ}C$ to constant weight.

Macrophyte density is expressed in $kg\ m^{-2}$, wet or dry weight. The area

used in the denominator can be the total pond surface area at sampling time or the pond surface area over macrophyte growth.

Along with four of the diurnals, 2 pairs of light and dark bottles were incubated for the full daylight period near the sampling station and at approximately the same depth as the pond diurnal samples were taken from.

Every two hours total alkalinity was determined by titration with 0.02N standard acid (APHA 1965). Temperature was recorded on the alternate hours and Secchi depth measured at the same time, but only during the daylight hours.

Benthic Invertebrates. Two ponds (N1 and S1) were sampled at 4 different times throughout the summer for benthic organisms, one pond (N2) twice and three ponds (N3, S2, S3) once. Two to four random samples were taken within each meter contour interval with a 225 cm^2 Eckman dredge. Each sample was washed through a #30 mesh brass sieve bucket, the residue placed into white stove pans and brought to shore for sorting.

Animals were fixed and preserved in 80% ethanol in baby food jars. Later, the individuals were identified as accurately as possible according to Pennak (1953), counted and lengths taken. These samples were then oven-dried at 105°C for 1½ hours.

The lengths of benthic animals is the greatest anterior-posterior distance indicative of the species in question, exclusive of filaments and the like. Mean biomass, as used in later discussions, is the average dry weight within a contour interval, summed over all such intervals.

Fish. Two seine hauls were taken at each pond in late August 1975 using a ¼" mesh 20' bag seine. Fish were measured for length and weight, then the guts removed to 80% ethanol and the fish to 10% formalin. To compare fish populations between ponds, the mean wet weight per seine haul per

square meter total surface area was used.

Gut samples analyzed in the lab are expressed as Y, the average contribution of a food item to a gut. Y goes from 0% to 100% and is calculated as follows:

Let f_i be the fraction of all guts with item i present out of all the guts sampled. Then:

$$Y = \left(\frac{f_i}{\sum\limits_{i=1}^{n} f_i}\right) \times 100\%, \text{ where n is the number of food items.}$$

III. RESULTS

Morphometry. The results of morphometric measurements in Table 1 show total surface areas ranging from 0.305 to 0.575 hectares. These ponds do not differ considerably in shape (FIGURE 6) except for S1, which has a small finger-like extension.

Primary Production. Each diurnal began at local sunrise which was arbitrarily set to 0600 (Figure 7). Oxygen measurements were interrupted by severe weather during the night at two ponds, N1 and N2. Most of the nighttime readings were unobtainable for N1(1) and the hourly average for the available data was used in computations. Only two hours readings were lost for N2 and no correction was necessary.

Total gross production (Table 2) ranged from 2.22 to 14.71 gms. C m^{-2} day^{-1}, phytoplankton production from 1.03 to 5.69 and littoral production (as the difference) ranged from 1.18 to 12.15. In the two ponds where replicates are available, one decreased in production (N1) and the other (S1) increased; although in each case the change was small. In later discussions the values for N1 and S1 production estimates are the average of the two diurnals.

As total production increases, the macrophytic and phytoplanktonic components do not increase proportionately (Figure 8). Macrophytes (and associated periphyton) account for most of the increase in total production (r=+0.94, P < 0.05), rather than the phytoplankton (r=+0.22, NS).

Given an assumed competitive relationship (Hasler and Jones 1944, Moore 1952, Goulder 1969, Nichols 1973) between algae and the aquatic hydrophytes with respect to light and nutrients, one may expect, a priori, an inverse relationship between their production rates. From these data the correlation between phytoplankton and macrophyte gross production is

r=-0.14 (NS) and our confidence in the inverse relationship is not increased. However, when the points are plotted in Figure 9, the southside points lie on a line above the northside points. The trend seems clear over this range of data: phytoplankton production is inverse to benthic production, but the southside ponds have higher phytoplankton productivities (P < 0.05, Mann-Whitney Test).

There may be an explanation for the difference between north and south: early in the spring, before these experiments began, the southside of the ranch was burned as part of a range management program. Although there does not seem to be any data to support the idea, burning may result in increased nutrient runoff (L. C. Hulbert, personal communication). If that were the case, the algae might be able to respond to and exploit that resource more quickly and efficiently than the macrophytes.

The carboy diurnals, which are assumed to estimate phytoplankton production were correlated (r=+0.96, P < 0.05) with gross production from the dark/light bottle experiment (Table 4), although the estimates, themselves, differ (Table 2).

Macrophyte biomasses (Table 3) range from 0.055 to 0.265 kg m^{-2} of total surface area on the sampling date. These are estimates of relative biomasses at the time of sampling. Repeated sampling to determine the point of maximum biomass was not possible so the values given here probably underestimate net annual production (Penford 1956, Ryther 1950, Wetzel 1965).

Macrophyte biomasses correlate negatively with the estimates of gross production (Table 4). There seems to be less benthic mass in the higher production ponds, although the trend is not statistically significant.

From Table 4, the average Secchi depth is negatively correlated with gross production and positively with macrophyte biomass (r=+0.97, P < 0.01).

Thus the ponds richer in macrophyte growth are clearer, and from Figure 9, have reduced phytoplankton productivities. The variable of non-algal turbidity is unaccounted for, but there are no data to show that it does or does not contribute strongly to turbidity in these ponds.

Community Structure. Faunal diversity (see Table 5 for species list) is rather similar in these ponds. The most common taxa (in percent biomass, see Table 6) are the aquatic stages of: Chaoborus, the phantom midge; Palpomyia, the biting midge; the midge genus Chironomus; Caenis, the mayfly; Ischnura, the damselfly, Sialis, the alderfly, and the mollusks Physa, Pisidium and Musculium.

The simple food chain based on the macrophyte-epiphyte complex is illustrated in Figure 10. This diagram is merely one subsystem within the overall pond ecosystem, but a system amenable to quantification.

The producer level is represented by the macrophyte-periphyton complex (P). A relatively diverse group of creatures are the primary consumers (C1). The basic criteria (based on the literature) for placing a species into the C1 were (1) feeding directly on the macrophyte complex and/or (2) being strongly associated with that complex, feeding on smaller animals (protozoa or rotifers, for example) or scavenging. Odonates, primarily Ischnura, and the alderfly larvae, Sialis comprise the secondary consumers (C2) along with two Coleopterans. Members of the Centrarchidae, the large-mouth bass (Micropterus salmoides) and the bluegill (Lepomis macrochirus) are the top carnivores (C3). It is generally known that these fish species are opportunistic, and gut analysis (Table 7) here does nothing to dispel that fact. As a result, then, lines are drawn connecting both C1 and C2 levels to the Centrarchidae.

Standing Crops. The standing crops of each trophic level (P, C1, C2, C3)

are plotted (Figure 11) against total gross primary production of the farm ponds. Macrophyte density is negatively correlated with production (r= -0.46, NS) and the primary consumers increase with production (r=+0.49, NS). The C2 density decreases with production (r=-0.84, P=0.07) while the C3 increased (r=+0.78, NS). Although three of these correlations are not significant, I will suppose the sign of the correlation to be biologically meaningful in later discussions.

Size-Frequency Distributions. The mean length of all secondary consumers decreases with primary production (r=-0.85, P=0.06; see Figure 12). The high production ponds seem to have smaller individuals, but the C2 contain at least two different species which bear examining.

Sialis was not found in N1 or S3, but Ischnura occurred in all 5 ponds and was most abundant in the absence of the alderfly larvae (Figure 13). Since mean Sialis length shows no pattern with production; the overall decrease in average C2 length is attributable to Ischnura.

In N1, Ischnura's size distribution expands towards mid-season (Figure 14) with new additions to the smaller size classes, then collapses to two modes, one at 4 mm., the other at 10 mm. Sialis, in S1, seems to follow the same expansion trend, although displaced forward in time.

IV. DISCUSSION

The Predictions. Because both the primary producers and the secondary
consumers in the model are subjected to greater predation as enrichment
increases, they were predicted to reflect the effects of predation in their
behavior, morphology or growth rates. The first is not testable here, but
body size changes and growth rates can be examined for the C2 and P,
respectively.

Body size measurement of the C2 showed a decrease in length that was
attributable to Ischnura in the high production ponds (Figures 12, 13 and
14). Although that correlation does not demonstrate predator-related
effects, it shows that a change has occurred in the high production ponds
where predation is presumably (and apparently,see below) greater.

Macrophyte production was strongly and positively correlated to total
production, but not macrophyte biomass (Tables 3 and 4). The implication
is that the macrophyte complex is turning over faster in the high production
ponds. This agrees with the hypothesized increase in growth rates as a
compensation for grazing losses. Since no direct evidence for grazing was
obtained other than the increase in primary consumer density in the high
production ponds, this agreement between data and predictions is qualified
and needs further testing.

The hypothesis that led to this study predicted patterns in the trophic
structure of an ecosystem influenced by primary production and predation.
Because of vertical predator isoclines, the densities of the secondary
consumers and primary producers were expected to remain the same as production
increased,while the densities of the C1 and C3 levels should increase. From
Figure 11, the C1 and C3 level densities do increase with production as
predicted, but the P and C2 levels decreased rather than remaining constant.

How are the results interpretable?

The two general predictions relative to the development of predator-limited adaptations are weakly confirmed, but the standing crop data are not in complete agreement with the predictions of the model. Something may be incorrect about the model given the evidence that the divergence from the predictions occurs in both prey groups (P and C2) that are presumably becoming more predator-limited (as their predators' densities are increasing). This consistent deviation suggests that assumption 4 concerning the vertical predator isoclines is not correct.

Recall from the introduction that 3 different predictions are possible based on the form of the predator isoclines. Particularly, the density patterns between the 3 and 4 link systems of Figure 4b, the so-called predator-assistance isoclines, are the same as the data presented in Figure 11: the P and C2 densities decrease and the C1 and C3 increase. There was no apparent reason why assuming that predators assist each other should hold for either fish or the primary consumers (the predators on the C2 and P, respectively). In the herbivore-plant link, for example, the macrophytes are not patchy, nor in any way (it seems) distributed in a fashion conducive to the predator-assistance hypothesis. The implication of sociality in the C1 and C3 still seems unreasonable at this time.

The structural role of macrophytes in providing habitat for both primary and secondary consumers has not been explored here. Decreased macrophyte density in higher productivity ponds may lead to a space-limited damselfly population in spite of increased primary production. Thus diminished secondary consumer populations could be a result of the synergistic effects of increased fish predation (there are more fish and/or their prey are more exposed in the scantier weed beds) and decreased macrophyte density.

Graphical predation theory is thought to be robust (Rosenzweig 1973b), but the assumption that coevolution is negligible may be critical. Would the evolutionary responses of the prey to their predator lead to the patterns in the data? The link between benthic invertebrates and their piscine predators has not been studied with evolutionary hypotheses, but the zooplankton have. Zooplankton response to vertebrate predation is well known (Brooks and Dodson 1965, Hrbacek 1962): size selective predation takes larger forms and leaves the smaller. In these ponds, smaller C2 appear in the high production ponds where they seem to be exposed to greater predation.

That correspondance is inviting and suggests that evolutionary factors associated with predation may be operating in these ponds. However, there may not have been enough time, not enough isolation for evolutionary mechanisms to be a strong determinant of these community patterns.

I am presently unable to assess the relative importances of either the evolutionary effects of the various ecological alternatives (fish predation or reduced macrophyte density). If, however, the secondary consumer populations are evolutionarily divergent, that divergence may be reflected in the adult populations or in nymphal morphology other than body size.

A New Model. This simple model assumes that the increases in production that a system (as described in the introduction) is subjected to are not only infinitesimally small, but that they occur over time periods in which adjustments between the n-1 predator-prey pairs can take place.

An important additional assumption concerns the type of responses between the predator and its prey. Based on the zooplankton studies mentioned earlier, the response of zooplankton to size-selective vertebrate predation is to become smaller. In that case, when predation is high, shorter

generation times and higher growth rates should be favored at the expense of standing crop.

The equations (from Gilpin 1975) for the vertical predator isocline and the humped victim isocline are, respectively:

$$V = -r_p/a \qquad (1)$$

$$P = \frac{r_v}{b} + \frac{c}{b}V + \frac{d}{b}V^2 \qquad (2)$$

V is the victim, r_v is its low density growth rate and 'a' is a constant approximating the efficiency of conversion of prey into predator. P is the predator, r_p is its low density growth rate and b, c and d are constants.

As a result of increased predation, three changes can be identified in the victim isocline: (1) r_v should increase as energy is diverted away from standing crop; this causes the hump (Figure 14) to move leftward, (2) the peak of the hump should increase since at higher turnover rates more predators can be supported by the same standing crop and (3) increased nutrient input should produce a greater victim carrying capacity, K^*. This third change results in a rightward movement of the prey isocline. The shift rightward is not as great as it would be if no extra energy were going into reproduction. The net result is an expansion and leftward drift of the victim isocline (Figure 15).

The predators are also in this "race" and selection will favor their greater efficiency. The constant 'a' in equation 1 is an approximation of that efficiency. As 'a' increased, $-r_p/a$ decreases and the predator isocline moves leftward (Figure 15).

The intersection of the two isoclines as drawn (Figure 15) is a stable equilibrium point, represented by some density of predator and victim.

Successive increases of production and time are represented by thicker isoclines, and at successive intersections the predator density increases ($P_3 > P_3 > P_1$) and victim density decreases ($V_3 < V_2 < V_1$). This provides a mechanism by which, through coevolution, the result of enrichment is to decrease the victim's density.

This relationship is drawn in Figure 16 in three dimensions. The time and enrichment axis comes out of the plane of the paper in which sits the predator-prey isoclines. (Gilpin 1975 shows a similar diagram for his group selection argument, but the third axis is gene frequency.) The line marked "no selection" shows how the victim isocline at the front of the drawing would look if there were no coevolution. Some measure of the energetic cost of shifting energy to reproduction and away from growth is indicated by the distance between points A and B.

This new model incorporating an evolutionary argument into predator-prey theory can not be used to test these data. Following Peter's (1976) advice, the prediction of this new model (that victim density will decrease with increasing production) may only be regarded as a "correspondance" to the data since the biomass density decrease is logically dependent on the assumption of a higher growth rate: the argument is circular.

This most certainly is not a fault of graphical predation theory as used here; correspondances can be quite useful in organizing knowledge and designing future experiments. However, whether and to what extent evolution is responsible for the observed decline in density and size of the secondary consumers remains for others to determine.

Conclusions. In much the same way as the variation between and within ecosystems can be divided into extrinsic and intrinsic factors, these latter biological factors can also be partitioned. In this particular case,

predation, the biological factor modeled, seems to produce patterns
influenced by both ecological events and evolutionary processes. While
this study is not able to determine the relative weights of influence,
it does demonstrate the value of an integrated approach.

This thesis has shown the application of predator-prey theory to farm
pond ecosystems to be interesting and synthetic, given the complexities
of seasonality and food webs. Examination of the data lead to the
supposition that evolutionary processes may be more important in these
ponds than first thought although the structural role of macrophytes and
the responses of fish and their prey to change in that structure are also
important determinants of the community patterns observed in these ponds.
While predator-prey dynamics and nutrient input do not (nor are shown to)
completely regulate this farm pond ecosystem, they seem to account for
some of the observed variation.

Figure 1. Predator-Prey Isoclines for Two-Species Systems. PD and V
are, respectively, the predator and victim densities in arbitrary units.
The K's represent the victim's carrying capacity. In 1a the outer isoclines
represent more enriched states, so K, the right intercept, increases. The
vertical line is the predator isocline. As enrichment occurs the prey
isocline enlarges and the intersection (dots) of both isoclines moves.
That intersection represents some equilibrium density of PD and V, and
the changes in those densities are plotted in 1b against victim K. See
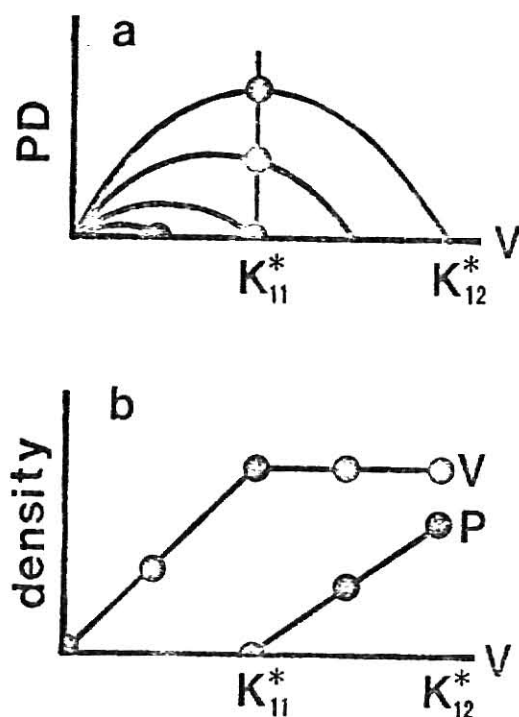text for explanation of K subscripts.

Figure 2. Predator-Prey Isoclines for Four-Species Systems. See the

text for general explanation. The dashed lines are extensions of predator

isoclines if the predator did not have its own predator. For example,

the C1 predator isocline extends upward from K_{11}^*, but the realized isocline

turns right when the C1 become prey for the C2. The vertical C2 isocline

"forces" this change in the C1 isocline. Also, note the juxtaposition of

the K^* for any level n_i with the intersection of the n_i and n_i-1 predator-

prey isoclines. Thus, K^* for the C1 just below K_{24}^* is the density

determined by the intersection of the C1 and P isoclines (arrow). These

arguments are summarized from Fretwell (MS).
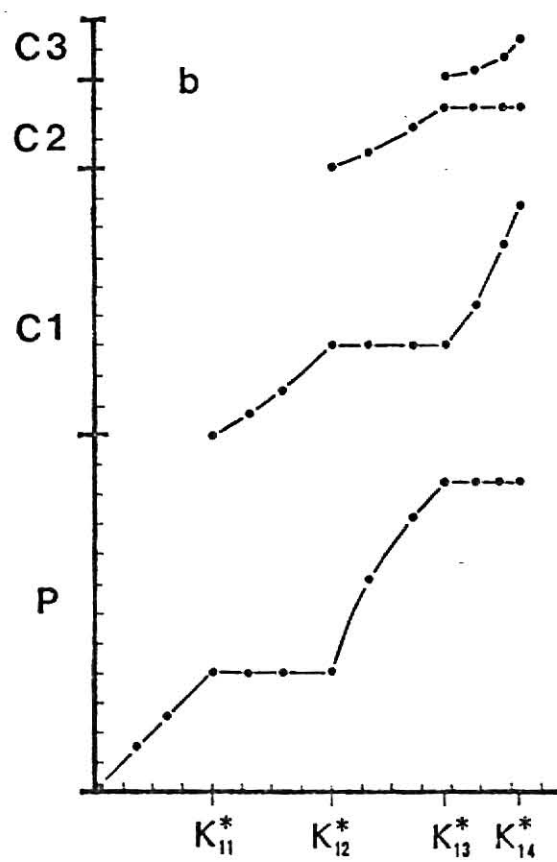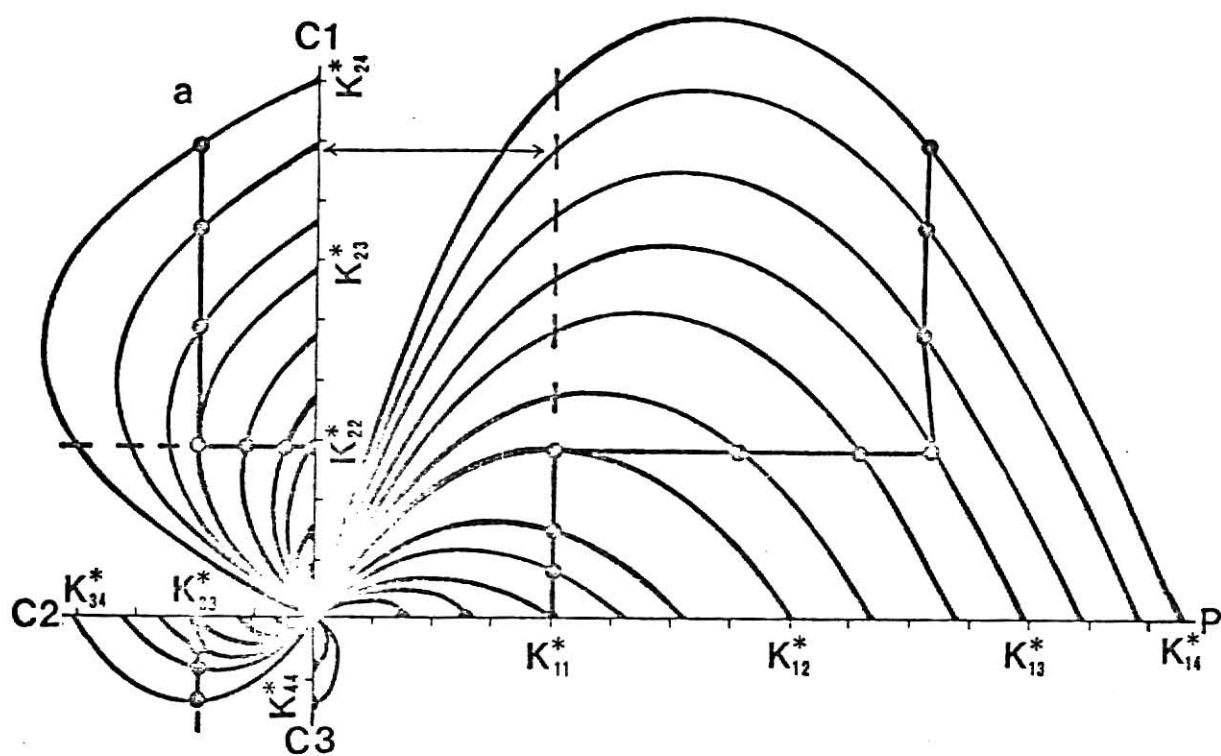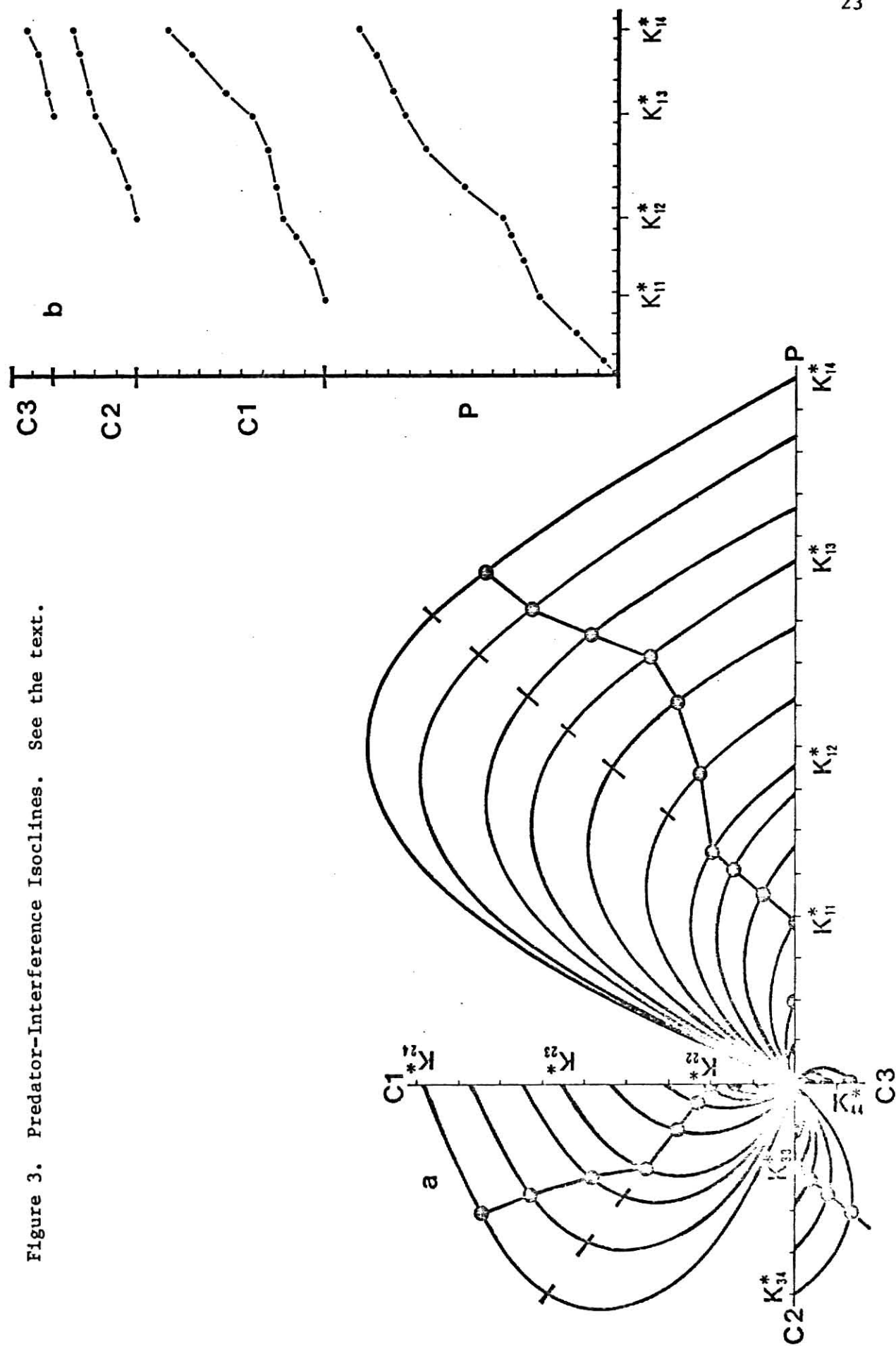
Figure 3. Predator-Interference Isoclines. See the text.

Figure 4. Predator-Assistance Isoclines. See the text.
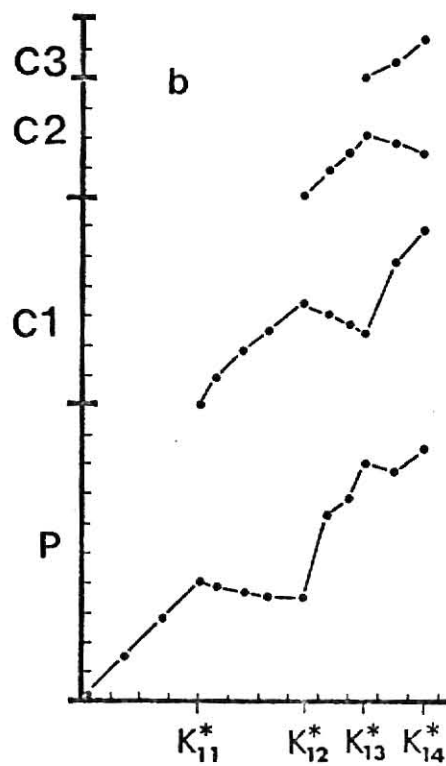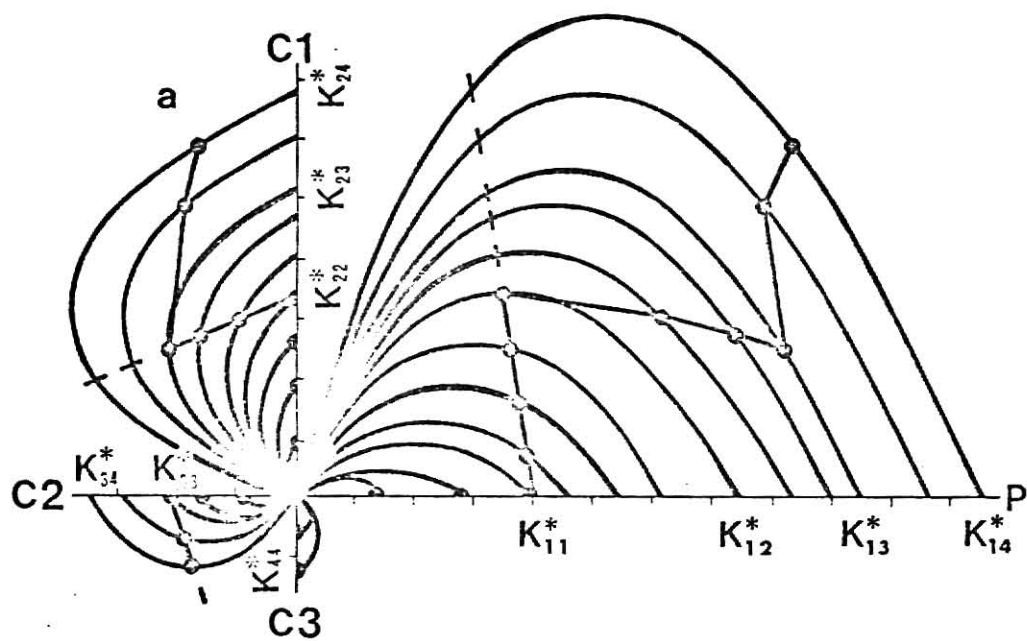
Figure 5. Location of Field Sites. The study area is located 9 miles east-southeast of Junction City T12S, R7E of Geary County, Kansas on the 6,000 acre Simpson Hereford Ranch. McDowell Creek Road approaches the ranch from the east off I-70, and Humbolt Road from the west off I-70. Only the ponds used in the study are shown; there are many others.
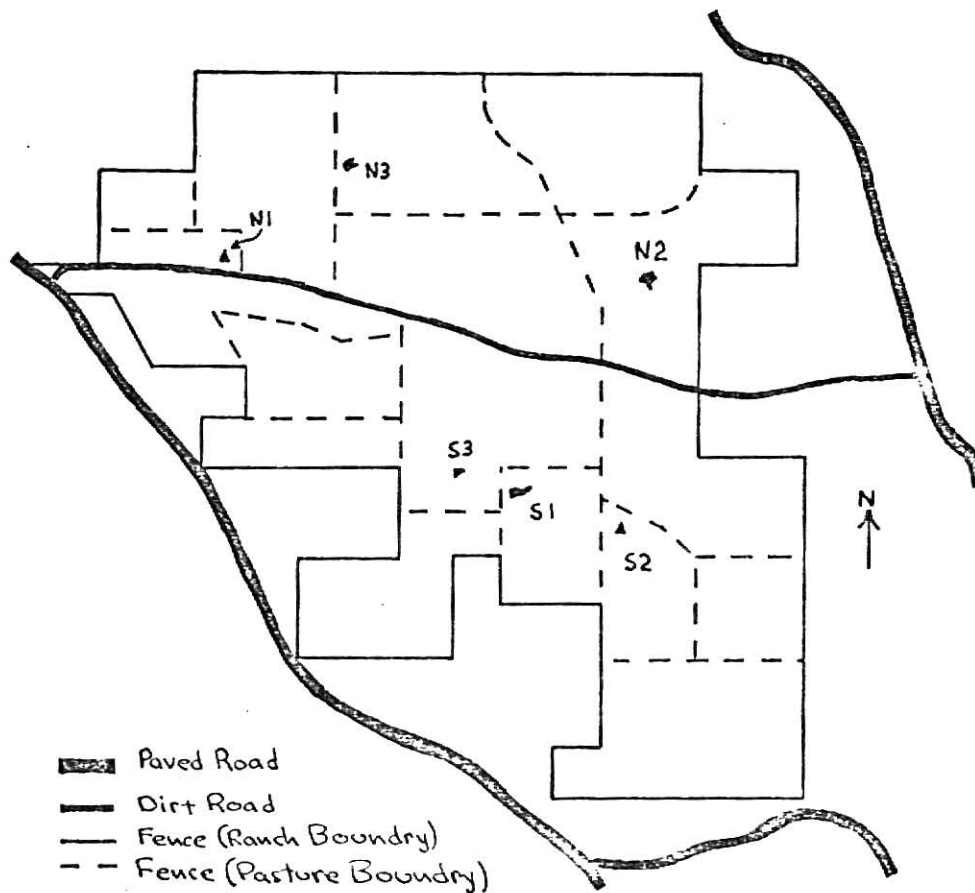
Figure 6. Pond Contours. The thick outer lines are the pond perimeters when water level is at the trickle tube height. Water's edge at sampling is the thin line just inside. Other lines are the depth contours in one meter intervals at the sampling date. Each small dot indicates one meter of depth and the maximum depth is given in meters.
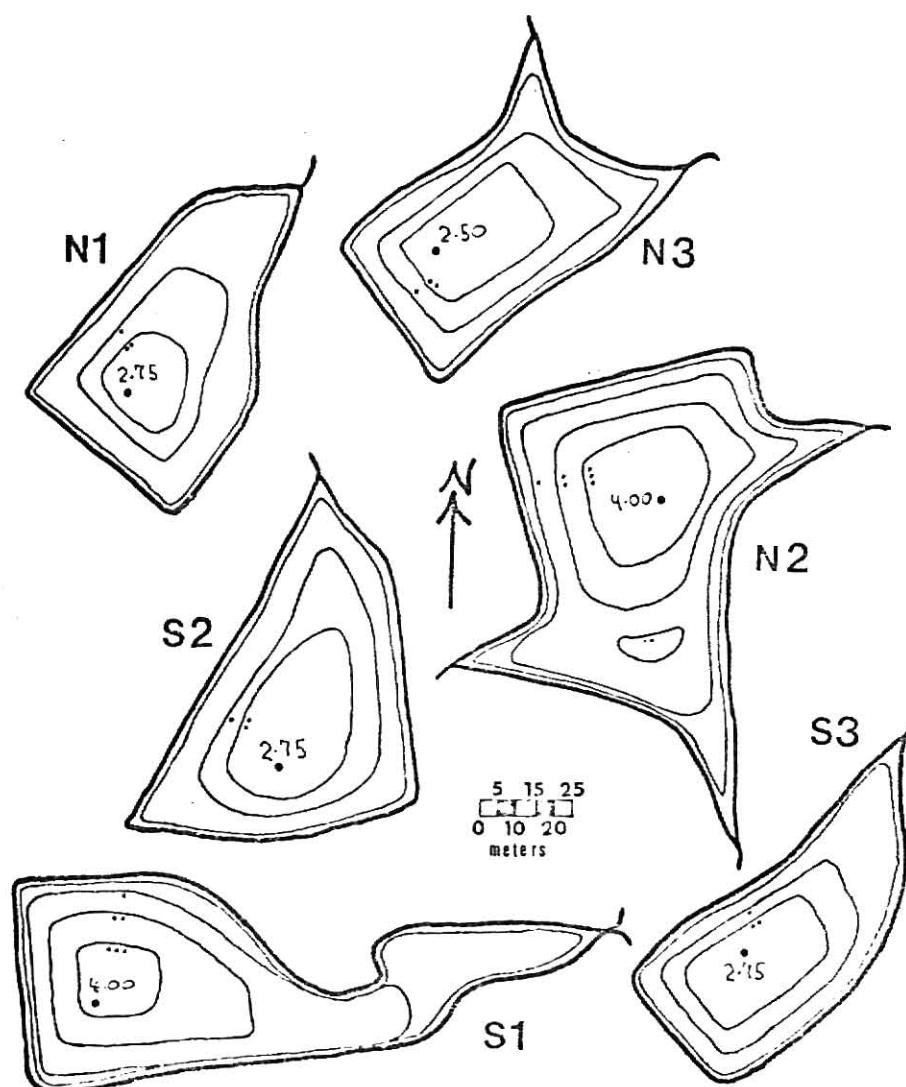
Figure 7. Diurnal Oxygen Curves. Time is hours from sunrise at 0600 except for N3 and S2 where sunrise came just after 0600. Closed circles represent the pond diurnal and the open squares are the carboy diurnal. The dashed line represents saturation, but for cases in which saturation is off the scale, the values are indicated at the top or bottom of the graph for the first sunrise and sunset. Thin vertical lines set off sunrise (sr) and sunset (ss).

O_2 (ppm)

TIME (hours)
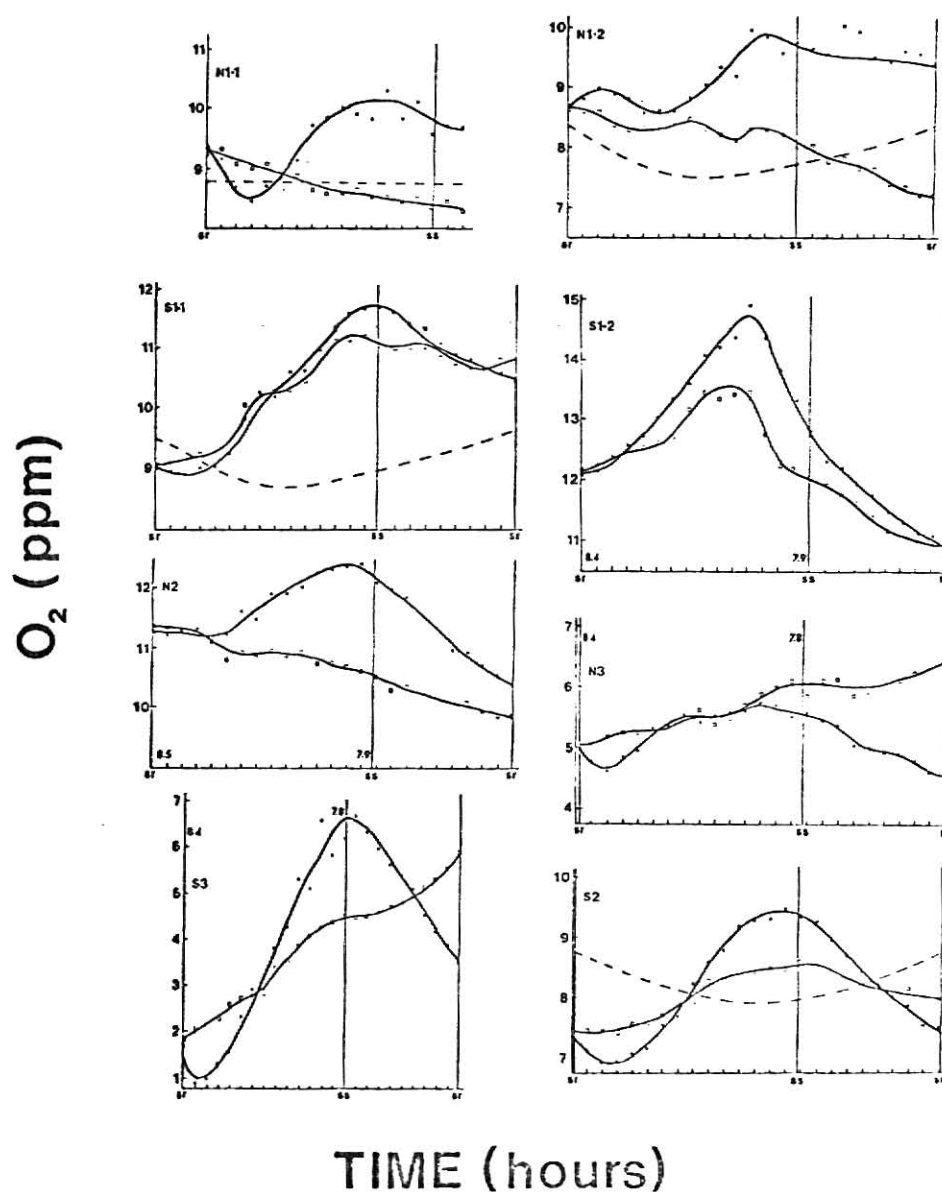
Figure 8. Components of Gross Primary Production. The ordinate may be read as total, planktonic or macrophytic production. Since the top line is total production and the lower is macrophyte production, the area between the two is phytoplanktonic production and the area below the lower line is macrophytic production. Macrophytes account for a greater proportion of total production at high production levels. See text for correlations.
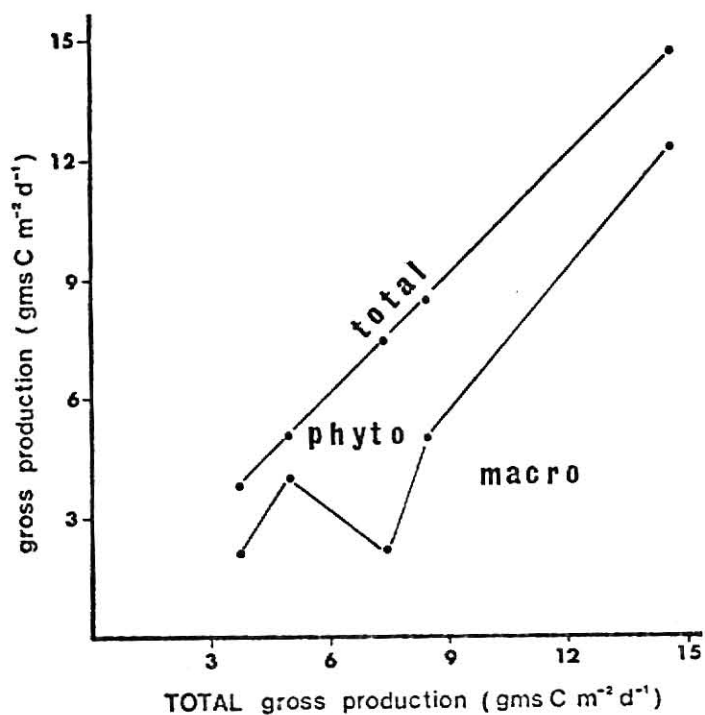
Figure 9. Relationship Between Planktonic and Macrophytic Production. The points are labled by pond and show that within each pasture (N is north and unburned, S is south and burned) there is an inverse relationship between planktonic and macrophytic production, but the ponds on the burned pasture seem to have higher planktonic production values.
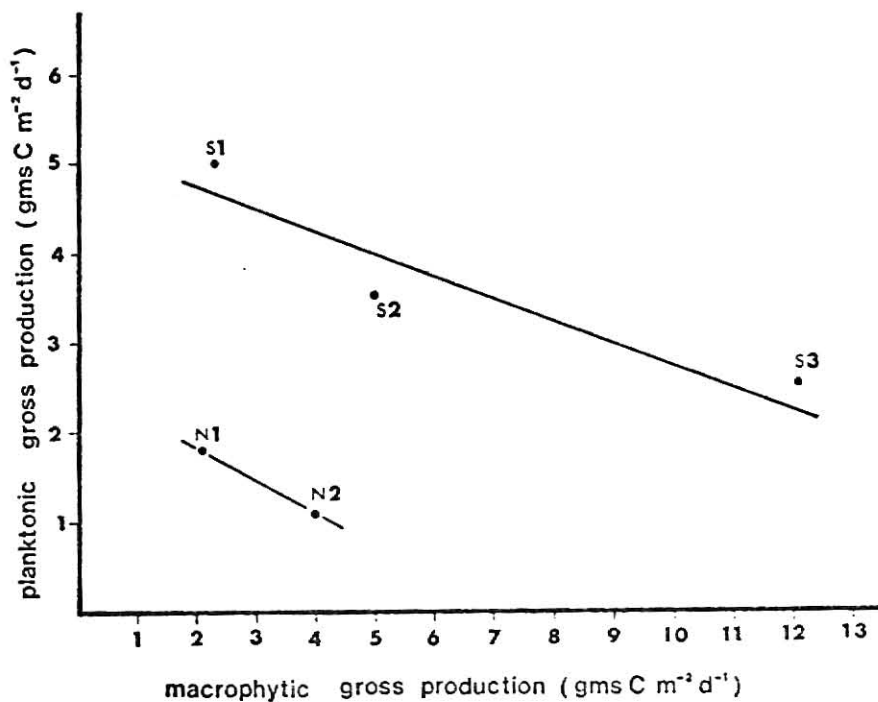
Figure 10. Macrophyte Community Structure: Trophic Concept. Idealized trophic structure of the macrophyte 'sub-system'. See the text for discussion.
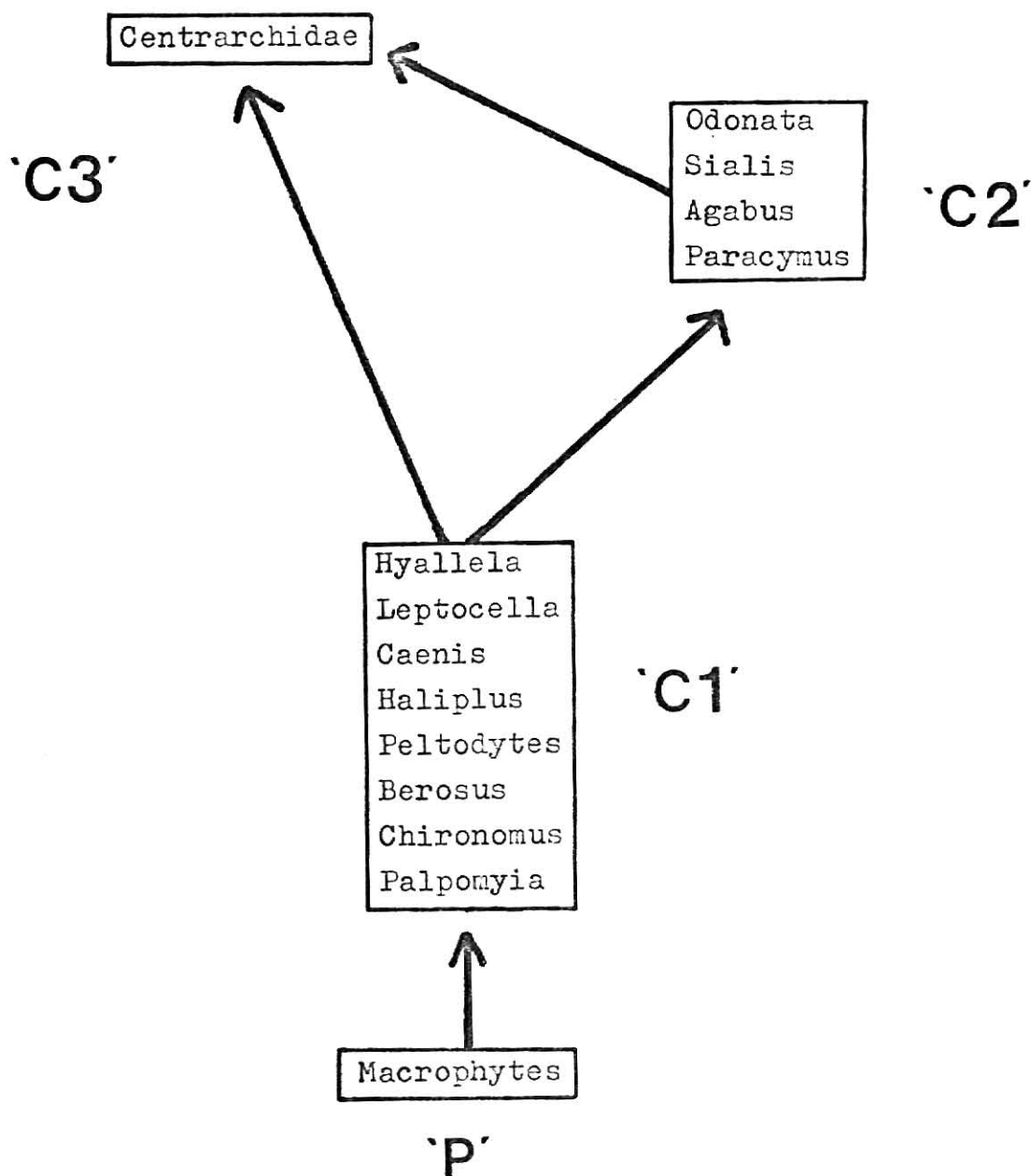
Figure 11. Trophic Level Standing Crop Versus Primary Production.
See text.
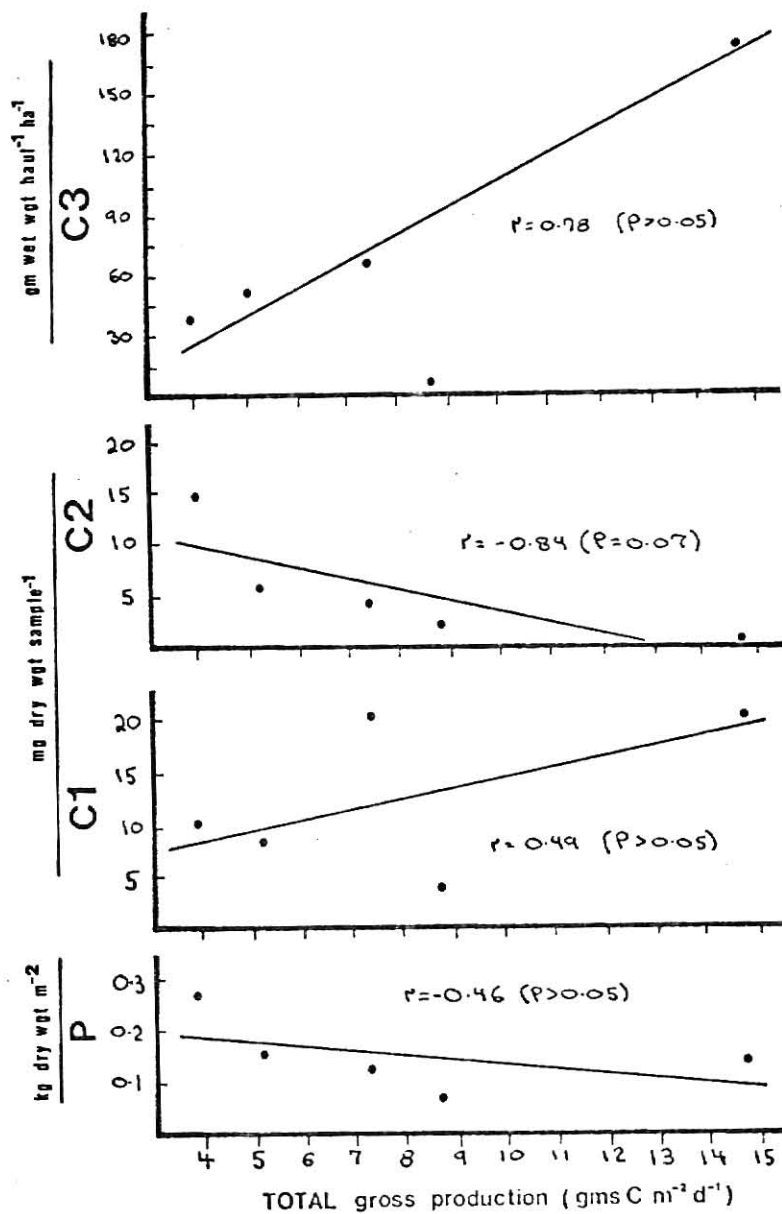
Figure 12. C2 Length Versus Primary Production. See text.
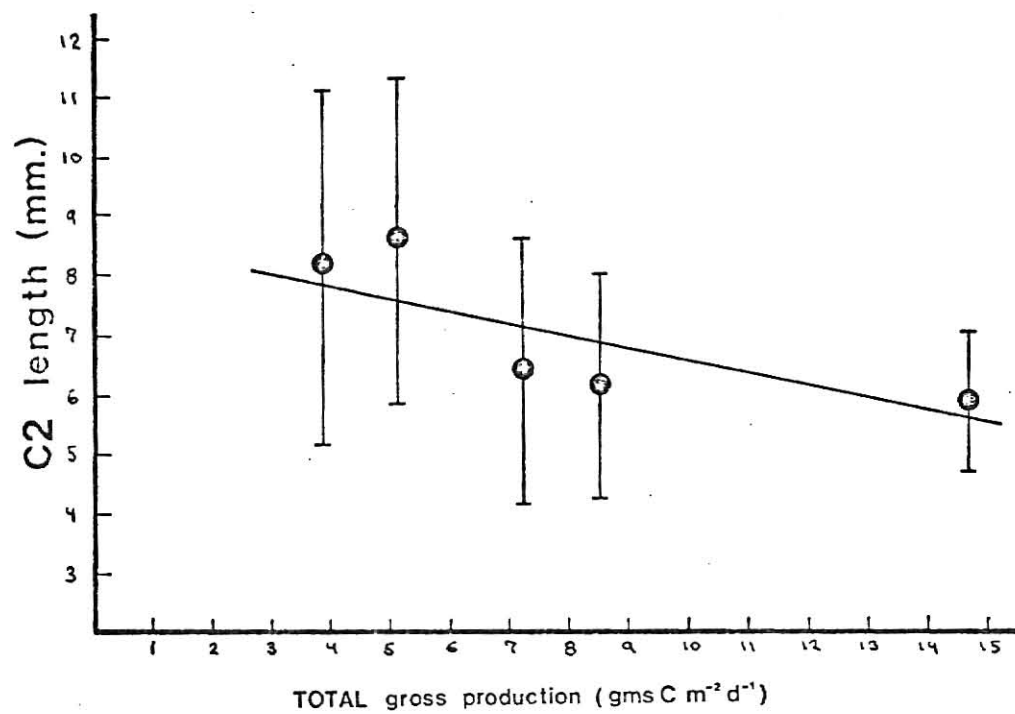
Figure 13. C2 Length-Frequency Histogram: Between Ponds. Sample identification is in upper left corner, n is the total number of individuals sampled and the figures in parentheses are the mean length (mm.) and standard deviation.
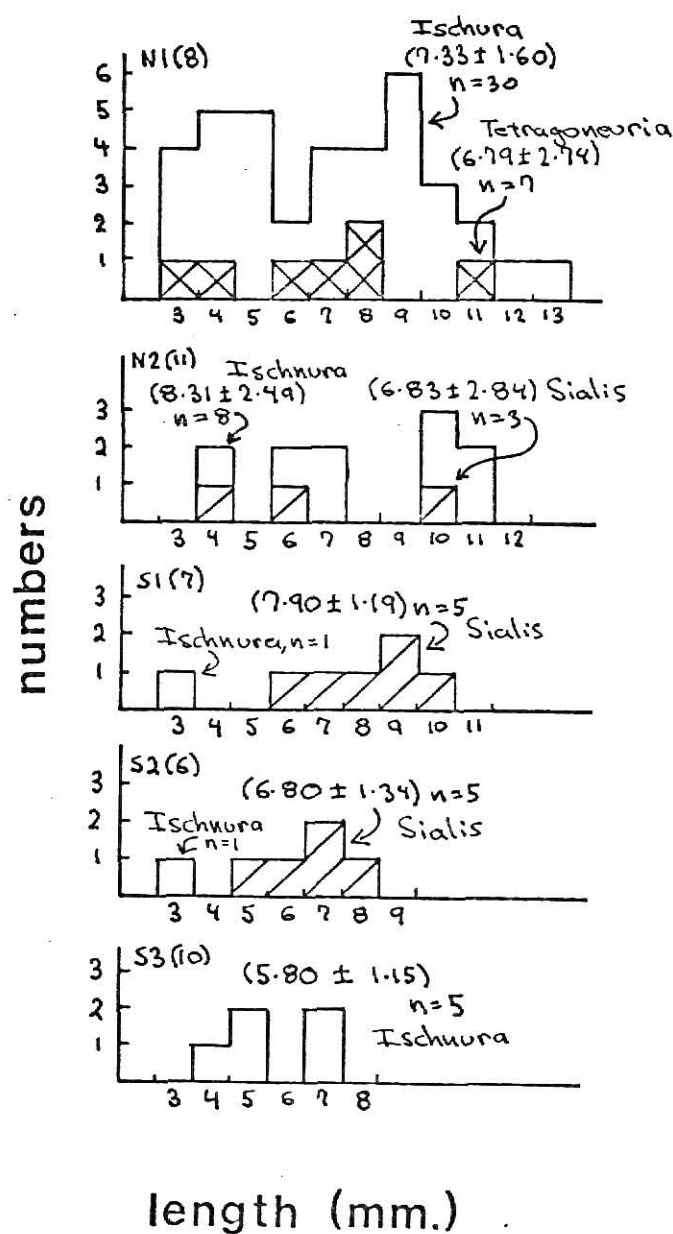
Figure 14. C2 Length-Frequency Histogram: Seasonal Changes. Sample identification is in upper left corner, n is the total number of individuals sampled and the figures in parentheses are the mean length (mm.) and standard deviation.

length (mm.)
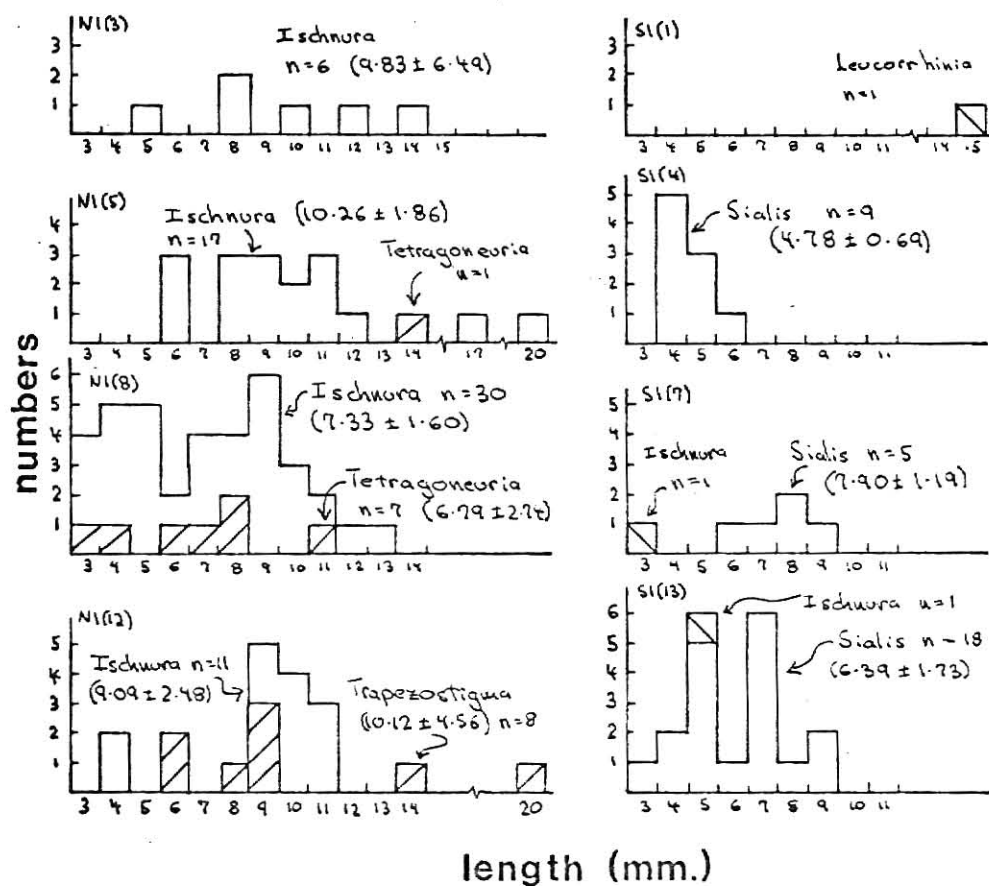
Figure 15. Evolutionary Effects on Predator and Victim Isoclines. Both axes are density in arbitrary units. See text.
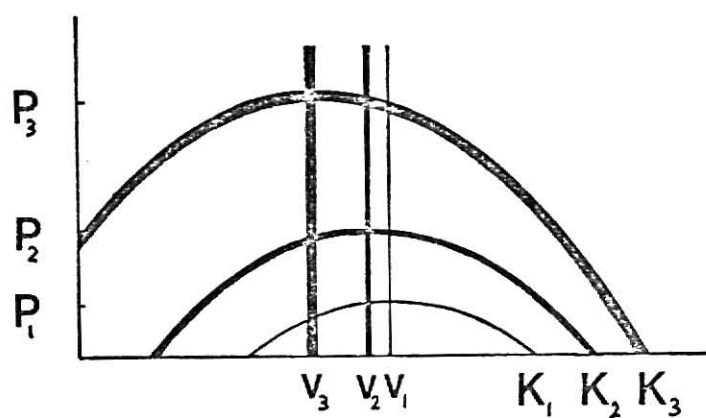
Figure 16. Energetic Cost of Selection in Co-evolving Predator-Prey System. In three dimensions, these are the predator and prey isosurfaces where dP/dt = 0 on the plant oblique to the V = 0 surface and where dV/dt = 0 on the airplane hanger shape. The dashed line traces the movement of the intersection of the two isosurfaces through (t, G), some function representing increases in time and enrichment. Along the (t, G) axis both predator-prey dynamics and evolution take place. See text for further discussion.
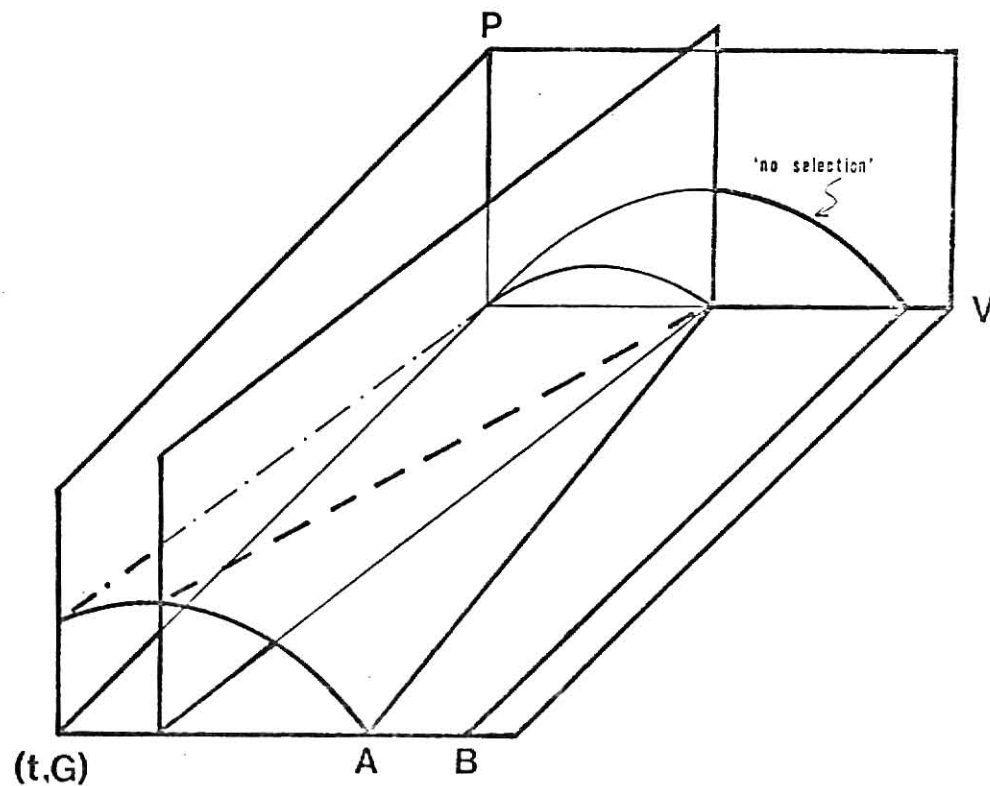
TABLE 1. Morphometric Data Summary. Sampling dates are the days on which diurnal oxygen measurements were taken.

POND	SAMPLE DATE	SURF. AREA (ha)			DEPTH (m)		VOLUME (x10³ m³)	AREA OVER CONTOUR INTERVAL (ha)				
		FULL	SAMPLE DATE	% FULL	MAX-IMUM	MEAN		0-1m	1-2m	2-3m	3-4m	4-5m
N1	25 V	0.331	0.296	89.5	2.75	1.06	4.54	0.173	0.074	0.050	–	–
N1	1 VII	0.331	0.331	100.0	3.50	1.37	4.54	0.155	0.087	0.061	0.029	–
N2	6 VI	0.575	0.523	91.0	4.00	1.86	9.74	0.115	0.196	0.118	0.092	–
N3	29 VII	0.392	0.269	81.9	2.50	1.38	3.72	0.093	0.093	0.082	–	–
S1	30 V	0.497	0.455	91.6	4.00	1.62	9.29	0.142	0.155	0.118	0.038	–
S1	24 VI	0.497	0.497	100.0	4.75	1.87	9.29	0.131	0.158	0.113	0.077	0.017
S2	14 VII	0.415	0.378	91.2	2.75	1.32	4.99	0.160	0.112	0.106	–	–
S3	5 VIII	0.305	0.262	85.9	2.74	1.32	3.47	0.115	0.072	0.076	–	–

TABLE 2. Primary Production Results. In the rows for each pond the top figure represents the pond diurnal, the lower figure is the carboy diurnal. Mean temperature, alkalinity and Secchi depth, as well as the dark/light values are for the pond water, not the carboy. NA means not done.

POND	SAMPLE DATE	$gm\ C\ m^{-2}\ day^{-1}$			GROSS KG C DAY^{-1}	MEAN TEMP. C°	TOTAL ALKALIN-ITY (ppm)	MEAN SECCHI (cm)	DARK/LIGHT BOTTLE, GROSS ($gm\ C\ m^{-2}\ day^{-1}$)
		GROSS	NET	RESPIRATION					
N1	25 V	5.54	4.54	1.00	16.4	22.0	70.9	110.0	NA
		3.12	2.82	0.30	9.2				
N1	1 VII	2.26	2.24	0.02	7.5	27.4	194.5	192.1	0.168
		1.08	0.76	0.32	3.6				
N2	6 VI	5.03	2.54	2.49	26.3	26.2	97.6	104.0	NA
		1.03	0.28	0.75	5.4				
N3	29 VII	4.69	1.53	3.16	12.7	28.9	170.6	38.6	0.019
		1.13	0.82	0.31	3.0				
S1	30 V	6.95	4.07	2.88	31.6	20.9	1167.1	75.4	NA
		5.69	3.87	1.82	25.9				
S1	24 VI	7.78	5.24	2.54	38.7	27.8	145.6	76.2	0.944
		4.30	3.15	1.15	21.4				
S2	14 VII	8.54	4.43	4.11	32.3	24.6	127.8	67.5	0.405
		3.54	2.13	1.41	13.0				
S3[a]	5 VIII	14.71	8.05	6.66	38.6	27.2	139.2	100.0	0.069
		2.56	-	-	6.7				

[a]Net production exceeded gross due to rise in carboy dissolved oxygen all night. The diffusion coefficient used was insufficient to correct this.

TABLE 3. Macrophyte Biomasses. TOTAL is kg per unit total surface
area on the sampling date, MP is per unit surface area over
macrophyte growth.

| POND | KG M^{-2} DRY | | | KG M^{-2} WET | | | % DRY |
	TOTAL	MP	KG DRY	TOTAL	MP	KG WET	WEIGHT
N1	0.265	0.352	658.9	1.520	2.020	3779.1	17.43
N2	0.155	0.276	562.3	1.352	2.407	4910.2	11.45
S1	0.125	0.326	446.3	0.737	1.927	2636.6	16.93
S2	0.055	0.113	181.7	0.295	0.607	976.3	18.61
S3	0.141	0.288	297.7	0.912	1.857	1921.5	15.49

TABLE 4. Production Parameter Correlation Matrix. For all correlations, n = 5.

VARIABLE	1	2	3	4	5	6	7	8	9
1 total gross production[a]	1.00								
2 gross phytoplankton production[a]	0.218	1.000							
3 gross macrophyte production[a]	0.936*	-0.139	1.000						
4 total macrophyte biomass[b]	-0.724	-0.343	-0.611	1.000					
5 macrophyte density[c]	-0.456	-0.466	-0.294	0.847	1.000				
6 macrophyte density[d]	-0.224	-0.188	-0.185	0.819	0.807*	1.000			
7 mean Secchi depth[e]	-0.406	-0.610	-0.192	0.733	0.969*	0.654	1.000		
8 total surface area[f]	-0.481	-0.030	-0.477	0.243	-0.287	-0.080	-0.381	1.000	
9 dark/light gross production[a]	-0.304	-0.962*	-0.546	0.102	-0.369	-0.038	-0.570	0.980*	1.000

[a] gm C m^{-2} day^{-1}

[b] kg dry weight

[c] kg m^{-2} dry weight, total surface area at sampling

[d] kg m^{-2} dry weight, surface area over macrophyte beds

[e] centimeters

[f] m^2, area if pond were full

* $P < 0.05$

TABLE 5. Benthic Species List. Species that were sampled, but not included in FIGURE 10, are listed here. A question mark indicates further identification not made.

Annelida   Oligochaeta   Chaetogaster
              Hirudinea   Helobdella

Arthropoda   Crustacea   Amphipoda   Hyallela azteca
                          Decapoda   Cambarinae (?)

              Insecta   Ephemeroptera   Caenis
                                        Cinygmula
                                        Hexagenia
                        Odonata   Leucorrhinna
                                  Tetragoneuria
                                  Trapezostigma
                                  Ischnura
                        Megaloptera   Sialis
                        Trichoptera   Leptocella
                        Coleoptera   Haliplidae   Peltodytes
                                                  Haliplus
                                     Dytiscidae   Agabus
                                     Hydrophilidae Berosus
                                                   Paracymus
                                     Elmidae (?)
                        Diptera   Culicidae   Chaoborus
                                  Chironomidae Chironomus
                                  Ceratopogonidae   Palpomyia

Molluska   Gastropoda   Physidae   Physa
                        Planorbidae   Heliosoma
                                      Gyraulus
           Pelecypoda   Sphaeriidae   Pisidium
                                      Musculium

TABLE 6. Percent Abundances of Benthic Invertebrates. For each species and pond the mean dry weight (mg per sample) is given on the left and the percent of total dry weight on the right. The sampling date is given below the pond name. Species that were sampled, but not included in FIGURE 10, are listed here. The crayfish weights are in parentheses.

TAXA	N1 24 V		N1 30 VI		N1 26 VII		N1 15 VIII		N2 7 VIII		N3 28 VII	
Chaetogaster												
Helobdella							0.39	0.52	6.34	7.43	18.96	92.40
Hyallela									2.38	2.79		
Cambarinae			0.58	0.77	0.43	0.46	0.18	0.24	0.79	0.93	(46.94)	
Caenis	0.31	2.02	6.05	8.06	0.35	0.38	0.20	0.27	1.44	1.69		
Cinygmula			0.28	0.37			0.29	0.39				
Hexagenia												
Leucorrhinia												
Tetragoneuria			6.71	8.94	3.36	3.61	14.14	18.81				
Trapezostigma												
Ischnura	3.36	21.90	11.08	14.76	11.49	12.38	7.24	9.63	6.06	7.10		
Sialis					3.12	3.35	0.13	0.17	2.00	2.34		
Leptocella	2.29	14.93							1.67	1.96		
Peltodytes	0.30	1.96										
Haliplus					0.78	0.84						
Agabus	1.09	7.11										
Berosus					0.34	0.37	0.17	0.23				
Paracymus			0.01	0.01								
Elmidae			1.89	2.52								
Chaoborus	1.09	7.11	1.48	1.97	6.20	6.66	2.88	3.83	40.20	47.08		
Chaoborus (pupae)			0.13	1.73	0.75	0.81	0.31	0.41	5.46	6.39		
Chironomus	0.19	1.24	0.92	1.23	5.87	6.30	10.38	13.81	2.58	3.02	1.56	7.60
Palpomyia			0.17	0.23	1.59	1.71	5.40	7.18	0.21	0.25		
Physa	0.38	2.48	21.68	25.88	45.29	48.64	29.77	39.61	11.64	13.63		
Heliosoma					0.19	0.20						
Gyraulus	6.32	41.20	9.95	13.26	7.70	8.27	2.08	2.77				
Pisidium			14.13	18.82								
Musculium					5.66	6.08	1.60	2.13	4.61	5.40		

TABLE 6: Percent Abundances of Benthic Invertebrates. Continued.

TAXA	S1 20 V	S1 23 VI	S1 25 VII	S1 15 VIII	S2 13 VII	S3 6 VIII
Chaetogaster		0.60	1.53	0.01	0.27	0.52
Helobdella				0.02	0.15	0.53
Hvallela		0.06	0.15	0.26	0.58	0.71
Cambarinae	(6.73)			(39.24)	(14.85)	2.49
Caenis	0.46	0.50	0.48	0.39	0.49	0.90
Cinygmula	1.29	1.27	1.08	0.75	1.72	1.86
Hexagenia						
Leucorrhinia	0.57	9.99	0.23	0.52		
Tetragoneuria						
Trapezostigma						
Ischnura		1.11	0.06	0.16	0.06	0.21
Sialis		2.83	4.12	9.25	13.47	2.26
Leptocella						0.22
Peltodytes						
Haliplus		0.04	0.10		0.23	0.47
Agabus						
Berosus						0.46
Paracymus						
Elmidae						
Chaoborus	11.55	5.90	15.04	40.48	31.72	14.96
Chaoborus (pupae)	20.14	3.08	0.35	0.68	3.85	0.53
Chironomus	24.95	63.62	17.70	39.76	5.40	10.09
Palpomyia	0.73	1.86	0.04	0.09	0.84	0.54
Physa	1.50	3.82	6.78	8.10	28.32	1.43
Heliosoma	0.12	0.31	0.48	1.08	8.07	2.95
Gyraulus				8.07	15.60	5.23
Pisidium	0.22	0.56		0.24	0.54	1.11
Musculium	0.41	1.05	0.10	0.22	10.00	20.64

TABLE 7. Fish Gut Analysis. Y indicates the average percent occurence of a food item in a gut. Rank is from most abundant to least; average ranks are used in the case of ties. All taxa are aquatic larvae or nymphs, except those with *, which are adults.

POND	RANK	TAXA	Y
N1	1.0	Anisoptera	33.33
	3.5	Ceriodaphnia	16.67
	3.5	Zygoptera	16.67
	3.5	Ephemeroptera	16.67
	3.5	Hemiptera*	16.67
N2	1.5	Anisoptera	21.43
	1.5	Ephemeroptera	21.43
	4.5	Amphipoda	14.36
	4.5	Cladocera	14.36
	4.5	Chironomus	14.36
	4.5	Chaoborus	14.36
S1	1.0	Chironomus	25.58
	2.5	Copepoda	15.09
	2.5	Ostracoda	15.09
	4.0	Chydorinae	12.02
	5.5	Ephemeroptera	6.14
	5.5	Palpomyia	6.14
	7.5	Physa	4.60
	7.5	Anisoptera	4.60
	9.5	Heliosoma	3.07
	9.5	Other	3.07
	12.0	Trichoptera	1.53
	12.0	Cladocera	1.53
	12.0	Cambarinae	1.53
S2	1.5	Cladocera	50.00
	1.5	Ostacoda	50.00
S3	3.0	Amphipoda	20.00
	3.0	Cladocera	20.00
	3.0	Notonectidae*	20.00
	3.0	Other	20.00
	3.0	Ephemeroptera	20.00

ACKNOWLEDGEMENTS

A dedication: for yesterday's friends.

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A THEORETICAL AND EMPIRICAL CONSIDERATION
OF TROPHIC DYNAMICS
IN SOME KANSAS FARM PONDS

by

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B.S., Southeastern Massachusetts University, 1972

AN ABSTRACT OF A MASTER'S THESIS

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Diverse causal agents can be assigned to observed patterns in nature, but they may generally be classified into extrinsic (abiotic or systems effects) and intrinsic (biological) factors. In this study, I consider a model of an idealized ecosystem influenced by the extrinsic factor of nutrient input and incorporating the intrinsic factor of predation. This model generates the following predictions: as an ecosystem between 3 and 4 links is enriched, the densities of the producer and secondary consumer levels should remain the same, while the primary and tertiary consumer level densities should increase. The primary producer and secondary consumer levels become subject to greater predator pressure as enrichment increases in the model, therefore the organisms in those levels should display such predator-limited adaptations as temporal or spatial displacement (predator-avoidance), altered body morph or increased growth rates. The aquatic farm pond ecosystem, particularly the subsystem based on the macrophyte-epiphyte complex, was used to test the predictions.

The body length of the most abundant secondary consumer, Ischnura (Odonata: Zygoptera), decreases with increases in primary production, and the production rates in the macrophyte-epiphyte complex are higher in the high production ponds where predator pressure is higher. Biomass densities of the primary and tertiary consumers increase with production as predicted, but the primary producer and secondary consumer levels decrease instead of remaining constant, as predicted.

This combination of verification and falsification must cause the model to be rejected in this system and modified. The theoretical thrust of the model which merges enrichment and predation into a general theory is shown to be valid by noting that the divergence from the predictions occurs within both prey groups that are presumably becoming more predator limited as production increases. This suggests that an assumption of the model has been

violated, or a new variable, perhaps coevolution between predator and prey or the structural effects of diminished macrophyte densities, needs to be accounted for.

The original model is modified to incorporate prey and predator evolution and predicts decreasing prey densities with enrichment over evolutionary time.