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PREDATION COMPONENTS AS REVEALED BY DISTRIBUTIONAL ANALYSIS OF THE *CHAOBORUS PUNCTIPENNIS* - *MESOCYCLOPS EDAX* INTERACTION

A Dissertation

Presented for the

Doctor of Philosophy

Degree

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ABSTRACT

Literature suggests that often predatory interactions cannot be adequately described as random events occurring in time. Factors that could complicate this simple description might be: intervals of no predator behavior associated with predation; digestion or some other behavior associated with predation sufficient to inhibit or prevent more events; predator learning; changed in predator search strategies; prey grouping; changes in prey defensive strategies; environmental heterogeneity; relative predator-prey size differences. Furthermore, it is suggested that Chaoborus spp. (Diptera; Culicidae) predation might be arranged such that only digestion is affecting the underlying random process.

Proportional increases in the average number of prey eaten per predator with increasing prey density are expected from random events in time. The non-proportionality of increases observed with Chaoborus predation is considered the result and confirmation of digestive interference. If digestion affects the average eaten, distributions of individual predator responses at any prey density should likewise show a digestive pause effect.

Female Mesocyclops edax (Copepoda; Cyclopoida) copepods were counted before and after 6 hours in 880ml filtered lake water with a fourth instar C. punctipennis larva. Missing copepods were assumed eaten by the larva.

7100+ observations ranging between 3 and 40 introduced prey were analyzed by a single regression of average eaten to prey density. Linear regression showed that a negative quadratic expression provided an adequate fit. A digestive pause estimate of 2.5 ± 1.0 hours per each prey item was provided through non-linear regression.

However, all empirical distributions of this data set were similar to those representing random events in time with no digestive pause; Poisson distributions. When the empirical distributions were compared to stochastically created computer simulations incorporating just 0.5 hours of digestive pause per prey item, statistical differences were detected. It was concluded that some process other than digestion was producing the observed non-proportionality.

It is suggested through elimination of complicating factors that only some form of rudimentary prey grouping, perhaps conceived as trailing, can be responsible for the non-proportionality. If so, it seems that sufficient predation attrition must implant the behavior throughout the prey population.

PREFACE

The volume of literature germane to the subject has necessitated a novel method for the presentation of cited material in order to maintain readability. At some points within the Introduction and elsewhere if necessary, where literature is to be cited, a parenthetical number indicates where in Appendix A a list of cited literature may be found. Each list may be divided. Contributory Literature is that which is most applicable to the present situation and from which a particular theoretical concept may have been developed. Pertinent Literature refers to that material in which a discussion of the particular subject is presented or where applicable material resides but has not directly aided in conception or has employed materials more distantly related to those used here.

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CHAPTER I

INTRODUCTION

A. The Implication that Predation Alters the Structure of Prey Populations

It has been shown through the study of ecosystems perturbed by the elimination (1)* or introduction (2) of predator populations, that predators have profound effects on their prey populations. Of natural, unperturbed ecosystems, those in which certain predators occur have different community structures than systems lacking these predators (3). Even the characteristic prey morphology can be different between such systems. The differences in density and genotype distribution which characterize a prey population corroborate the assumption that predation is effective in altering those characteristics. Correlations have been drawn between predator density or activity and the mortality rates of prey populations by monitoring population dynamics and demography (4). If the substantial predation pressure imposed by constant attrition is sufficient to control or regulate (5) natural prey populations as implied by the observations above, observed natural stability of prey density might result (6). It is therefore important to provide some measure of the predation pressure as applied in natural

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*Appendix A contains lists which appear parenthetically in the text, a brief description of the subject referenced, and the page number of text appearance. The complete reference may be found in the Bibliography.

situations. Furthermore, the evolutionary tendencies of populations having differing phenotypes, already correlated to variable predation rates (7), might become predictable with predation pressure quantification.

There have been some attempts to compare predation rates derived from observed laboratory behavior to estimated field mortality rates (8). However, lack of precision in the estimation of these rates precludes the dismissal of other factors potentially involved in the construction of prey population characteristics. It seemed that much difficulty experienced in these investigations might have arisen from the injudicious selection of interactions that were too complicated. It became apparent then, that the least complicated type of predator-prey interaction might have the greatest potential for providing the necessary precision for application of laboratory derived predation rates to entire predator populations. In order to determine what might be an uncomplicated or simple predator-prey interaction, it is necessary first to provide a definition of such an interaction, secondly to provide a list of possible complications, and finally to examine the particular predator-prey interaction used in this study as potentially lacking these complications.

B. A Definition of a Simple Predator-Prey Interaction

The predation rate is the number of interactions between individual prey and predators within a specific time interval that result in predator success or, in other words, consumption of the prey item (9). A predator can be considered a stationary or moving point in

space surrounded by a volume defined by isopleths of successful predation probabilities for dimensionless prey items. Kerfoot (1978) illustrated response probabilities in this fashion and it is similar to that discussed by Riessen et al. (1984). The probability of a successful predation event is conditional on the probabilities of the occurrence of the following events:

a. the item will be recognized by the predator,

b. the recognition elicits a response,

c. the response results in capture,

d. and the captured item is ingested (10).

If the probabilities of these events remain constant for individual predators and if their averages remain constant for the population, the predation rate will only depend on the rate at which prey appear in the volume of successful predation probabilities surrounding the predators. If animals are randomly distributed, moving at a constant mean rate, and the prey density remains constant, the prey appearance rate and therefore the predation rate will be random and can be modelled as a Poisson process (11). Under these conditions, the Poisson parameter becomes the mean appearance rate, a constant, multiplied by the prey density and the time interval during which predation can occur (12). The above, a process which can be explained as a Poisson process, defines a simple predator-prey interaction.

C. Characteristics of Specific Predator-Prey Interactions Which Can Complicate the Simple Description

It is possible that this simplistic predator-prey interaction does not exist. Complications can interpose by altering the prey appearance rate or the conditional probabilities (see above). These complications can arise from changes in predator or prey behavior, spatial or temporal heterogeneity, or a synergism of these.

Predator Behavior

Behavior unallied with but precluding predation. Predator behavior alterations can decrease or increase the predation rate. Perhaps the most easily recognizable behavior alteration decreasing the predation rate occurs when the predator is involved with something unassociated with but precluding predation such as reproduction or rest (13). Previous authors (14) have undoubtedly included intervals of this type when calculating predation rates (15) and this can jeopardize the estimation of other behavior alterating agents (see below).

Sensory perception of prey sufficient to reduce or eliminate the probability of an immediately subsequent predation act. Behavior initiated and sustained by sensory contact with a particular prey item sufficient to prevent additional predation acts (pursuit, handling, and digestion) may also effectively reduce the time allotted for predation (16). These intervals may vary due to prey items of differing description. This would seem particularly true if wide variation in

size and morphology exists within the prey community (17). It may also be possible that a predator can reduce this interval by practice on a particular prey type (18).

It has been suggested that the internal sensory perception of a prey item or items, while not absolutely precluding predation, may reduce the conditional probabilities, particularly the probability of responding to a recognized prey item (19). This inhibition in the propensity to prey may vary with the exposed prey type (20) but should be generally distributed to all prey species. The inhibition may increase with the accumulation of undigested prey (21) and may gradually dissipate as consumed prey items are digested. If this is a true representation of the digestive process, the mathematical description must be far more involved and the quantification equally more difficult than that required for a simple pause.

Probabilities of predator success increased by learning. Prey characteristics, if remembered by the predator, may allow the predator to improve the chance of it getting more of the same. Investigations have revealed this predator ability to remember certain prey characteristics (22). Any alternative prey species may also have their probability of being eaten altered by the consumption of a different species. The alternative's chances of being eaten would increase if its characteristics were similar to those of a recent food item but, in natural circumstance, it will probably be dissimilar and thus less likely recognized as food. With learning emplaced, the successful probability volume for each prey species surrounding each predator

would be constantly changing depending on what the predator has eaten and when.

Ultimately, the chances of a predator discovering a particular type of prey depends on the number of that prey available. If an individual becomes a prey item, it alters for that predator the successive conditional probabilities for all prey types. Therefore, the probability of any individual becoming a meal depends on its species density and also the densities of all alternative prey types. Even events no longer remembered by the predator, by having affected its behavior, have individualized its probability of recognizing and taking any prey type. When considered with the natural, spatial heterogeneity of prey availability, enormous variability is possible, if not expected, in the probabilities of predation within and between predator populations. This factor, perhaps more than any other, confounds the estimation of predation rates.

Learning ability has been exhibited by vertebrate predators (23). Perhaps even some invertebrates possess the ability to distinguish prey based on experience (24), but the opinion is by no means unanimous. To avoid this complication requires much care in selecting the participants for predation rate estimation.

Probability of contact with prey increased by predator search behavior alteration. A predator may increase the prey appearance rate by altering its search technique (25). This alteration is usually conceived as a maintenance of position close to where recent contact with prey occurred. If the contact were unsuccessful, the prey item

may remain in the vicinity. Of course, the success of this ploy is dependent on prey behavior.

Prey may also congregate (26). If so, maintenance of position may effectively increase prey density and therefore the prey appearance rate (27). If prey associate with a particular environmental assemblage, predator recognition and response to the assemblage alone could increase the probability of success. Furthermore, when inundated with prey, a predator might familiarize itself with that prey's attributes to allow an increase in contact and capture probabilities and/or a decrease in the handling time (28), with a resultant increase in its own potential predation rate.

Prey Behavior: Congregation and Changes in Defensive Strategies

If prey maintain groups, the rate of appearance within the successful predation probability volume surrounding a predator becomes dependent upon the number of groups which can potentially enter that volume and not the number of individual prey. If this volume, within which prey recognition is possible, does not increase proportionally with the size of a group, then the prey appearance rate would be expected lower than if the prey were randomly distributed. If, in addition, the predator were likely to lose contact with the group after consuming only a small proportion of them, such as might be expected from a predator incorporating substantial pursuit and handling intervals or a long digestive pause, the predation rate could be expected to be lower than if the predator were making more frequent

contact with isolated prey items (29). This is particularly true for ambush predators which do not have the luxury of changing hunting behavior (30). Furthermore, if detection of predators substantially lowers the probability of capture, vigilance might be better maintained by a group (31). Predator confusion within a congregation may reduce the capture probability (32).

The implementation of various defensive strategies by prey may increase the variability of the conditional probabilities or even the prey appearance rate if predator presence is determined or predicted prior to recognition by the predator (33). If different populations employ different strategies, characteristic predation rates might exist.

Physical Conditions

Spatial and temporal heterogeneity. Spatial and temporal variation of environmental characteristics may introduce variation in the predation rates between the populations or the same population over time. Objects within the successful predation probability volume would reduce or alter the shape of that volume. Variation between areas in the effect of objects on those volumes could result in characteristic predation rates for each area (34). If prey associate with environmental assemblages and the size, quantity, and quality of those assemblages vary, predation rates could be different for populations inhabiting different areas. Even within a population, quantification of the predation rate might be impossible due to complications induced by environmental heterogeneity.

By offering refuges, spatial heterogeneity may remove, as potential prey items, a constant proportion of the prey population, thus lowering the prey density relative to a predator. Refuges may be located within or immediately adjacent to the predators' feeding volume into which small numbers of prey can escape predation for only short periods (35). Otherwise, refuges to which large numbers of prey can migrate and remain indefinitely or for extended periods (36) may even contain entirely different predator populations (37).

Heat and light vary both diurnally and seasonally and can present vastly different conditions at different times. Different sets of conditions may have greatly different associated predation rates (38). This type of variation restricts the interval during which constant predation rates might exist. Behavioral change can be cued into circannual rhythms by small changes in external stimuli. When the cues are unknown, the prediction of intervals of constant behavior is even more difficult.

Relative participant sizes. Relative sizes of participants in predator-prey interactions are extremely important in determination of predation rates (39). Frequently size is a reflection of age. Each predator age class may therefore have a characteristic set of associated conditional probabilities (40). The same can be true for each prey age class, with the extreme example of invulnerable classes (41). Even the prey appearance rate may be characteristic for specific age class interactions, especially if movement varies with the age of either or both participants (42).

D. The Application of Predation Rates to Field Situations

If experimental predation rates are to be compared to field mortality estimates, the physical complexity of a natural system may increase the difficulty of monitoring necessary prey and predator population characteristics. Finally, all forms of predation in the system must be evaluated in order to assign the total impact of predation.

E. Discussion on the Possibility that the *Chaoborus*-*Mesocyclops* Interaction Is Simple

Diptern larvae of the genus *Chaoborus* are the only insects that truly inhabit the limnetic zone of lakes. They accomplish this with diurnal migration. Propelling themselves with a fan of setae at the tail of the half-inch, slender, wormlike body, they tumble upwards for tens to hundreds of meters. By dawn, some species and instars have resettled to the benthos where they bury themselves and disappear. As the clear larvae are seldom seen, they have been given the common name, phantom midge.

While settling from the surface, the older instars of the larvae catch, with grasping antennae, their food which is primarily a wide variety of crustacean zooplankton. Among these, *Mesocyclops* species, scavengers and part-time predators, are represented. The size, shape, armor, and amazing speed of these powerful copepods must demand a most adroit predator to affect capture.

Besides offering abundant and experimentally manipulatable organisms, the Chaoborus-Mesocyclops interaction described below would seem to contain few if any of the complicating factors described above. The following discussion presents each complicating factor as it applies to this interaction. The discussion is based on information gleaned from the literature.

Predator Behavior

Behavior unallied with but precluding predation. Chaoborus larvae feed on Mesocyclops in the limnetic zone of lakes, frequently close to the surface. The fourth and final instar of Chaoborus, particularly C. punctipennis (Say), which was used in this study, only visits this zone nocturnally and remains in the sediments during the day (43). The ploy has probably evolved as a defense against visual vertebrate predation (44). The clear bodies of the larvae support this contention (45) but also indicate that even under the cover of darkness, the zone is dangerous for the larvae. A strong selective advantage must be gained through migration to offset both the danger entailed and what must be a tremendous expenditure of energy through the upward tumbling.

No advantage directly related to reproduction can be gained by larvae but it has been suggested that an oxygen debt, incurred while in the sediments and relieved during migration, might cause migration initiation (46). However, larvae have survived for weeks in anaerobic conditions (47) so it seems unlikely that daily migration would be necessary for oxygen debt relief. Furthermore, oxygen debt relief

would hardly need migration to the lake surface, where most larvae arrive daily (48), but could be achieved far closer to the sediments.

The only other suggested selective advantage of migration is exposure to prey (49). As feeding leads to pupation and reproduction, those individuals feeding more quickly might pupate earlier and thus spend less time in their threatened position in the limnetic zone. Some authors have gone so far as to suggest that during the sojourn in the limnetic zone, larval behavior is totally restricted to that directly related to hunting (50).

Sensory perception of prey sufficient to reduce or eliminate the probability of an immediately subsequent predation act. Extended pursuit has never been observed for Chaoborus (51). Handling time is relatively short, usually less than five minutes (52), and the prey consumed with little mastication (53). Monchadskii (1945) and Pastorok (1980a) observed that the capture and swallowing of prey was not dependent on the physical condition of previously consumed prey in the digestive tract of Chaoborus. Smyly (1980) observed that Chaoborus flavicans (Meigan) would stop feeding when their pharynx was filled, which required three to five adult Mesocyclops leuckarti (Claus). This could be achieved only at or above prey densities of one prey for every four to eight milliliters, which seems extremely high for natural conditions. It seems that the larvae might possess the potential for continuous recognition and reaction to prey.

In summary, each limnetic zone feeding:

a. requires a large energy expenditure,

b. is life threatening,

c. is a restricted interval,

and the resultant necessary digestion can be accomplished during the subsequent twelve to fifteen hours the larvae spend interred. It seems more than reasonable that a process should have evolved which requires the fewest limnetic zone feedings to achieve reproductive potential, that is, that each feeding is as productive as possible. The presence of any digestive relaxation of hunting concentration during limnetic zone feeding seems unlikely.

Probability of predator success increased by learning. As was stated earlier, predator learning produces a predation rate dependent not only on the density of the particular prey species under consideration but on the structure of the entire prey community. Many authors believe invertebrates are incapable of increasing their probability of prey capture through learning (54). This is particularly true for Chaoborus (55). The problems potentially created by this most crucial complication are presumably inoperative.

Probability of contact with prey increased by predator search behavior alteration. The only observed method of prey capture employed by planktoric Chaoborus larvae has been from ambush (56). If no other search strategy exists, no alteration can occur.

Prey Behavior: Congregation and Changes in Defensive Strategies

No mention was found in the literature of zooplankton deliberately congregating. Congregations do exist (57) but are often

attributed to wind induced water movements (58). It seems then that with the selection of a small and well protected study area, these complications might be avoided.

Zooplankters recognize other organisms primarily through mechanoreception of water disturbances caused by their movement (59). Since the search strategy of Chaoborus does not produce such disturbances, it seems unlikely that vigilance could be important to the interaction (60). Planktonic animals, particularly copepods, possess the ability of chemoreception (61) and are known to use this in tracking wounded prey (62). However, it is not known if this ability has reached the degree of sophistication necessary for predator detection.

The defensive strategies of copepods are swift, evasive maneuvers and seem to have a consistent methodology (63). Although scantily observed, prey behavior does not seem likely to complicate the predation process.

Physical Conditions

Spatial and temporal heterogeneity. The physical homogeneity of water column, where Chaoborus is potentially a major predator (64) provides few, if any objects capable of distorting the prey recognition volume surrounding the predator (65). Neither does it provide assemblages with which the prey can associate. The homogeneity also precludes small physical refuges in the water column large enough for large zooplankters (66).

Refuge for zooplankton in small, regularly-shaped bodies of water from which they are unable to escape (67) is confined to littoral and benthic regions. Limited mobility of zooplankton restricts use of the littoral zone for refuge. Pelagic zooplankton even exhibit a distinct avoidance of the littoral zone (68). Refuge in the benthos may occur. However, for organisms adapted to pelagic living, the benthos, with its complete community including predators, not the least of which are Chaoborus larvae (69), seems to provide poor, if any refuge. In any case, refuge seeking in this type of system is usually ignored (70).

As can be ascertained from the preceding discussion, any temporal fluctuation in light can be disregarded as experimentation is initiated after dusk and concluded before dawn. Short-term temperature fluctuations are suppressed by the system's aqueous medium. Moreover, advanced Chaoborus larval instars do not seem greatly affected by temperature fluctuation (71), which seems reasonable for an animal that routinely moves through a thermocline. Since Chaoborus individuals do not remain in any instar long enough to be affected by long-term temperature fluctuations and since all individuals of a cohort are extremely close to the same age, any comparisons to indicate feeding behavior changes induced by temperature fluctuation must include differences between cohorts, completely distinct populations with radically different life histories (71). It will be seen that differences between cohorts completely obscure any possible long-term temperature induced changes.

Relative participant sizes. The identifiable and discrete stages of the copepod life cycle facilitate division of the population into subunits within which little size variability exists. Each subunit would have associated predation probabilities with a particular predator population subunit, also identifiable, discrete, and with little size variability in Chaoborus larvae (72). If initially only adult copepods are used, several problems can be avoided. Adult copepods do not increase in size with age. Maturational losses to the next age class need not be considered. However, prey "population" recruitment would arrive from the penultimate age class and could not be simply estimated from fecundity.

The Application of Chaoborus-Mesocyclops Predation Rates to Field Situations

Many conditions normally producing difficulty in the compilation of population characteristics necessary to provide field mortality estimates do not exist in the homogenous medium of the limnetic system. In addition, numerous organisms are easily collected to allow for quantitative data.

Frequently, small ponds and lakes cannot support large effective limnetic vertebrate planktivore populations (73). Even the number of large invertebrate planktivore populations may be severely restricted. It is common to find only one such planktivore, Chaoborus sp., in a small pond (74). In this type of situation, additional predation occurs only within the microcrustacean community. Frequently, the largest predatory member of the crustacean community is a cyclopoid

copepod (75). It is possible then, if the investigated prey were adult Mesocyclops, that no simultaneous predation other than cannibalism could produce enough attrition to alter population characteristics.

The Repudiation of the Chaoborus-Mesocyclops Predation Interaction as a Simple Process

While it seems reasonable that circumstances might allow representation of the Chaoborus-Mesocyclops, predator-prey interaction as a Poisson process, collected evidence refutes the argument (76). In reported situations, similar or identical to what is attempted herein, the second derivative of the predation rate as a function of prey density is negative (see Figure I, Appendix E). With a Poisson process, this derivative and therefore the predation rate velocity over prey density is constant. Where identified, the complicating factor producing deceleration is always assumed to be an internal sensory perception of previously consumed prey or in other words, a digestive feature. This feature can be in the form of a pause, a probability reduction for a successful predation act, or otherwise.

Two basic types of confirmation of the assumption that the predation process is complicated by a digestive feature have been attempted. The first involves the time required to resume feeding after complete satiation (77). The necessary assumption here is that the pause or probability reduction caused by a single prey item is constant regardless of the volume of undigested gut contents. This assumption may be reasonable within a lower range of gut content

volumes; but as a complete satiation is approached, it seems quite likely that the digestive effect would appreciate considerably.

In the second type of confirmation, two or more prey species, for which the predator has different initial preferences when gut content is low, are presented simultaneously. As gut content increases, the predator more often consumes the preferred prey (78). However, due to the many variations of initial situations which must be tested (gut content, relative and absolute prey densities), it is difficult to provide the necessary replication at all situations to achieve statistical significance if preference actually changes with gut content. Furthermore, it seems a questionable practice to compare situations where multiple prey species are presented to that where the predator has no choice in prey type.

A much simpler confirmation is available. As the average number of consumed prey per predator is being developed from the observed number of prey eaten by many individual predators, necessary for the regression of predation rate as a function prey density, a discrete distribution of the proportion of individual predators exhibiting specific responses in the number of prey eaten is also developed (see Figure II, Graph A, Appendix E). One can assume that if a digestive feature is affecting the average number of prey eaten, it would also affect the proportion of predators exhibiting specific responses. In particular, if a digestive feature is operating, the proportion of individual predators consuming large numbers of prey should be reduced from that where the predators can consume constantly as is assumed in a Poisson process. Furthermore, to offset this and maintain the same

average, more individual predators must consume some prey when a digestive feature is operating than when a few individuals exhibit large numbers of prey eaten as in a Poisson process (see Figure II, Graphs B and D, Appendix D). Here, the problem of comparing data collected under different conditions is avoided.

Two major problems arise from this type of analysis. Distributional comparisons require extremely large numbers of individual responses at any particular set of circumstances to allow fine differentiation. Secondly, a method for the prediction of the effect of a digestive feature on distributions was not found to be immediately available. It is hoped that the reader will agree that an adequate solution has been found for both problems.

CHAPTER II

METHODS AND MATERIALS

The basic experimental design was to place a single fourth instar Chaoborus punctipennis larvae with a particular number of adult, female Mesocyclops edax, with or without eggs, in a known volume of filtered lake water. Those M. edax which were not recovered after a specific period of time were assumed eaten by the larvae. Controls indicated that while some prey were either physically lost or miscounted, mistakes normally involved less than one percent of the total count (see Controls, Methods 1, Appendix B).

Organisms were collected from I. C. King Lake, a shallow, eutrophic, two-acre lake, four miles south of Knoxville, Tennessee. This lake was completely destroyed in September 1986 for road construction. A plankton net 30cm in diameter with apertures of 245 microns was towed at or near the surface some time after sunset. The total distance towed varied from 150 to 200m. Water filtered from I. C. King Lake and replaced every three or four days was used for all isolation and experimental procedures.

Collected organisms were taken to the laboratory, with those destined for experimentation isolated as soon as possible. The sample was poured through a net, 10cm in diameter with 500 micron apertures, floating just below the water surface in a large finger bowl. Small organisms passed through this net. The net was removed from the finger

bowl and quickly inverted onto filtered lake water in a 100 by 15mm petri dish, thereby releasing the organisms.

Chaoborus larvae were individually removed from the petri dish with a Kahn serological pipette and placed on depression slides. At the beginning of the study a dozen or more larvae from each of the several morphologically distinguishable types present were identified using Cook (1956) and all were found to be C. punctipennis. As no other morphological types were seen throughout the study, it seemed reasonable to assume that only that species was present. Length was more easily determined than instar development and seemed to provide a reliable method for limiting experimental subjects to those with similar feeding habits. Preliminary evidence indicated that larvae smaller than 7mm would not eat as many of the large M. edax adult females as larger larvae predator size (see Methods 2, Appendix B). Larvae larger than 8mm frequently pupated before termination of the experiment, invalidating that observation. Therefore, experimental subjects were restricted to larvae between 7 and 8mm in length. All individuals of this size which were checked were of the fourth instar. Larvae were measured from the base of the antennae to the posterior end of the anal segment with a clear disk of known diameter attached to the stage of a dissecting microscope (7.5-30 power).

Individual larvae between 7mm and 8mm were transferred by Kahn pipette to shell vials containing approximately 30ml filtered lake water. Preliminary observations revealed no statistical evidence that extended intervals of predator isolation (starvation) affected feeding behavior (see Isolation Interval, Methods 3, Appendix B). However,

since the average number of prey eaten was somewhat higher for fresh predators, perhaps a result of greater vigor, larvae were never held in isolation longer than sixteen hours before being used in experimentation. To avoid a carry over digestive pause, the isolation interval was never less than twelve hours.

As ambient temperatures could not be held constant throughout the laboratory experience of either predator of prey; the revelation of temperature effects requires an as yet unestablished baseline; the projected analysis requires large amounts of poolable data collected under similar conditions; and finally as there is reason to believe that the effect of temperature variation may be relatively unimportant to this particular predator-prey interaction (see Experimental Temperature, Methods 4, Appendix D), temperature manipulation, whenever possible, was conducted solely to promote constancy. To this end incubation temperatures were arbitrarily set at 20°C.

Before sunset the day following collection, the individual larvae were transferred with the water in the vials each to its own quart canning jar containing 820ml filtered lake water. The animals seemed to react well with that volume, natural occurring prey densities could be approximated, and there is precedence for both that approximate volume and the use of a single volume throughout a study (see Experimental Chamber Size, Methods 5, Appendix B). The larvae were inspected at the time of transfer for death, pupation, or aberrant behavior. The jars were placed in darkened incubators and the larvae allowed to acclimate for three to five hours.

Copepod prey were found to concentrate toward or directly opposite a fluorescent light placed at the edge of the petri dish. These concentrations were transferred to depression slides with a Kahn pipette. When viewed under a dissecting scope, all organisms other than adult, female M. edax were easily removed with needles or Pasteur pipettes. The isolated M. edax were then transferred to a 250ml beaker containing filtered lake water. Normally, over 2,000 prey were needed for each experiment run of 100 or more observations.

It was necessary to design an apparatus for counting the strong swimming copepods into groups of between 3 and 40 as capturing them individually is decidedly too slow (see Counting Apparatus, Methods 6, Appendix B). With this apparatus, it was possible to count accurately 1,000 or 2,000 copepods in any size lot in about an hour. Vials containing counted copepods were inspected, dead organisms replaced (usually no more than 10 individuals for the entire count), and filled to approximately 30ml with filtered lake water.

Prey were transferred to the quart jars containing the larvae the evening following their collection. This transfer, considered the initiation of the experiment, was begun at 10:30PM and required about half an hour for completion. Transfer was conducted under red light so as to disturb the larvae as little as possible. As it was impossible, under red light, to inspect the vials to ensure that no prey remained in them following transfer, the vials were dunked in the quart jars after pouring. Control data indicated that dunking improved precision (see Controls). This transfer raised the final volume in the

jars to approximately 880ml. The quart jars were returned to the darkened incubators.

It was felt that the larvae might not maintain a constant feeding rate throughout the nocturnal period. Other activities, such as migration, could conceivably divert their attention (see Introduction, page 11). It is also conceivable that such diversions may continue in artificial surroundings even though the objective, such as migration, is impossible. For that reason, experimental initiation was begun well after sunset, 10:30PM, with the conclusion before sunrise, 4:30AM. Preliminary data indicated that the predation might not remain constant for a longer interval (see Experimental Interval, Methods 7, Appendix B).

At the end of the six hours, the contents of each jar were poured through its own 250 micron screen, 20mm in diameter. It required no more than half an hour to screen all jars. It was assumed that no feeding could occur on screens before death. After the screens had dried, the remaining copepods were easily counted under the dissecting scope.

CHAPTER III

RESULTS

Data analysis consisted of four phases:

1. an estimation of the effect of a digestive feature was established from the regression of average predation rates, derived through experimentation, across a range of prey densities;
2. distributions, with parameters (mean number consumed at specific prey densities) equal to those of specific data distributions, were created in a manner which includes the effect of a digestive feature, the estimation of which was provided by the regression above;
3. these created distributions incorporating a digestive feature were compared to distributions created as if no digestive feature existed to indicate where comparisons of data distributions to both distributional types might have statistically different results;
4. those data distributions identified above were compared to each created distributional type.

Based on the preceding discussion, it seems reasonable that if no digestive feature were operating, the distributional results of this particular predator-prey interaction might be estimated as a Poisson process. However, if a digestive feature were operating, no method for direct distributional estimation was discovered. Therefore, stochastic

computer simulation was employed to provide distributional estimation affected by a digestive feature. As the implementation of distributional analysis of predator-prey interactions did not appear in the previous studies reviewed here, it seemed advisable, for an initial analysis, to choose a simple description for the digestive feature.

An accepted representation of a simple digestive feature, a pause absolute in both duration and predator inhibition, is described by the traditional Holling Disk formula (Holling, 1959a). The non-linear regression of data with this formula provided the regression estimation of a digestive pause for the first phase of data analysis. The range of initial densities chosen for analysis extended from three prey per 880ml to 40 prey per 880ml. This range was such that a significant proportion of the exposed prey were removed during experimentation (see Methods 1, Appendix B), any rough estimation of natural prey density was included, and the ability to supply counted prey was not strained.

In the Holling Disk formula,

$$MU = \frac{TOT * AHT * D}{1 + AHT * DP * D}$$

where:

a. MU is the average number of prey consumed per predator;

b. TOT is the interval during which predatory acts can occur;

c. AHT is the average hunting time, the average interval between that instant when a predator will respond to prey to when capture is affected;

d. D is prey density;

e. DP is the digestive pause, the interval from when capture is affected until the predator will again respond to prey presence and is a constant.

This formula and the partial derivatives of MU with respect to both AHT and DP were introduced into the SAS Non-linear Regression model along with data in the form of MU's over a range of D's. From this estimations of both AHT and DP were obtained.

For the second phase of data analysis, stochastic computer simulations provided distributions where the predation process was affected by a digestive pause. As in the Holling Disk formula, the proposed model was based on the time required by a "predator" to perform certain tasks relative to the total amount of time available. Those tasks were again prey detection, or hunting, and digestion. Detection was considered accomplished only when it results in prey consumption.

The model tracked the intervals, during which the behavioral patterns are performed, for a series of individual "predators." The initial hunting interval for each "predator" (it was assumed that there was no initial pause) was a pseudo random number generated from an exponential distribution. If this interval was less than the total time allocated for the "experiment," a "prey item" was considered to have been eaten. If this initial interval, summed with a constant digestive pause, was less than the total allocated interval, a second random interval was generated, summed with the previous intervals and compared to the total allocated interval. Again, if less than the total, a second "prey item" was considered to have been eaten. The

process was continued for each "predator" until the total allocated time was expended. The operation was repeated for any number of "predators" with each placed in a category as to how many "prey items" it had eaten. As hunting time intervals were generated from an exponential distribution, if the digestive pause was excluded, the resultant distributions were homogeneous with Poisson distributions (see Results 1, Appendix C).

In the third phase of data analysis, distributions created through the process incorporating a digestive pause as suggested by regression were compared to distributions of the same average number of prey eaten per predator where no digestive pause was involved. A Poisson distribution is, theoretically, appropriate as a representation of the results of a process unaffected by digestion.

However, the assumption of a Poisson process, that the number of possible events, or density, is constant, is violated by experimental procedures. In an experiment, every time a prey item was eaten, the density was reduced from (n) to (n - 1). Whereas, before that consumption the Poisson parameter (λ) was equal to (n) times the probability of a predation event (p), following the removal or consumption, the Poisson parameter becomes (n - 1) times that probability (p).

It was deemed necessary to determine if this reduction altered resultant distributions such that they were distinguishable from Poisson estimations. Furthermore, mean predation rates might have been substantially reduced by this process, perhaps more important to field comparisons than the present analysis (see Density Reduction

Phenomenon, Results 2, Appendix C). Analysis revealed that the complication of density reduction did not produce a necessarily accountable effect in either distributional or mean regressional methods at observational numbers experimentally possible. At approximately those observational levels (1000 observations in each distribution), homogeneity was reduced by less than 12%. Average homogeneity between Poisson and exponential simulation distributions was 0.981. Average homogeneity between Poisson and exponential simulation incorporating density reduction distributions was 0.866 (see Tables 5 and 6, Appendix D). Means were reduced by only about 2% across the range (see Table 7, Appendix D).

The comparison of digestive pause estimations from distributional and mean regressional analysis created a dilemma in experimental data collection. Precision in the pause estimation through regression can be improved by data collection at as many points within the independent variable range (here density) as possible. Alternatively, the pause estimation from distributional data is improved by concentrating collection at a single initial density. Replicative capability and organismal availability dictated that temporally segregated data groups would necessarily be pooled if adequate empirical data were to be provided for both types of analysis.

Within years, mean predation rates gathered within as little as a ten day period can be significantly different from rates developed before and after as indicated by covariance analysis (see Seasonal Variation, Results 3, Appendix). This suggested that variation between years might exist. Owing to the necessary provision of large groups of

observations at a few densities, it was not possible to compare data from all years by analysis of covariance as in some years data was collected at only a few densities (see Table 13, Appendix D). It was possible to conduct that type of comparison between the summer data of 1983 and 1984 (see Table 14, Appendix D). While the probability that both groups of data belong to the same population is only approximately 0.25 and is not as high as that normally suggested for pooling (0.75, Sokal and Rohlf, 1969), pooling still seemed reasonable as data of this type had never been collected to this extent before (see Table 15, Appendix D).

This pooled data set provided mean numbers consumed at many points across a wide range of densities. From this, a pause and its possible variability could be estimated through regression. It was felt, that if further pooling of other data sets with this set neither increased the digestive pause estimate through regression nor reduced its predicted variability, any undiscoverable differences in the mean rates would not produce false conclusions in the comparative analysis.

Far more serious problems may develop when distributions are summed. Homogeneity between distributions collected in different years was occasionally quite low (see Table 16, Appendix D). Unlike regression analysis where the addition of a few disparate means would have little effect, heterogeneous distributions might provide equal volumes of data for summation. A feature of Poisson distributions, the summation of two distributions with different parameters results in a Poisson distribution having as its parameter the mean of the originals, did not appear to extend to distributions where digestive pauses were

involved in the creation (see Distributional Summation, Results 4, Appendix C). This summation may indicate a shorter digestive pause than was actually operating but constitutes only a slight threat to the integrity of comparisons to pauses estimated through regression as the estimated pause should never be lowered by more than 10% to 12% from the actual with conditions experienced here.

Nevertheless, to avoid controversy, empirical data were organized into three groups. The complete comparative analysis was first conducted for all distributions within the pooled 1983 and 1984 data only. The average p-value from X-square tests of homogeneity through the 14 comparisons of 1983 and 1984 distributional data was 0.62. When distributions from 1980 and 1981 were compared to each other and to the distributions of 1983 and 1984, the average p-value from 18 tests was 0.54. Of the 31 comparisons of 1979 and 1982 data distributions to each other and those of 1980, 1981, 1983, and 1984, the average p-value was but but 0.39 (see Table 16, Appendix D). Complete analysis was conducted on each of these three poolings.

The regressed pooled data set means showed that a highly significant amount of variability was explained through a quadratic expression in all three pooling group instances (see Table 18, Appendix D). Therefore, it seemed appropriate to estimate through SAS non-linear regression parameters for both a hunting time probability distribution (λ) and a digestive pause from each of the three data sets.

The digestive pause indicated by the regression of the pooled 1983 and 1984 empirical data set was somewhat greater than that where

more data were included. However, the startling aspect, regardless of the data group, was the large size of the pause estimation, 2.5 to 3.2 hours, practically half the time of the experiment (see Table 19, Appendix D). Even at the lower limit of the 95% confidence interval, the pause estimated for any set was greater than 1.5 hours, one fourth the time allotted for the experiment. With this digestive pause, one would never expect to have more than three prey consumed in an experimental observation. Even if the actual pause were only just within the 95% confidence interval, never more than four prey could have been consumed and that by only a few lucky predators.

From an inspection of empirical distributions, it can be seen that only seldom were more than four prey items consumed (see Table 15, Appendix D). Thus, perhaps the lowest regression estimate is not far off that which will be estimated from distributional analysis. Still, this value was only about half that expected. It seems obvious, then, that distributional analysis will give a lower estimate of the digestive pause than regression analysis.

Even should the actual pause have been immeasurably small and thus approach a Poisson process, not all experimental distributions could have been expected to show significant differences with distributions incorporating pauses equal to that suggested by regression. This would seem particularly true for distributions with low means, occurring at low densities, where, as predators ate fewer times, proportionally less of their time was spent in digestive pause. Also, distributions might not contain a sufficient number of observations to indicate significant differences.

It seemed advisable then, to identify those empirical distributions where the parameter combination of mean number consumed and the number of observations might allow a significant difference between simulated distributions incorporating a pause less than that suggested by regression and Poisson distributions. Homogeneity suggested by empirical distributions of different parameters could not be considered conclusive as heterogeneity could not be revealed (see Digestive Pause and Poisson Distributional Comparisons, Results 5, Appendix C).

The identification process revealed many distributions which should show significant differences when compared to Poisson distributions if a digestive pause as indicated by regression was operating. In addition, several distributions should show significantly different comparisons if the pause is far lower than that expected.

However, not one empirical distribution showed a significant difference when compared to a Poisson distribution of the same mean (see Table 21, Appendix D). The empirical distributions were then compared to simulated distributions. The digestive pause of the simulations was that discovered through comparisons of simulation and Poisson distributions (see Results 5). There, a pause just a tenth hour longer would likely produce significant heterogeneity but at the pause used, the Poisson and simulated distributions were not likely to be significantly different.

Eleven distributions of isolated empirical data were each compared to three simulated distributions incorporating a pause of the

duration discussed above. In nine of these cases, the likely probability that the distributions were different was not only significant but had an average less than 0.005, an order of magnitude below that which might be expected, 0.05 (see Digestive Pause and Empirical Distributional Comparisons, Results 6, Appendix C).

This suggests that:

1. the actual process was affected by a complication quite unlike the conceived digestive feature,
2. this complication contributed to the heterogeneity between empirical and Poisson distributions,
3. without this complication, empirical and Poisson distributions would have appeared even more homogeneous,
4. the existence of a pause, such as suggested by regression, was even less likely than as it may first have appeared from inspection of the homogeneity between empirical and Poisson distributions (see Figures II, III, IV, V, Appendix E).

Inspection comparisons of the nine empirical distributions mentioned above with Poisson distributions of identical means showed in each case a greater number of individual predators consumed no prey in the empirical data. Of the 26 isolated empirical distributions of the final pooling, 23 had an identifiable proportion of individuals consuming no prey above that suggested by Poisson estimation. This proportion averaged almost 15% of the observations (see Table 24, Appendix D).

When the excess number of non-consumers was removed from the four most important isolated distributions (densities 15, 16, 20, and

23 of the final pooling), the p-values from homogeneity tests of the remaining consuming population subset to Poisson distributions averaged 0.92 (see Refusal to eat, Results 7, Appendix C). (Including any non-consuming individuals in comparisons to Poisson distributions as herein may be inappropriate and should be investigated.) When the heterogeneity from non-consumers was included, the average probability of homogeneity was below 0.5 (see Table 23, Appendix D).

This unexpected increased level of non-consuming predators could have resulted from:

1. an experimental artifact induced by handling the organism,
2. individuals not feeing at every migration,
3. some individuals collected for experimentation during migration that would not have participated in the subsequent migration when experimentation took place.

In any case, the result is easily understandable.

It seems evident that by far the greatest source of differences between empirical and Poisson distributions was being contributed by non-consuming individual predators, just those animals which had no possibility at all of being affected by any type of digestive feature. Perhaps the most interesting case is the empirical data collected at a density of 20 prey per 880ml. When the non-consumers were removed, the p-value from a test of homogeneity with a Poisson estimation was greater than 0.99 (see Table 23). However, at the same parametric level, the distributional differences induced by a pause of but a half-hour would likely have reduced the p-value to around 0.5 (see Table 20, Appendix D). This half-hour is less than a fourth that of the most

conservative estimate by regression and far below the 95% confidence interval (see Refusal to Eat Regressional Analysis, Appendix C).

CHAPTER IV

DISCUSSION AND CONCLUSIONS

From the preceding discussion, it seems reasonable to assume that:

1. regression analysis is an inappropriate method to estimate a digestive pause,
2. a digestive pause does not exist in the volume necessary to produce the curvilinearity exposed in regression analysis,
3. while other methods of digestive feature representation (Metz and van Batenburg, 1985) might create less of a conflict between regression and distributional analyses, some other process was producing the greatest part of regression curvilinearity.

In an effort to promote parsimony, it seems most reasonable to assume the non-existence of a digestive feature operating within the C. punctipennis-M. edax interaction.

It becomes incumbent then upon this author to describe a process which would colligate results observed in both the regression and distributional analyses. Perhaps a suitable manner for the discovery of such a process, particularly in the light of the simplified situation, is that of elimination.

Since the experimental design included only two variables, prey density and the number of prey eaten, these are the only factors that can affect behavior of prey or predators to produce the observed

results. In the theory that a digestive feature produces deceleration, the number of prey eaten affects the behavior of the predator. Although differences between adjacent means of the number of prey eaten across the density range were small, there was still an observable deceleration when those means were compared by regression. One might have expected then, when comparing the responses of individuals where there were large differences between the number of prey eaten by those individuals, the differences in the effect on predator behavior would be even more pronounced. In fact, there was no observable effect. A similar argument exists if the number of prey eaten were affecting prey behavior. There must be an observable effect through distributional analysis. The only possibility remaining then is that prey density is the variable producing deceleration. With that, the effect on any predator at a particular density would be identical, allowing the production of a Poisson distribution with no evidence of behavioral change.

Prey density can affect deceleration only through the behaviors of the prey or predators. In either case, differences in prey density must be discerned prior to any successful predation acts. Otherwise, even though the predation act itself is not affecting the probabilities of subsequent acts, the effect of prey density is changing those subsequent probabilities. With distributional analysis, the results would be indistinguishable from those affected by the number of prey eaten and, as above, could not have produced observed results, Poisson distributions.

It seems unreasonable that hungry predators could or would estimate prey density before acting. Even if we assume that the predator does estimate prey density, we must also assume that the predator changes its behavior accordingly. Alteration of behavior to fit environmental conditions assumes the ability to learn, at best questionable with Chaoborus. Finally, if one assumes that the more an organism eats the more likely it will reproduce, the behavioral change is disadvantageous for the actor. How could it have evolved?

Conversely, a process by which observed results can be derived through a density effect on prey behavior seems easier to accept. If prey behavior reduces the likelihood of becoming consumed and is a response to the presence of other prey, the behavior might not need to change in intensity to produce observed results, deceleration. As density increases, the probability of behavior elicitation simply increases. The prey need not estimate the density but need only react to the presence of other prey individuals. If it is more likely that prey contact each other than a predator, the behavior will be elicited prior to predation acts. If all encounters are random, the differences between predator and prey densities used during the observations herein would have insured this. Finally, the result is evolutionarily advantageous for the actor.

A description of the nature of the behavior must at this point be speculative. However, it is known that copepods can keenly differentiate sources of water column disturbances (Strickler, 1975b; Strickler and Twombly, 1975; Kerfoot, 1978; Landry, 1980; Williamson, 1980; Williamson, 1983; Kirk, 1985) and produce by their own motion

distinctive trails (Strickler, 1975a). Furthermore, males must necessarily find females more frequently than random encounters (Strickler and Bal, 1973). It seems more than reasonable then that copepods have the ability to discern and follow turbulence trails left by their conspecifics.

If the distance at which prey follow requires less time to travel than that required for handling by the predator, perhaps immeasurably short by distributional analysis, the following prey item would be invulnerable to an ambush predator. Even should the predator fail in an attempt at the leader, the turbulence created by the action might precipitate an escape response by the follower. The density relative to the predator would actually be reduced by the number of prey followers.

As long as the average interval spent following a single trail is independent of the possibility of finding another trail and is a limited interval, and the interval required for contacting appropriate trails random, the density relative to the predator would increase but at a rate less than the absolute density increase. If one were to regress the relative density with the absolute, deceleration such as the function of the predation rate to the absolute density might be observed. However, at any particular initial absolute density, the relative density would be the same for all predators resulting in a Poisson distribution. The process is evolutionarily advantageous not only for the followers but for the population as well (Hamilton, 1971; Vine, 1971; Lazarus, 1972; Theisman, 1975a; Taylor, 1976; Kiltie, 1980).

It is not intuitively obvious that trailing behavior alone could produce deceleration. Certainly the absolute density could be reduced relative to the predator. However, if trail finding were a random process, its rate should have a direct and constant relationship to prey density. If the propensity to follow trails were then a random variable with a constant mean, would not:

1. the actively trailing subset of the population increase proportionally with absolute density increases,
2. the relative density rise in a direct and constant proportion to the absolute density,
3. the predation rate, dependent on the relative density, rise with a direct and constant relationship to the absolute density?

A mathematical investigation might disclose a not yet apparent source of deceleration but it must be consistent with the amount of trailing involved, an as yet undefined quantity.

A possible source of deceleration might be found if behavioral capabilities, hitherto attributed to predators, are projected to prey behavior. Theoretically, for some predators there is a resistance to attacking specific, if not all prey types. However, after a successful encounter, precipitated perhaps by extreme proximity of predator and prey, the threshold to attack is immediately lowered. Gradually thereafter, resistance increases. A less provocative encounter shortly after a successful encounter can elicit behavior (Holling, 1965).

Perhaps trailing behavior is a threshold response. Once a trail has been followed, shortly after losing it encounters with older trails

or encounters further from the center of the trail might elicit the response. Moving through low to high density areas, elicitation of the trailing behavior would accelerate. Initially, cutting the center of a fresh trail might elicit the response but it might even be necessary to cut several trails in close succession before any response. One would expect to see little trailing at low density. This explanation is not entirely satisfactory as it intimates some sort of learning capability, not something expected from copepods.

Perhaps the trailing behavior is elicited only in high density areas. Pheromone concentration, reasonably expected to be directly related to density, might elicit the behavior.

If in some manner trailing does produce deceleration, then the greatest benefit is derived when prey are located in high density areas. This could be particularly necessary if the behavior entails some disadvantages such as a reduction in foraging capabilities. Even without deceleration, the prey could spend more time following trails in high density areas and thus more time invulnerable as the average interval between losing and finding trails is shorter than in low density areas. Are natural prey densities consistently high enough to produce through attrition reduction an evolutionary imperative for the behavior? While high densities may have been true in I. C. King lake, high densities hardly seem possible for all the populations exhibiting deceleration (78).

Perhaps trailing behavior itself produces high densities. Mathematical investigation and computer simulation might prove instrumental to the solution of that question.

A behavior has been described for beetle larvae that seems to promote maintenance of position in a high prey density area. The predatory larvae simply turned more often shortly after discovering a prey item (Fleshner, 1950; Banks, 1957). If, in the case of copepods, after losing a trail in a high density area, an individual moved with frequent turns, position could be more likely maintained in the high density pocket until trail rediscovery. In itself, this does not explain the generation of pockets but in combination with trailing behavior might produce and maintain high densities such that maximum benefit from the trailing behavior might be derived.

Perhaps some process other than predation caused the evolution of trailing behavior. However, deceleration indicates that if predation attrition is sufficient to control the average prey density, high prey density is maintained in patches and if the behavior is ever present in the gene pool, its implantation throughout the population is assured. The theoretical involvement of any other process is not parsimonious.

The obvious method for proving the existence of trailing behavior, direct observation, was beyond the scope of this study. Additionally, trailing behavior might be extremely difficult or even impossible to observe under natural conditions. In working with copepods, it was obvious how easily natural behavior was disrupted, especially by artificial lighting. However, the behavior might produce peculiarities even within the type of data collected here that would support the theory.

In 1983 and 1984, data were collected in 93 separate groups across a range of 21 densities from 3 prey per jar to 23 prey per jar

(see Table 13, Appendix D). In previous analyses, the separate groups at each density were pooled. However, when all 93 group means were subjected to regression, an interesting phenomenon was exposed. A cubic regression removed a significant amount of variation (see Table 26, Appendix D, and Figure VI, Appendix E). In other words, acceleration was at first negative at low densities and then at a flex point, apparently close to a density of 13, become positive.

If real, the cubic regression, the change in acceleration from negative to positive can only be interpreted as a behavioral change. If the tenet is true that predator behavior is unchanging, developed from distributional analysis, it seems inescapable that prey behavior is changing.

In conjunction with the cubic regression, the group means at a density of nine were significantly higher than the means at a density of 13. Does the predation rate actually go down with increasing density to rise again?

In the middle area of the density range which contains the flex point, there seems to be a rise in the standard deviation of group means at each density (see Table 26). If behavior is changing in this middle area, one could not expect all individuals to change behavior at the same moment. One might expect an increase in variation as different groups would have different proportions of their constituents performing differently.

Finally, two of the three most outlying points, from a total of 93 points, determined by the difference between those points and the average of the remainder of their group means at the same density,

occurred on the same night out of a total of 48 nights. Was the collection of the two outlyers on the same night by chance? The third group of data collected that night was at a density of nine, below where the suggested behavioral change occurs. It was exactly the average of all other data collected at that density. Could the animals of that one night have simply failed to change behavior?

The interaction between Chaoborus and its prey appears simplistic to the extent that facts as yet unknown for any predator-prey relationship might be revealed from its study. Already, evidence of a possible prey social behavior has been collected. Using the techniques employed here, computer simulation, regressional and distributional analyses, and data collection methods, along with the techniques of mathematics and direct observation, it may be possible to develop incontrovertible evidence that this behavior is a direct result of attrition by predation.

To this end, areas of further investigation should include:

1. direct observation of the trailing behavior perhaps with photography and radioisotope marking,
2. mathematically or through computer simulation determining if trailing behavior can produce either or both deceleration and high densities,
3. determining through experimentation if the cubic regression, the predation rate reduction through certain ranges of increasing density, and the differences in variance between density ranges are real,

4. solidly establishing laboratory derived predation rates for application to field situations.

Based on the results of this study, there is a reasonable expectation that these investigations can be concluded successfully.

BIBLIOGRAPHY

BIBLIOGRAPHY

Abramson, M. 1979. Vigilence as a factor influencing flock formation among curlews Numenius arquata. Ibis 121:213-216.

Akre, E. G., and D. M. Johnson. 1979. Switching and sigmoid functional response curves by damselfly naiads with alternate prey available. Journal of Animal Ecology 48:703-720.

Alcock, J. 1974. Cues in searching for food by red-winged blackbirds Agelais phoeniceus. Behavior 46:174-188.

Allan, J. D. 1973. Competition and the relative abundances of two cladocerans. Ecology 54:484-498.

Allen, J. A. 1972. Evidence for stabilising and apostatic selection by wild blackbirds. Nature 237:348-349.

Allen, J. A. 1974. Further evidence for apostatic selection by wild passerine birds; training experiments. Heredity 33:361-372.

Allen, J. A. 1976. Further evidence for apostatic selection by wild passerine birds - 9:1 experiments. Heredity 36:173-180.

Allen, J. A., and B. C. Clarke. 1968. Evidence for apostatic selection on the part of wild passerines. Nature 220:501-502.

Ambler, J. W., and B. W. Frost. 1974. The feeding behavior of a predatory planktonic copepod, Tortanus discaudatus. Limnology and Oceanography 19:446-451.

Anderson, R. S. 1970. Predator-prey relationships and predation rates for crustacean zooplankters from some lakes in western Canada. Canadian Journal of Zoology 48:1229-1240.

Anderson, R. S. 1971. Crustacean plankton of 146 alpine and subalpine lakes and ponds in western Canada. Journal of the Fisheries and Research Board of Canada 28:311-321.

Anderson, R. S. 1972. Zooplankton composition and change in an alpine lake. Internationale Vereinigung fur Theoretiache und Angewandte Limnologie Verhandlunger 18:264-268.

Anderson, R. S. 1980. Relationships between trout and invertebrate species as predators and the structure of the crustacean and rotiferan plankton in mountain lakes. Pages 635-641 in W. C. Kerfoot, editor. Evolution and ecology of zooplankton communities. American Society of Limnology and Oceanography

Special Symposium 3, University of New England, Hanover, New Hampshire, USA.

Ball, R. C., and D. W. Hayne. 1952. Effects of the removal of the fish population on the fish-food organisms of a lake. Ecology 33:41-48.

Banks, C. D. 1957. The behavior of individual coccinellid larvae on plants. British Journal of Animal Behavior 5:12-24.

Barnard, C. J. 1980. Flock feeding and time budgets in the house sparrow (Passer domesticus L.). Animal Behavior 28:295-309.

Beavers, R. A., and R. H. Stavn. 1975. Seasonal changes in diaptomid copepod populations as a function of vertebrate predation. Internationale Vereinigung fur Theoretische und Angewandte Limnologie Verhandlungen 19:2966-2975.

Benke, A. C. 1976. Dragon fly production and prey turnover. Ecology 57:915-927.

Benke, A. C. 1978. Interactions among coexisting predators - a field experiment with dragonfly larvae. Journal of Animal Ecology 47:335-350.

Bernardi, R. de, and G. Guissani. 1975. Population dynamics of three cladocerans of Lago Maggiore related to predation pressure by a planktophagous fish. Internationale Vereinigung fur Theoretische und Angewandte Limnologie Verhandlungen 19:2906-2912.

Bertram, B. C. R. 1980. Vigilance and group size in ostriches. Animal Behavior 28:278-286.

Bohrer, R. N. 1980. Experimental studies on diel vertical migration. Pages 111-121 in W. C. Kerfoot, editor. Evolution and ecology of zooplankton communities. American Society of Limnology and Oceanography Special Symposium 3, University of New England, Hanover, New Hampshire, USA.

Boulding, E. G., and T. K. Hay. 1984. Crab response to prey density can result in density-dependent mortality of clams. Canadian Journal of Fisheries and Aquatic Sciences 41:521-525.

Brambilla, D. J. 1980. Seasonal changes in size at maturity in small pond Daphnia. Pages 438-455 in W. C. Kerfoot, editor. Evolution and ecology of zooplankton communities. American Society of Limnology and Oceanography Special Symposium 3, University of New England, Hanover, New Hampshire, USA.

Brandl, Z., and C. H. Fernando. 1974. Feeding of the copepod Acanthocyclops vernalis on the cladoceran Ceriodaphnia reticulata under laboratory conditions. Canadian Journal of Zoology 52:99-105.

Brandl, Z., and C. H. Fernando. 1978. Prey selection by the cyclopoid copepods Mesocyclops edax and Cyclops vicinus. Internationale Vereinigung fur Theoretische und Angewandte Limnologie Verhandlungen 20:2505-2510.

Brandl, Z., and C. H. Fernando. 1981. The impact of predation by cyclopoid copepods on zooplankton. Internationale Vereinigung fur Theoretische und Angewandte Limnologie Verhandlungen 21:1573-1577.

Brockleman, W. Y. 1969. An analysis of density effects and predation in Bufo americanus tadpoles. Ecology 50:632-644.

Brooks, J. L. 1965. Predation and the relative helmet size in cyclomorphic Daphnia. Proceedings of the National Academy of Sciences (USA) 53:119-126.

Brooks, J. L., and S. I. Dodson. 1965. Predation, bodysize, and composition of plankton. Science 150:28-35.

Brown, J. L. 1982. Optimal group size in territorial animals. Journal of Theoretical Biology 95:793-810.

Byron, E. R. 1982. The adaptive significance of calanoid copepod pigmentation: a comparative and experimental analysis. Ecology 63:1871-1886.

Caraco, T. 1979a. Time budgeting and group size: a theory. Ecology 60:611-617.

Caraco, T. 1979b. Time budgeting and group size: a test of theory. Ecology 60:618-627.

Carter, J. C. H., and J. K. Kwik. 1977. Instar distribution, vertical distribution and interspecfic competition among four species of Chaoborus. Journal of the Fisheries Research Board of Canada 34:113-118.

Caswell, H. 1978. Predator-mediated coexistence: a non-equilibrium model. American Naturalist 112:127-154.

Charnov, E. L. 1976. Optimal foraging: attack strategy of a mantid. American Naturalist 110:141-151.

Chaston, I. 1969a. The light threshold controlling the vertical migration of Chaoborus punctipennis in a Georgia impoundment. Ecology 50:916-920.

Chaston, I. 1969b. A comparison of the activity patterns of the aquatic larvae Protonemura meyeri (Plecoptera) and Chaoborus punctipennis (Diptera). American Midland Naturalist 82:302-307.

Chiszar, D., and J. T. Windell. 1973. Predation by the bluegill sinfish (Lepomis macrochirus Rafinesque) upon mealworm larvae (Tenebrio molitor). Animal Behavior 21:536-543.

Confer, J. L. 1971. Intrazooplankton predation by Mesocyclops edax at natural prey densities. Limnology and Oceanography 16:663-667.

Confer, J. L., and P. I. Blades. 1975. Omnivorous zooplankton and planktivorous fish. Limnology and Oceanography 20:571-579.

Confer, J. L., and J. M. Cooley. 1977. Copepod instar survival and predation by zooplankton. Journal of the Fisheries Research Board of Canada 34:703-706.

Confer, J. L., G. L. Howick, M. H. Corzette, S. L. Kramer, S. Fitzgibbon, and R. Landesberg. 1978. Visual predation by planktivores. Oikos 31:27-37.

Connell, J. L. 1961. Effect of competition, predation by Thias lapillus, and other factors on natural populations of the barnacle Balanus balanoides. Ecological Monographs 31:61-104.

Connell, J. H. 1970. A predator-prey system in the marine intertidal region. I. Balanus glandula and several predatory species of Thias. Ecological Monographs 40:49-78.

Cook, E. F. 1965. Family Choaboridae. Pages 102-105 in A. Stone, editor. A catalog of the Diptera of America North of Mexico. U.S. Department of Agriculture, Agricultural Handbook, Agricultural Research Service 276.

Cook, R. M., and B. J. Cockrell. 1978. Predator ingestion rate and its bearing on feeding time and the theory of optimal diets. Journal of Animal Ecology 47:529-547.

Cooper, S. D., and C. R. Goldman. 1980. Opossom shrimp (Mysis relicta) predation on zooplankton. Canadian Journal of Fisheries and Aquatic Sciences 37:909-919.

Cooper, S. D., and C. R. Goldman. 1982. Environmental factors affecting predation rates of Mysis relicta. Canadian Journal of Fisheries and Aquatic Sciences 39:203-208.

Cornell, H., and D. Pimentel. 1978. Switching in the parasitoid Nasonia vitripennis and its effects on host competition. Ecology 59:297-308.

Cramer, J. D., and G. R. Marzolf. 1970. Selective predation on zooplankton by gizzard shad. Transactions of the American Fisheries Society 99:320-332.

Crawley, M. J. 1975. The numerical responses of insect predators to changes in prey density. Journal of Animal Ecology 44:877-892.

Crook, J. H., J. E. Ellis, and J. D. Goss-Custard. 1976. Mammalian social systems: structure and function. Animal Behavior 24:261-274.

Culver, D. 1980. Seasonal variation in the sizes at birth and at first reproduction in Cladocera. Pages 358-366 in W. C. Kerfoot, editor. Evolution and ecology of zooplankton communities. American Society of Limnology and Oceanography Special Symposium 3, University of New England, Hanover, New Hampshire, USA.

Cummins, K. W., R. R. Costa, R. E. Rowe, G. A. Moshir, R. M. Scanlon, and R. K. Zajdel. 1969. Ecological energetics of a natural population of the predaceous zooplankter Leptodora kindtii Focke (Cladocera). Oikos 20:189-223.

Davies, R. W. 1969. Predation as a factor in the ecology of triclads in a small weedy pond. Journal of Animal Ecology 38:577-584.

Davies, R. W., and T. B. Reynoldson. 1969. The incidence and intensity of predation on lake-dwelling triclads in the laboratory. Ecology 50:845-853.

Deither, V. G., and A. Gelperin. 1967. Hyperphagia in the blowfly. Journal of Experimental Biology 47:191-200.

Dimond, S., and J. Lazarus. 1974. The problem of vigilance in animal life. Brain, Behavior and Evolution 9:60-79.

Dixon, A. F. G. 1959. An experimental study of the searching behavior of the predatory coccinellid beetle Adalia decempuctata (L.). Journal of Animal Ecology 28:259-281.

Dixon, A. F. G. 1970. Factors limiting the effectiveness of the coccinellid beetle, Adalia bipunctata (L.), as a predator of the sycamore aphid, Drepanosiphon platanoides (Schr.). Journal of Animal Ecology 39:739-751.

Dodson, S. I. 1970. Complementary feeding niches sustained by size-selective predation. Limnology and Oceanography 15:131-137.

Dodson, S. I. 1972. Mortality in a population of Daphnia rosea. Ecology 53:1011-1023.

Dodson, S. I. 1974a. Zooplankton competition and predation: an experimental test of the size-efficiency hypothesis. Ecology 55:605-613.

Dodson, S. I. 1974b. Adaptive change in plankton morphology in response to size-selective predation: a new hypothesis of cyclomorphosis. Limnology and Oceanography 19:721-729.

Dodson, S. I. 1975. Predation rates of zooplankton in artic ponds. Limnology and Oceanography 20:426-433.

Drenner, R. W., and S. R. McComas. 1980. The roles of zooplankter escape ability and fish size selectivity in the selective feeding and impact of planktivorous fish. Pages 587-593 in W. C. Kerfoot, editor. Evolution and Ecology of Zooplankton Communities. American Society of Limnology and Oceanography Special Seminar 3, University of New England, Hanover, New Hampshire, USA.

Drenner, R. W., J. R. Strickler, and W. J. O'Brien. 1978. Capture probability: the role of zooplantor escape in the selective feeding of planktivorus fish. Journal of the Fisheries Research Board of Canada 35:1370-1373.

Dunbar, R. I. M., and E. P. Dunbar. 1980. The pairbond in Klipspringer. Animal Behavior 28:219-229.

Eggars, D. M. 1978. Limnetic feeding behavior of juvenile sockeye salmon in Lake Washington and predator avoidence. Limnology and Oceanography 23:1114-1125.

Eggers, D. M. 1977. The nature of prey selection by planktivorus fish. Ecology 58:46-60.

Elgar, M. A., and C. P. Catterall. 1981. Flocking and predator surveillance in house sparrows: test of an hypothesis. Animal Behavior 29:868-872.

Enright, J. T. 1977. Diurnal vertical migration: adaptive significance and timing. Part I. Selective advantage: a metabolic model. Limnology and Oceanography 22:856-872.

Eveleigh, E. S., and D. A. Chant. 1981. Experimental studies on acarine predator-prey interactions: effects of predator age and feeding history on prey consumption and the functional response (Acarina: Phytoseiidae). Canadian Journal of Zoology 59:1387-1406.

Fedorenko, A. Y. 1975a. Feeding characteristics and predation impact of Chaoborus (Diptera, Choaboridae) larvae in a small lake. Limnology and Oceanography 20:250-258.

Fedorenko, A. Y. 1975b. Instar and species-specific diets in two species of Chaoborus. Limnology and Oceanography 20:238-249.

Fedorenko, A. Y., and M. C. Swift. 1972. Comparative biology of Chaoborus americanus and Chaoborus trivittatus in Eunice Lake, British Columbia. Limnology and Oceanography 17:721-730.

Fleshner, C. A. 1950. Studies on the searching capacity of the larvae of three predators of the citrus red mite. Hilgardia 20:233-265.

Fox, L. R., and W. W. Murdoch. 1978. Effects of feeding history on short-term and long-term functional responses in Notonecta hoffmanni. Journal of Animal Ecology 47:945-959.

Friedman, M. M., and J. R. Strickler. 1975. Chemoreceptors and feeding in calanoid copepods (Arthropoda:Crustacea). Proceedings of the National Academy of Sciences (USA) 72:4185-4188.

Galbraith, M. G. 1967. Size-selective predation on Daphnia by rainbow trout and yellow perch. Transactions of the American Fisheries Society 96:1-10.

Galbraith, M. G. 1975. The use of large Daphnia as indices of fishing quality for rainbow trout in small lakes. Internationale Vereinigung fur Theoretische und Angewandt Limnologie Verhandlungen 19:2485-2492.

Gause, G. F. 1934. The struggle for existence. Williams and Wilkens Company, Baltimore, Maryland, USA.

George, D. G., and R. W. Edwards. 1973. Daphnia distribution within Langmuir circulations. Limnology and Oceanography 18:798-800.

Gerritsen, J. 1978. Instar-specific swimming patterns and predation of planktonic copepods. Internationale Vereiningung fur Theoretische und Angewandte Limnologie Verhandlungen 20:2531-2536.

Gerritsen, J. 1980. Adaptive responses to encounter problems. Pages 52-62 in W. C. Kerfoot, editor. Evolution and ecology of zooplankton communities. American Society of Limnology and Oceanography Special Symposium 3, University of New England, Hanover, New Hampshire, USA.

Gerritsen, J., and J. R. Strickler. 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. Journal of the Fisheries Research Board of Canada 34:73-82.

Gibb, J. A. 1962. L. Tinbergen's hypothesis of the role of specific search images. Ibis 104:106-111.

Gigue're, L. A. 1979. An experimental test of Dodson's hypothesis that Amblystoma (a salamander) and Chaoborus (a phantom midge) have complementary feeding niches. Canadian Journal of Zoology 57:1091-1097.

Gigue're, L. A. 1980. Metabolic expenditures in Chaoborus larvae. Limnology and Oceanography 25:922-928.

Gigue're, L. A. and L. M. Dill. 1979. The predatory response of Chaoborus larvae to acoustic stimuli, and the acoustic characteristics of their prey. Zeitschrift Tierpsychologie 50:113-123.

Gigue're, L. A., and L. M. Dill. 1980. Seasonal patterns of vertical migration: a model for Chaoborus trivittatus. Pages 122-128 in W. C. Kerfoot, editor. Evolution and ecology of zooplankton communities. American Society of Limnology and Oceanography Special Symposium 3, University of New England, Hanover, New Hampshire, USA.

Gigue're, L. A., A. Delage, L. M. Dill, and J. Gerritsen. 1982. Predicting encounter rates for zooplankton: a model assuming a cylindrical encounter field. Canadian Journal of Fisheries and Aquatic Sciences 39:237-242.

Gliwicz, Z. M. 1981. Food and predation in limiting clutch size of cladocerans. Internationale Vereinigung fur Theoretische und Angewandte Limnologie Verhandlungen 21:1562-1566.

Gliwicz, Z. M., A. Ghilarov, and J. Pijanowska. 1981. Food and predation as major factors limiting two natural populations of Daphnia cucllata Sars. Hydrobiologia 80:205-218.

Goldman, C. R., M. D. Morgan, S. T. Threlkeld, and N. Angeli. 1979. A population dynamics analysis of the cladoceran disappearance from Lake Tahoe, California-Nevada. Limnology and Oceanography 24:289-297.

Gophen, M. 1977. Food and feeding habits of Mesocyclops leuckarti (Claus) in Lake Kinnert (Israel). Freshwater Biology 7:513-518.

Goss-Custard, J. D. 1970. The responses of redshank (Tringa tatanus L.) to spatial variations in their prey density. Journal of Animal Ecology 39:91-113.

Grant, J. W. G., and I. A. E. Bayly. 1981. Predator induction of crests in morphs of the Daphnia carinata King complex. Limnology and Oceanography 26:201-218.

Green, J. 1971. Associations of Cladocera in the zooplankton of the lake sources of the White Nile. Journal of Zoology (London) 165:373-414.

Green, J., S. A. Corbett, and E. Betney. 1973. Ecological studies on crater lakes in West Cameroon. The blood of endemic cichlids in Barombi Mbo. in relation to stratification and their feeding habits. Journal of Zoology (London) 170:299-308.

Gresens, S. E., M. L. Cothran, and J. H. Thorp. 1982. The influence of temperature on the functional response of the dragonfly Celithemis fasciata (Odonata: Libellulidae). Oecologia (Berlin) 53:281-284.

Griffiths, D. W. 1973. The food of animals in an acid moorland pond. Journal of Animal Ecology 42:285-293.

Hairston, N. G., Jr., and R. A. Pastorok. 1975. Response of Daphnia population size and age structure to predation, Internationale Vereinigung fur Theoretische und Angewandte Limnologie Verhandlungen 19:2898-2905.

Hall, D. J. 1964. An experimental approach to the dynamics of a natural population of Daphnia galeata mendotae. Ecology 45:94-111.

Hall, D. J., S. T. Threlkeld, C. W. Burns, and P. H. Crowley. 1976. The size-efficiency hypothesis and the size structure of zooplankton communities. Annual Review of Ecology and Systematics 7:177-208.

Hamilton, W. D. 1971. Geometry for the selfish herd. Journal of Theoretical Biology 31:295-311.

Hamner, P., and W. M. Hamner. 1977. Chemosensory tracking of scent trails by planktonic shrimp Acetes sibogae australis. Science 195:886-888.

Hardman, J. M., and A. L. Turnbull. 1974. The interaction of spatial heterogeneity, predator competition and the functional response to prey density in a laboratory system of wolf spiders (Araneae: Lycosidae) and fruit flies (Diptera: Drosophilidae). Journal of Animal Ecology 43:155-171.

Hassell, M. P., J. H. Lawton, and J. R. Beddington. 1977. Sigmoid functional responses by invertebrate predators and parasitoids. Journal of Animal Ecology 46:249-262.

Hassell, M. P., and R. M. May. 1974. Aggregation of predators and insect parasites and its effect on stability. Journal of Animal Ecology 43:567-594.

Havel, J. E., and S. I. Dodson. 1984. Chaoborus predation on typical and spined morphs of Daphnia pulex: behavioral observations. Limnology and Oceanography 29:487-494.

Hayne, D. W., and R. C. Ball. 1956. Benthic productivity as influenced by fish predation. Limnology and Oceanography 1:162-175.

Haynes, D. L., and P. Sisojevic. 1966. Predatory behavior of Philodromus rufus Walckenaer (Araneae: Thomisidae). Canadian Entomologist 98:113-133.

Hebert, P. D. N. 1974. Enzyme varability in natural populations of Daphnia magna. I. Population structure in East Anglia. Evolution 28:546-556.

Hebert, P. D., and J. M. Loaring. 1980. Selective predation and the species composition of artic ponds. Canadian Journal of Zoology 58:422-426.

Henrikson, L., and H. G. Oscarson. 1978. Fish predation limiting abundance and distribution of Glaenocorisa p. propinqua (Hemiptera). Oikos 31:102-105.

Henrikson, L., and H. G. Oscarson. 1981. Corixids (Hemiptera-Heteroptera), the new top predators in acidified lakes. Internationale Vereinigung fur Theoretische und Angewandte Limnologie Verhandlungen 21:1616-1620.

Hildrew, C. W., and C. R. Townsend. 1977. The influence of substrate on the functional response of Plectrocnemia conspersa (Curtis) larvae (Trichoptera: Polycentropodidae). Oecologia (Berlin) 31:21-26.

Hodgkin, E. P., and R. J. Rippingale. 1971. Interspecies conflict in esturine copepods. Limnology and Oceanography 16:573-575.

Holling, C. S. 1959a. The components of predation as revealed by a study of small-mammal predation of the european pine sawfly. Canadian Entomologist 91:292-320.

Holling, C. S. 1959b. Some characteristics of simple types of predation and parasitism. Canadian Entomologist 91:385-398.

Holling, C. S. 1961. Principles of insect predation. Annual Review of Entomology 6:163-182.

Holling, C. S. 1963. An experimental component analysis of population processes. Memoirs of the Entomological Society of Canada 32:22-32.

Holling, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. Memoirs of the Entomological Society of Canada 45:1-60.

Holling, C. S. 1966. The functional response of invertebrate predators to prey density. Memoirs of the Entomological Society of Canada 48:1-86.

Holling, C. S., and S. Buckingham. 1976. A behavioral model of the predator-prey functional responses. Behavioral Science 21:183-195.

Hoogland, J. L. 1979. The effect of colony size on individual alertness of prairie dogs (Sciuridae: Cynomys spp.). Animal Behavior 27:394-407.

Hrb'acek, J. 1969. On the possibility of estimating predation pressure and nutrition level of populations of Daphnia (Crustacea, Cladocera) from their remains in sediments. Internationale Vereinigung fur Theoretische und Angewandte Limnologie Verhandlungen 17:269-274.

Hrb'acek, J. 1977. Competition and predation in relation to species composition of freshwater zooplankton, mainly Cladocera. Chapter 10 in J. Cairns Jr., editor. Aquatic microbial communities. Garland Publishing, Inc., New York, New York, USA.

Huffaker, C. B. 1958. Experimental studies on predation. II. Dispersion factors and predator-prey oscillations. Hilgardia 27:343-383.

Huffaker, C. B., P. S. Messenger, and P. DeBach. 1971. The natural enemy component in natural control and the theory of biological control. Pages 16-67 in C. B. Huffaker, editor. Biological control. Plenum Press, New York, New York, USA.

Hunt, B. P. 1958. Limnetic distribution of Chaoborus larvae in a deep Florida lake (Diptera: Culicidae). Florida Entomologist 41:111-116.

Hurlbert, S. H., J. Zedler, and D. Faribanks. 1972. Ecosystem alteration by the mosquitofish (Gambusia affinis) predations. Science 175:639-641.

Hutchinson, B. P. 1971. The effect of fish predation on the zooplankton of ten Adirondack lakes with particular reference to

the alewife (Alosa pseudoharengus). Transactions of the American Fisheries Society 100:325-335.

Inglis, I. R., and A. J. Isaacson. 1978. The responses of dark-bellied Brent Geese to models of geese in various postures. Animal Behavior 26:953-958.

Ivelev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, Connecticut, USA.

Jacobs, J. 1977. Coexistence in similar zooplankton species by differential adaptation to reproduction and escape in an environment with fluctuating food and enemy densities. II. Field data analysis of Daphnia. Oecologia 30:313-329.

Jacobs, J. 1978a. Coexistence of similar zooplankton species by differential adaptation to reproduction and escape in an environment with fluctuating food and enemy densities. III. Laboratory experiments. Oecologia 35:35-54.

Jacobs, J. 1978b. The influence of prey size, light intensity, and alternative prey on the selectivity of plankton feeding fish. Internationale Vereinigung fur Theoretische und Angewandte Limnologie Verhandlungen 20:2461-2466.

James, H. G. 1957. Mochlonyx velutinus (Ruuthe) (Diptera: Culicidae), an occasional predator of mosquito larvae. Canadian Entomologist 89:470-480.

Jamieson, C. D. 1980. The predator feeding of copepodid stages III to adult Mesocyclops leuckarti (Claus). Pages 518-537 in W. C. Kerfoot, editor. Evolution and the ecology of zooplankton communities. American Society of Limnology and Oceanography Special Symposium 3, University of New England, Hanover, New Hampshire, USA.

Janssen, J. 1976. Feeding modes and prey size selection in the alewife (Alosa pseudoharengus). Journal of the Fisheries Research Board of Canada 33:1972-1975.

Jennings, T., and S. M. Evans. 1980. Influence of position in the flock and flock size on vigilance in the starling, Sturnus vulgaris. Animal Behavior 28:634-635.

Johnson, D. M. 1973. Predation by damselfly naiads on cladoceran populations: fluctuating intensity. Ecology 54:251-268.

Johnson, D. M., and B. G. Akre, and P. H. Crowley. 1975. Modeling arthropod predation: wasteful killing by damselfly naiads. Ecology 56:1081-1094.

Johnson, D. M., and P. H. Crowley. 1980. Odonate "hide and seek": habitat-specific rules? Pages 569-579 in W. C. Kerfoot, editor. Evolution and ecology of zooplankton communities. American Society of Limnology and Oceanography Special Symposium 3, University of New England, Hanover, New Hampshire, USA.

Juday, C. 1921. Observations on the larvae of Corethra punctipennis Say. Biological Bulletin 40:271-286.

Kerfoot, W. C. 1974. Egg-size cycle of a cladocern. Ecology 55:1259-1270.

Kerfoot, W. C. 1975. The divergence of adjacent populations. Ecology 56:1298-1313.

Kerfoot, W. C. 1977a. Implications of copepod predation. Limnology and Oceanography 22:316-321.

Kerfoot, W. C. 1977b. Competition in cladocern communities: the cost of evolving defenses against copepod predation. Ecology 58:303-313.

Kerfoot, W. C. 1978. Combat between predatory copepods and their prey: Cyclops, Epischura, and Bosmina. Limnology and Oceanography 23:1089-1102.

Kerfoot, W. C. 1980a. Perspectives on cyclomorphosis: separation of phenotypes and genotypes. Pages 470-496 in W. C. Kerfoot, editor. Evolution and ecology of zooplankton communities. American Society of Limnology and Oceanography Special Symposium 3, University of New England, Hanover, New Hampshire, USA.

Kerfoot, W. C. 1980b. Commentary: transparency, body-size, and prey conspicuousness. Pages 609-617 in W. C. Kerfoot, editor. Evolution and ecology of zooplankton communities. American Society of Limnology and Oceanography Special Symposium 3, University of New England, Hanover, New Hampshire, USA.

Kerfoot, W. C., D. L. Kellogg Jr., and J. R. Strickler. 1980. Visual observations of live zooplankters: evasion, escape, and chemical devices. Pages 10-27 in W. C. Kerfoot, editor. Evolution and ecology of zooplankton communities. American Society of Limnology and Oceanography Special Symposium 3, University of New England, Hanover, New Hampshire, USA.

Kerfoot, W. C., and R. A.Pastorok. 1978. Survival versus competition: evolutionary compromises and diversity in the zooplankton. Internationale Vereinigung fur Theoretische und Angewandte Limnologie Verhandlungen 20:362-374.

Kerfoot, W. C., and K. Peterson. 1980. Predatory copepods and Bosmina: replacement cycles and further influences of predation upon prey reproduction. Ecology 61:417-431.

Kettle, D., and W. J. O'Brien. 1978. Vulnerability of artic zooplankton species to predation by small lake trout. Journal of the Fisheries Research Board of Canada 35:1495-1500.

Kiltie, R. A. 1980. Application of search theory to the analysis of prey aggregation as an antipredator tactic. Journal of Theoretical Biology 87:201-206.

Kirk, K. L. 1985. Waterflows produced by Daphnia and Diaptomus: implications for prey selection by mechanosensory predators. Limnology and Oceanography 30:679-686.

Krueger, D. A., and S. I. Dodson. 1981. Embryological induction and predation ecology in Daphnia pulex. Limnology and Oceanography 26:219-223.

Kwik, J. K., and J. C. H. Carter. 1975. Population dynamics of limnetic Cladocera in a beaver pond. Journal of the Fisheries Research Board of Canada 32:341-346.

Laing, J. 1938. Host-finding by insect parasites. II. The chance of Trichogramma evanescens finding its host. Journal of Experimental Biology 15:281-302.

Landenberger, D. E. 1966. Learning in the Pacific starfish Piaster giganteus. Animal Behavior 14:414-418.

Landenberger, D. E. 1968. Studies on the selective feeding in the Pacific starfish, Piaster, in Southern California. Ecology 49:1062-1075.

Landry, M. R. 1978. Predatory feeding behavior of a marine copepod Labidocera trispinosa. Limnology and Oceanography 23:1103-1113.

Landry, M. R. 1980. Detection of prey by Calanus pacificus: implications of the first antennae. Limnology and Oceanography 25:545-549.

Lane, P. A. 1979. Vertebrate and invertebrate predation intensity on fresh-water zooplankton communities. Nature 280:391-393.

Lane, P., M. Klug, and L. Louden. 1976. Measuring invertebrate predation in situ on zooplankton assemblages. Transactions of the American Microscopic Society, 95:143-155.

LaRow, E. J. 1968. A persistent diurnal rhythm in Chaoborus larvae. I. The nature of the rhythmicity. Limnology and Oceanography 13:250-256.

LaRow, E. J. 1969. A persistent diurnal rhythm in Chaoborus larvae. II. Ecological significance. Limnology and Oceanography 14:213-218.

LaRow, E. J. 1970. The effect of oxygen tension on the vertical migration of Chaoborus larvae. Limnology and Oceanography 15:357-362.

LaRow, E. J. 1976. Population interaction: a synchronizer for the persistent rhythmicity of Chaoborus larvae. Hydrobiologia 48:85-88.

LaRow, E. J., and G. R. Marzolf. 1970. Behavioral differences between third and fourth instars of Chaoborus punctipennis. American Midland Naturalist 84:428-436.

Lawton, J. H., J. Beddington, and R. Bonser. 1974. Switching in invertebrate predators. Pages 75-105 in M. B. Usher and M. H. Williamson, editors. Ecological Stability. Chapman and Hall Publishers, New York, New York, USA.

Lawton, J. H., M. P. Hassell, and J. R. Beddington. 1975. Prey death rates and rate of increase of arthropod predator populations. Nature (London) 255:60-62.

Lazarus, J. 1972. Natural selection and the functions of flocking in birds: a reply to Murton. Ibis 114:556-558.

Lewis, W. J. Jr. 1975. Distribution and feeding habits of a tropical Chaoborus population. Internationale Vereinegung fur Theoretische und Angewandte Limnologie Verhandlungen 19:3106-3119.

Lewis, W. M. Jr. 1977. Feeding selectivity of a tropical Chaoborus population. Freshwater Biology 7:311-325.

Lewis, W. M. Jr. 1980. Evidence for a stable zooplankton community structure gradients maintained by predation. Pages 625-634 in W. C. Kerfoot, editor. Evolution and ecology of zooplankton communities. American Society of Limnology and Oceanography Special Symposium 3, University of New England, Hanover, New Hampshire, USA.

Li, J. L., and H. W. Li. 1979. Species-specific factors affecting predator-prey interactions of the copepod Acanthocyclops vernalis with its natural prey. Limnology and Oceanography 24:613-626.

Lipetz, V. E., and M. Bekoff. 1982. Group size and vigilance in pronghorns. Zeitschrift Tierpsychologie 58:203-216.

Lynch, M. 1977. Fitness and optimal body size in zooplankton populations. Ecology 58:763-774.

Lynch, M. 1979. Predation, competition, and zooplankton community structures: an experimental study. Limnology and Oceanography 24:253-272.

Lynch, M. 1980. Predation, enrichment, and the evolution of cladoceran life histories: a theoretical approach. Pages 367-376 in W. C. Kerfoot, editor. Evolution and ecology of zooplankton communities. American Society of Limnology and Oceanography Special Symposium 3, University of New England, Hanover, New Hampshire, USA.

Lynch, M., B. Monson, M. Sandheinrich, and L. Weider. 1981. Size-specific mortality rates in zooplankton populations. Internationale Vereinigung fur Theoretische und Angedwandte Limnologie Verhandlungen 21:363-368.

Macan, T. T. 1965. Predation as a factor in the ecology of water bugs. Journal of Animal Ecology 34:691-698.

Macan, T. T. 1977. The influence of predation on the composition of fresh-water animal communities. Biological Review 52:45-70.

MacMillen, R. E., and F. L. Carpenter. 1980. Evening roosting flights of the honey creepers Himatione saguinea and Vestiaria coccinea on Hawaii. Auk 97:28-37.

Maguire, B., D. Belk, and G. Wells. 1968. Control of the community structure by mosquito larvae. Ecology 49:207-210.

Maiorana, V. C. 1976. Predation, submergent, behavior, and tropical diversity. Evolutionary Theory 1:157-177.

Makarewicz, J. C., and G. E. Likens. 1975. Niche analysis of a zooplankton community. Science 190:1000-1003.

Maly, E. J. 1970. The influence of predation on the adult sex ratios of two copepod species. Limnology and Oceanography 15:566-573.

Manning, B. J., W. C. Kerfoot, and E. M. Berger. 1978. Phenotypes and genotypes in cladoceran populations. Evolution 32:365-374.

McNaught, D. C., and A. D. Hasler. 1961. Surface schooling and feeding behavior in the white bass Roccus chrysops (Rafinesque), in Lake Mendota. Limnology and Oceanography 6:53-60.

McPhail, J. D. 1969. Predation and the evolution of a stickleback (Gasterosteus). Journal of the Fisheries Research Board of Canada 26:3183-3208.

McQueen, D. J. 1969. Reduction of zooplankton standing stocks by the predaceous Cyclops bicuspidatus thomasi in Marion Lake, British Columbia. Journal of the Fisheries Research Board ofCanada 26:1605-1618.

Menge, B. A. 1972. Foraging strategy of a starfish in relation to actual prey availability and environmental predictability. Ecological Monographs 42:25-50.

Messenger, P. S. 1968. Bioclimatic studies of the apid parasite Praon exsoletum. I. Effects of temperature on the functional response of females to varying host densities. Canadian Entomologist 100:728-741.

Metcalfe, N. B. 1984. The effects of mixed-species flocking on the vigilance of shorebirds: who do they trust? Animal Behavior 32:986-993.

Metz, J. A. J., and F. H. D. van Batenburg. 1985. Holling's 'Hungry Mantid' model for the invertebrate functional response considered as a Markov process. Part 0: a survey of the main ideas and results. Pages 29-41 in S. Levin and T. G. Hallam, editors. Lecture notes in biomathematics. Mathematical Ecology Proceedings, Trieste 54, Springer-Verlag, Berlin.

Meyers, D. G. 1980. Duirnal vertical migration in aquatic microcrustacea: light and oxygen responses of littoral zooplankton. Pages 80-90 in W. C. Kerfoot, editor. Evolution and ecology of zooplankton communities. American Society of Limnology and Oceanography Special Symposium 3, University of New England, Hanover, New Hampshire, USA.

Milinski, M. 1977. Do all members of a swarm suffer the same predation? Zeitschrift Tierpsychologie 45:373-388.

Monchadskii, A. S. 1945. The mechanism of digestion in the larvae of Chaoborus (Diptera, Culicidae). (In Russian with English summary). Zool. Zh. (Moscow) 24:90-98.

Morgan, M. D., C. R. Goldman, and R. C. Richards. 1981. Impact of introduced populations of Mysis relicta on zooplankton in oligotrophic subalpine lakes. Internationale Vereinigung fur Theoretische und Angewandte Limnologie Verhandlungen 21:339-345.

Morgan, M. D., S. T. Threlkeld, and C. R. Goldman. 1978. Impact of the introduction of kokanee (Oncorhynchus nerke) and opossum

shrimp (Mysis relicta) on an alpine lake. Journal of the Fisheries Research Board of Canada 35:1572-1579.

Morris, R. F. 1963. The effect of predator age and prey defense on the functional response of Podisus maculiventris Say to the density of Hyphantria cunea Drury. Canadian Entomologist 95:1009-1020.

Murdie, G., and M. P. Hassell. 1973. Food distribution, searching success and predator-prey models. Pages 87-101 in R. W. Hiorns, editor. The Mathematical Theory of the Dynamics of Biological Populations, Academic Press, London, England.

Murdoch, W. W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. Ecological Monographs 39:335-354.

Murdoch, W. W. 1973. The functional response of predators. Journal of Applied Ecology 10:335-342.

Murdoch, W. W. 1977. Stabilizing effects of spatial heterogeneity in predator-prey systems. Theoretical Population Biology 11:252-273.

Murdoch, W. W., S. Avery, and M. E. B. Smyth. 1975. Switching in predatory fish. Ecology 56:1094-1105.

Murdoch, W. W., and J. R. Marks. 1973. Predation by coccinellid beetles: experiments on switching. Ecology 54:160-167.

Murdoch, W. W., and A. Oaten. 1975. Predation and population stability. Advanced Ecological Research 9:1-63.

Nachtigall, W. 1974. Locomotion: mechanics and hydrodynamics of swimming in aquatic. Pages 381-342 in M. Rockstein, editor. The Physiology of Insects, Academics Press, London, England.

Neill, W. E. 1978. Experimental studies on factors limiting colonization by Daphnia pulex Leydig of coastal montane lakes in British Columbia. Canadian Journal of Zoology 56:2498-2507.

Neill, W. E. 1981. Impact of Chaoborus predation upon the structure and dynamics of a crustacean zooplankton community. Oecologia (Berlin) 48:164-177.

Neill, W. E., and A. Peacock. 1980. Breaking the bottleneck: interactions of invertebrate predators and nutrients in oligotrophic lakes. Pages 715-724 in W. C. Kerfoot, editor. Evolution and ecology of zooplankton communities. American Society of Limnology and Oceanography Special Symposium 3, University of New England, Hanover, New Hampshire, USA.

Nelson, M. E., and L. D. Mech. 1981. Deer social organization and wolf predation in Northeastern Minnesota. Wildlife Monographs 77:5-53.

Northcote, T. G. 1964. Use of a high frequency echo sounder to record distribution and migration of Chaoborus larvae. Limnology and Oceanography 9:87-91.

Northcote, T. G., and R. Clarotto. 1975. Limnetic macrozooplankton and fish predation in some coastal British Columbia lakes. Internationale Vereinigung fur Theoretische und Angewandte Limnologie Verhandlungen 19:2378-2393.

Northcote, T. G., C. J. Walters, and J. M. B. Hume. 1978. Initial impacts of experimental fish introduction on the macrozooplankton of small oligotrophic lakes. Internationale Vereinigung fur Theoretische und Angewandte Limnologie Verhandlungen 20:2003-2012.

Oaten, A., and W. W. Murdoch. 1975. Switching, functional response, and stability in predator-prey systems. American Naturalist 109:299-318.

O'Brien, W. J. 1979. The predatory-prey interaction of planktivorous fish and zooplankton. American Scientist 67:572-581.

O'Brien, W. J., D. Keitle, and H. Riessen. 1979. Helmets and invisible armor: structures reducing predation from tactile and visual planktivores. Ecology 60:287-294.

O'Brien, W. J., D. Kettle, H. Riessen, D. Schmidt, and D. Wright. 1980. Dimorphic Daphnia longiremis: predation and competitive interactions between the two morphs. Pages 497-506 in W. C. Kerfoot, editor. Evolution and ecology of zooplankton communities. American Society of Limnology and Oceanography Special Symposium 3, University of New England, Hanover, New Hampshire, USA.

O'Brien, W. J., and D. Schmidt. 1979. Artic Bosmina morphology and copepod predation. Limnology and Oceanography 24:564-568.

O'Brien, W. J., N. A. Slade, and G. I. Vinyard. 1976. Apparent size as the determinant of prey selection of bluegill sunfish (Lepomis machrochirus). Ecology 57:1304-1310.

O'Brien, W. J., and G. L. Vinyard. 1978. Polymorphism and predation: the effect of invertebrate predation on the distribution of two varieties of Daphnia carinata in South India ponds. Limnology and Oceanography 23:452-460.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist 100:65-75.

Paine, R. T. 1969. The Pisaster-Tergula interaction: prey patches, predator food preference, and the intertidal community structure. Ecology 50:950-961.

Paine, R. T. 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia 15:93-120.

Paine, R. T. 1976. Size-limited predation: an observational and experimental approach with the Mytilus-Pisaster interaction. Ecology 57:858-873.

Parma, S. 1969. The life cycle of Chaoborus crystallinus (DeGeer) (Diptera, Chaoboridae) in a Dutch pond. Internationale Vereindgung fur Theoretische und Angewandte Limnologie Verhandlungen 17:888-894.

Pastorok, R. A. 1980a. The effect of predator hunger and food abundance on prey selection by Chaoborus larvae. Limnology and Oceanography 25:910-921.

Pastorok, R. A. 1980b. Selection of prey by Chaoborus larvae: a review and new evidence for behavioral flexibility. Pages 538-554 in W. C. Kerfoot, editor. Evolution and the ecology of zooplankton communities. American Society of Limnology and Oceanography Special Symposium 3, University of New England, Hanover, New Hampshire, USA.

Pastorok, R. A. 1981. Prey vulnerability and size selection by Chaoborus larvae. Ecology 62:1311-1324.

Pearre, S. Jr. 1973. Verrical migration and feeding in Sagitta elegans Verrill. Ecology 54:300-314.

Pennak, R. W. 1978. Fresh-water invertebrates of the United States (second edition). John Wiley and Sons, New York, New York, USA.

Pope, G. F., J. C. H. Carter, and G. Power. 1973. The influence of fish on the distribution of Chaoborus spp. (Diptera) and the density of larvae in the Matamek River system, Quebec. Transactions of the American Fisheries Society 102:707-714.

Porter, J. W. 1972. Predation by Acanthaster and its effect on coral species diversity. American Naturalist 106:487-492.

Powell, G. V. N. 1974. Experimental analysis of the social value of flocking by starlings (Sturnus vulgaris) in relation to predation and foraging. Animal Behavior 22:501-505.

Prepas, E., and F. H. Rigler. 1978. The enigma of Daphnia death rates. Limnology and Oceanography 23:970-988.

Readshaw, J. L. 1973. The numerical response of predators to prey density. Journal of Applied Ecology 10:342-351.

Real, L. A. 1977. The kinetics of functional response. American Naturalist 11:289-300.

Real, L. A. 1979. Ecological determinants of functional response. Ecology 60:481-485.

Reif, C. B., and D. W. Tappa. 1966. Selective predation: smelt and cladocerans in Harvey's Lake. Limnology and Oceanography 11:437-438.

Richards, R. C., C. R. Goldman, T. C. Frantz, and R. Wickwire. 1975. Where have all the Daphnia gone? The decline of a major cladoceran in Lake Tahoe, California-Nevada, Internationale Vereinigung fur Theoretische und Angewandte Limnologie Verhandlungen 19:835-842.

Riessen, H. P. 1982. Predatory behavior and prey selectivity of the pelagic water mite Piona constricta. Canadian Journal of Fisheries and Aquatic Sciences 39:1569-1579.

Riessen, H. P., W. J. O'Brien, and B. Loveless. 1984. An analysis of the components of Chaoborus predation on zooplankton and the calculation of relative prey vulnerabilities. Ecology 65:514-522.

Ringelberg, J. 1980. Introductory remarks: causal and teleological aspects of diurnal vertical migration. Pages 65-68 in W. C. Kerfoot, editor. Evolution and ecology of zooplankton communities. American Society of Limnology and Oceanography Special Symposium 3, University of New England, Hanover, New Hampshire, USA.

Rippengale, R. J., and E. P. Hodgkin. 1975. Predation effects on the distribution of a copepod. Australian Journal of Marine and Fresh-water Research 26:81-91.

Rogers, D. J. 1972. Random search and insect population models. Journal of Animal Ecology 41:369-383.

Rohlf, F. J., and H. R. Sokal. 1969. Statistical tables. W. H. Freeman and Company, San Francisco, California, USA.

Salt, G. W. 1974. Predator and prey densities as controls of the rate of capture by the predator Didinium nasutum. Ecology 55:434-439.

Sandness, J. N., and J. A. McMurtry. 1970. Functional response of three species of Phyoseiida (Acarina) to prey density. Canadian Entomologist 102:692-704.

Sandness, J. N., and J. A. McMurtry. 1972. Prey consumption behavior of Amblyseius largoensis in relation to hunger. Canadian Entomologist 104:461-470.

Sherman, P. W. 1977. Nepotism and the evolution of alarm calls. Science 197:1246-1253.

Siebeck, H. O. 1980. Optical orientation of pelagic crustaceans and its consequence in the pelagic and littoral zones. Pages 28-38 in W. C. Kerfoot, editor. Evolution and ecology of zooplankton communities. American Society of Limnology and Oceanography Special Symposium 3, University of New England, Hanover, New Hampshire, USA.

Siegfried, W. R., and L. G. Underhill. 1975. Flocking as an anti-predatory strategy in doves. Animal Behavior 23:504-508.

Simons, S., and J. Alcock. 1971. Learning and foraging persistence of white-crowned sparrows, Zonotrichia leucophrys. Ibis 113:477-482.

Sjoberg, S. 1980. Zooplankton feeding and queueing theory. Ecological Modelling 10:215-225.

Smith, F. E., and E. R. Baylor. 1953. Color responses in Cladocera and their ecological significance. American Naturalist 87:49-55.

Smith, J. N. M., and C. R. Dawkins. 1971. The hunting behavior of individual great tits in relation to spatial variation in their food density. Animal Behavior 19:695-706.

Smyly, W. J. P. 1976. Some effects of enclosure on the zooplankton in a small lake. Freshwater Biology 6:241-251.

Smyly, W. J. P. 1980. Food and feeding of aquatic larvae of the midge Chaoborus flavicans (Meigen) (Diptera: Chaoboridae) in the laboratory. Hydrobiologia 70:179-188.

Sokal, R. R., and F. J. Rohlf. 1969. Biometry. W. H. Freeman and Company, San Francisco, California, USA.

Spitze, K. 1985. Functional response of an ambush predator: Chaoborus americanus predation on Daphnia pulex. Ecology 66:938-949.

Sprules, G. 1972. Effects of size-selective predation and food competition on high altitude zooplankton communities. Ecology 53:375-386.

Stavn, R. H. 1971. The horizontal-vertical distribution hypothesis: Langmuir circulation and Daphnia distributions. Limnology and Oceanography 16:453-466.

Stavn, R. H. 1975. The effects of predator pressure on species composition and vertical distribution of Daphnia in piedmont lakes of North Carolina, USA. Internationale Vereinigung fur Theoretische und Angewandte Limnologie Verhandlungen 19:2891-2897.

Stenson, J. A. E. 1973. On predation and Holopedium gibberum (Zaddach) distribution. Limnology and Oceanography 18:1005-1010.

Stenson, J. A. E. 1976. Significance of predator influence on the composition of Bosmina spp. populations. Limnology and Oceanography 21:814-822.

Stenson, J. A. E. 1978. Differential predation by fish on two species of Chaoborus (Diptera, Chaoboridae). Oikos 31:98-101.

Stenson, J. A. E. 1980. Predation pressure from fish on two Chaoborus species as related to their visibility. Pages 618-622 in W. C. Kerfoot, editor. Evolution and ecology of zooplankton communities. American Society of Limnology and Oceanography Special Symposium 3, University of New England, Hanover, New Hampshire, USA.

Straskraba, M. 1965. The effect of fish on the number of invertebrates in ponds and streams. Internationale Vereinegung fur Theoretische und Angewandte Limnologie Verhandlungen 13:106-127.

Strickler, J. R. 1975a. Swimming of planktonic Cyclops species (Copepoda, Crustaceans): pattern, movements and their control. Pages 599-613 in T. Y. T. Wu, C. J. Brokaw, and C. Brennen, editors. Swimming and flying in nature. Volume 2. Plenum Press, New York, New York, USA.

Strickler, J. R. 1975b. Intra- and inter-specific information flow among planktonic copepods: receptors. Internationale Vereinigung fur Theoretische und Angewandte Limnologie Verhandlungen 19:2951-2958.

Strickler, J. R., and A. K. Bal. 1973. Setae of the first antennae of the copepod Cyclops scutifer (Sars): their structure and

importance. Proceedings of the National Academy of Sciences (USA) 70:2656-2659.

Strickler, J. R., and S. Twombly. 1975. Reynolds number, diapause and predatory copepods. Internationale Vereinigung fur Theoretische und Angewandte Limnologie Verhandlungen 19:2943-2950.

Sullivan, K. A. 1984. The advantages of social foraging in downy woodpeckers. Animal Behavior 32:16-22.

Swift, M. C. 1975. Simulation studies of Chaoborus vertical migration. Internationale Vereinigung fur Theoretische und Angewandte Limnologie Verhandlungen 19:3120-3126.

Swift, M. C. 1976. Energetics of vertical migration in Chaoborus trivittatus larvae. Ecology 57:900-915.

Swift, M. C., and A. Y. Fedorenko. 1975. Some aspects of prey capture by Chaoborus larvae. Limnology and Oceanography 20:418-425.

Swift, M. C., and R. B. Forward Jr. 1981. Chaoborus prey capture efficiency in the light and dark. Limnology and Oceanography 26:461-466.

Swuste, H. F., R. Cremer, and S. Parma. 1973. Selective predation by larvae of Chaoborus flavicans (Diptera, Chaoboridae). Internationale Vereinigung fur Theoretische und Angewandte Limnologie Verhandlungen 18:1559-1563.

Taylor, B. E. 1980. Size-selective predation on zooplankton. Pages 377-387 in W. C. Kerfoot, editor. Evolution and ecology of zooplankton communities. American Scoeity of Limnology and Oceanography Special Symposium 3, University of New England, Hanover, New Hampshire, USA.

Taylor, R. J. 1976. Value of clumping to prey and the evolutionary response of ambush predators. American Naturalist 110:13-29.

Thompson, D. J. 1975. Towards a predator-prey model incorporating age structure: the effects of predator and prey size on the predation of Daphnia magna by Ischnura elegans. Journal of Animal Ecology 44:907-916.

Thompson, D. J. 1978. Towards a realistic predatory-prey model: the effect of temperature on the functional response and life history of larvae of the damselfly, Ischnura elegans. Journal of Animal History 47:757-767.

Threlkeld, S. T. 1979a. Estimating cladoceran birth rates: importance of egg mortality and egg distribution. Limnology and Oceanography 24:601-612.

Threlkeld, S. T. 1979b. The midsummer dynamics of two Daphnia species in Wintergreen Lake, Michigan. Ecology 60:165-179.

Threlkeld, S. T., J. T. Rybock, M. D. Morgan, C. L. Folt, and C. R. Goldman. 1980. The effects of an introduced predator and food resource variation on zooplankton dynamics in an ultraoligotrophic lake. Pages 555-568 in W. C. Kerfoot, editor. Evolution and ecology of zooplankton communities. American Society of Limnology and Oceanography Special Symposium 3, University of New England, Hanover, New Hampshire, USA.

Timin, M. E. 1973. A multi-species consumption model. Mathematical Bioscience 16:59-66.

Tionbergen, L. 1960. The natural control of insects in pine woods. I. Factors influencing the intensity of predation by song birds. Archives Neerlandaises de Zoologie 13:265-343.

Tostowaryk, W. 1972. The effect of prey defense on the functional response of Podisus modestus (Hemiptera: Pentatomidae) to the densities of the sawflies Neodiprion swainei and N. pratti banksianae (Hymenoptera: Neodiprionidae). Canadian Entomologist 104:61-69.

Treisman, M. 1975a. Predation and the evolution of gregariousness. I. Models for concealment and evasion. Animal Behavior 23:779-800.

Treisman, M. 1975b. Predation and the evolution of gregariousness. II. An economic model for predator-prey interaction. Animal Behavior 23:801-825.

Underwood, R. 1982. Vigilance behavior in grazing African antelopes. Behaviour 79:81-107.

Vine, I. 1971. Risk of visual detection and pursuit by a predator and the selective advantage of flocking behavior. Journal of Theoretical Biology 30:405-422.

Vinyard, G. L., and R. A. Menger. 1980. Chaoborus americanus predation on various zooplankters: functional response and behavioral observations. Oecologia (Berlin) 45:90-93.

Vinyard, G. L., and W. J. O'Brien. 1976. Effects of light and turbidity on the reactive distance of bluegill (Lepomis macrochirus). Journal of the Fisheries Research Board of Canada 33:2845-2849.

Von Ende, C. 1979. Fish predation, interspecific predation, and the distribution of two Chaoborus species. Ecology 60:119-128.

Von Ende, C. N., and D. O. Dempsey. 1981. Apparent exclusion of the claodceran Bosmina longirostris by the invertebrate predator Chaoborus americanus. American Midland Naturalist 105:240-248.

Walters, C. J., and R. E. Vincent. 1973. Potential productivity of an alpine lake as indicated by removal and reintroduction of fish. Transactions of the American Fisheries Society 102:675-697.

Ware, D. M. 1971. Predation by rainbow trout (Salmo gairdneri): the effect of experience. Journal of the Fisheries Research Board of Canada 28:1847-1852.

Ware, D. M. 1972. Predation by rainbow trout (Salmo gairdneri): the influence of hunger, prey density, and prey size. Journal of the Fisheries Research Board of Canada 29:1193-1201.

Ware, D. M. 1973. Risk of epibenthic prey to predation by rainbow trout (Salmo gairdneri). Journal of the Fisheries Research Board of Canada 30:787-797.

Warshaw, S. J. 1972. Effects of alewives (Alosa pseudoharengus) on the zooplankton of Lake Wononskopomuc, Connecticut. Limnology and Oceanography 17:816-825.

Wells, L. 1970. Effects of alewife predation on zooplankton populations in Lake Michigan. Limnology and Oceanography 15:556-565.

Werner, E. E. 1974. The fish size, prey size, handling time relation in several sunfishes and some implications. Journal of the Fisheries Research Board of Canada 31:1531-1536.

Werner, E. E., and D. J. Hall. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (Lepomis macrochirus). Ecology 55:1040-1052.

Wetzel, R. G. 1975. Limnology. W. B. Saunders Co., Philadelphia, Pennsylvania, USA.

Wilkinson, G. S., and G. M. English-Loeb. 1982. Predation and colonality incliff swallows (Petrochelidon pyrrhonota). Auk 99:459-467.

Williamson, C. E. 1980. The predatory behavior of Mesocyclops edax: predator preferences, prey defenses, and starvation-induced changes. Limnology and Oceanography 25:903-909.

Williamson, C. E. 1981. Foraging behavior of a freshwater copepod: frequency changes in looping behavior at high and low prey densities. Oecologia 50:332-336.

Williamson, C. E. 1983. Behavioral interactions between a cyclopoid copepod and its prey. Journal of Plankton Research 5:701-711.

Williamson, C. E., and J. J. Gilbert. 1980. Variation among zooplankton predators: the potential of Asplanchna, Mesocyclops, and Cyclops to attack, capture, and eat various rotifer prey. Pages 509-517 in W. C. Kerfoot, editor. Evolution and ecology of zooplankton communities. American Society of Limnology and Oceanography Special Symposium 3, University of New England, Hanover, New Hampshire, USA.

Wright, J. C. 1965. The population dynamics and production of Daphnia in Caynon Fern Reservoir, Montana. Limnology and Oceanography 10:583-590.

Wright, D., W. J. O'Brien, and G. L. Vinyard. 1980. Adaptive value of vertical migration: a simulation model argument for the predation hypothesis. Pages 138-147 in W. C. Kerfoot, editor. Evolution and ecology of zooplankton communities. American Society of Limnology and Oceanography Speical Symposium 3, University of New England, Hanover, New Hampshire, USA.

Wong, C. K. 1981. Predatory feeding behavior of Epishura lacustris (Copepoda, Calanoida) and prey defense. Canadian Journal of Fisheries and Aquatic Sciences 38:275-279.

Wood, K. G. 1956. Ecology of Chaoborus (Diptera: Culicidae) in an Ontario lake. Ecology 37:639-643.

Zaret, T. M. 1969. Predation-balanced polymorphism of Ceriodaphnia cornuta Sars. Limnology and Oceanography 14:301-303.

Zaret, T. M. 1972a. Predator-prey interaction in a tropical lacustrine ecosystem. Ecology 53:248-257.

Zaret, T. M. 1972b. Predators, invisible prey, and the nature of polymorphism in the Cladocera (Class Crustacea). Limnology and Oceanography 17:171-184.

Zaret, T. 1975. Strategies for existence of zooplankton prey in homogeneous environments. Internationale Vereinegung fur Theoretische und Angewandte Limnologie Verhandlungen 19:1484-1489.

Zaret, T. 1978. A predation model of zooplankton community structure. Internationale Vereinigung fur Theoretische und Angewandte Limnologie Verhandlungen 20:2496-2500.

Zaret, T. 1980. The effect of prey motion on planktivore choice. Pages 594-603 in W. C. Kerfoot, editor. Evolution and ecology of zooplankton communities. American Society of Limnology and

Oceanography Special Symposium 3, University of New England, Hanover, New Hampshire, USA.

Zaret, T., and W. C. Kerfoot. 1975. Fish predation on Bosmina longirostris: body size selection versus visibility selection. Ecology 56:232-237.

Zaret, T., and R. T. Paine. 1973. Species introduction in a tropical lake. Science 182:449-455.

Zaret, T., and S. Suffern. 1976. Vertical migration in zooplankton as a predator avoidence mechanism. Limnology and Oceanography 21:804-813.

APPENDIXES

APPENDIX A

ANNOTATED CITATION LISTS

The following lists are subtitled with the appropriate number listed parenthetically in the text, a brief description of the subject referenced, and the page number of text appearance. The complete reference may be found in the Bibliography.

1. Predator Elimination; page 1.

Contributory Literature:

Paine, 1974
Smyly, 1976
Stenson, 1980
Walters and Vincent, 1973

Pertinent Literature:

Ball and Hayne, 1952
Benke, 1978
Bernardi and Guissani, 1975
Connell, 1961
Connell, 1970
Hayne and Ball, 1966
Hendrickson and Oscarson, 1978
Hendrickson and Oscarson, 1981
Lynch et al., 1981
Macan, 1965
Macan, 1977
Paine, 1966
Paine, 1969
Stenson, 1973
Stenson, 1978
Straskraba, 1965

2. Predator Introduction; page 1.

Contributory Literature:

Brooks and Dodson, 1965
Lynch, 1979
Morgan et al., 1981
Northcote et al., 1978
VonEnde, 1979

Pertinent Literature:

Anderson, 1972
Davies, 1969
Goldman et al., 1979
Hayne and Ball, 1956
Morgan et al., 1978
Readshaw, 1973
Rief, 1966
Richards, 1975
Stavn, 1975
Threlkeld et al., 1980
Walters and Vincent, 1973
Warshaw, 1972
Wells, 1970
Zaret and Paine, 1973

3. Community Comparisons; page 1.

Contributory Literature:

Giguere, 1979
Neill, 1981
Neill and Peacock, 1980
Northcote and Clarotto, 1975
Sprules, 1972
VonEnde and Dempsey, 1981

Pertinent Literature:

Anderson, 1980
Galbraith, 1975
Green, 1971
Herbert and Loaring, 1980
Hurlbert et al., 1972
Lewis, 1980
Maguire et al., 1968
Manning et al., 1978
O'Brien et al, 1979
O'Brien and Schmidt, 1979
O'Brien and Vinyard, 1978
Pope et al., 1973
Porter, 1972
Rippengale and Hodgkin, 1975
Stenson, 1976
Zaret, 1972
Zaret, 1978

4. Density and Mortality Correlations; page 1.

Contributory Literature:

Dodson, 1974a
Gliwicz et al., 1981
Hall, 1964
Threlkeld, 1979b
Threlkeld et al., 1980

Pertinent Literature:

Beavers and Stavn, 1975
Benke, 1976
Bernardi and Giussani, 1975
Brockleman, 1969
Cummins et al., 1969
Dodson, 1972
Gliwicz, 1981
Ivelev, 1961
Jacobs, 1977
Kerfoot, 1975
Lynch, 1979
Lynch et al., 1981
Threlkeld, 1979a
Wright, 1965

5. Control and Regulation; page 1.

Huffaker, Messenger, and DeBach, 1971

6. Natural Stability; page 1.

Gause, 1934
Holling, 1965
Huffaker, 1958
Salt, 1974

7. Evolutionary Tendencies; page 1.

Contributory Literature:

Brambilla, 1980
Havel and Dodson, 1984
Kerfoot, 1980a
Kerfoot and Peterson, 1980
O'Brien et al., 1980

Pertinent Literature:

Brooks, 1965
Culver, 1980
Jacobs, 1978
Kerfoot, 1974
Kerfoot, 1975
Kerfoot, 1977a
McPhail, 1969
Maiorana, 1976
Zaret, 1969
Zaret, 1972a
Zaret, 1972b
Zaret, 1980

Kerfoot, 1977b
Lynch, 1980
Zaret and Kerfoot, 1975

8. In Vitro Predation Rates; page 1.

Contributory Literature:
Fedorenko, 1975a
Neill, 1978
Smyly, 1980
Stenson, 1980

Pertinent Literature:
Allan, 1973
Brandl and Fernando, 1981
Confer, 1971
Dodson, 1970
Dodson, 1974b
Drenner and McComas, 1980
Hodgkin and Rippengale, 1971
Kerfoot, 1980b
Kerfoot and Pastorok, 1978
Lynch, 1979
McQueen, 1969
Maly, 1970
O'Brien et al., 1980
VonEnde, 1979

9. The Predation Rate; page 2.
Gerritsen and Strickler, 1977

10. Predation Probabilities; page 3.

Contributory Literature:
Gerritsen and Strickler, 1977
Reissen et al., 1984

Pertinent Literature:
Drenner and McComas, 1980
Drenner et al., 1978
Kettle and O'Brien, 1978
O'Brien, 1979
Williamson and Gilbert, 1980

11. Poisson Process; page 3.

Eggers, 1977
Gerritsen, 1980
Gerritsen and Strickler, 1977
Pastorok, 1981

12. Poisson Parameter; page 3.

Gerritsen and Strickler, 1977
Giguere et al., 1982

13. Reproduction and Rest; page 4.

Contributory Literature:
Hall et al., 1976
Johnson, 1973

Pertinent Literature:
Connell, 1961
Crawley, 1975
Morris, 1963
Sandness and McMurtry, 1972

Giguere, 1980
Haynes and Sisojevic, 1966
Timin, 1973

14. Use of Mean Predation Rates; page 4.

Contributory Literature:
Fedorenko, 1975a
Neill, 1978
Pastorok, 1980a
Smyly, 1980

Pertinent Literature:
Cooper and Goldman, 1980
Cooper and Goldman, 1982
Dodson, 1975
Johnson et al., 1975
Landry, 1978
Messenger, 1968
Riessen, 1982
Thompson, 1975

15. Calculation of Mean Predation Rates; page 4.

Eggers, 1977
Haynes and Sisojevic, 1966
Lane et al., 1976
Sandness and McMurtry, 1972

16. Sensory Contact; page 4.

Contributory Literature:
Holling, 1966
Sjoberg, 1980
Smyly, 1980
Spitze, 1985
Thompson, 1975

Pertinent Literature:
Akre and Johnson, 1979
Charnov, 1976
Chizar and Windell, 1973
Cook and Cockrell, 1978
Dethier and Gelperin, 1967
Dixon, 1959
Dixon, 1970
Hardman and Turnbull, 1974
Holling, 1959
Holling, 1961
Holling, 1965
Holling and Buckingham, 1976
Johnson et al., 1975
Lawton et al., 1975
Messenger, 1968
Morris, 1963
Murdoch and Marks, 1973
Sandness and McMurtry, 1970
Sandness and McMurtry, 1972
Ware, 1972

17. Interval Variations; page 4.

Werner, 1974

18. Interval Reduction; page 4.

Real, 1977

19. Conditional Probability Reduction; page 5.

Contributory Literature:
Holling and Buckingham, 1976
Johnson et al., 1975
Pastorok, 1980a

Pertinent Literature:
Holling, 1961
Kerfoot, 1978
Sandness and McMurtry, 1972
Ware, 1972
Werner, 1974

20. Reduction Variation; page 5.

Ivlev, 1961
Landenberger, 1968

21. Accumulation of Undigested Prey; page 5.

Thompson, 1975

22. Predator Learning Ability; page 5.

Gibb, 1962
Holling, 1961
Oaten and Murdoch, 1975
Tinbergen, 1960
Ware, 1971

23. Vertebrate Learning; page 6.

Contributory Literature:
Allen, 1976
Holling, 1965
Jacobs, 1978a

Pertinent Literature:
Alcock, 1974
Allen, 1972
Allen, 1974
Allen and Clarke, 1968
Murdoch et al., 1975
Simons and Alcock, 1971

24. Invertebrate Learning; page 6.

Contributory Literature:
Hassell et al., 1977
Johnson and Crowley, 1980
Murdoch, 1969

Pertinent Literature:
Cornell and Pimentel, 1978
Haynes and Sisojevic, 1966
Johnson, 1973
Landenberger, 1966
Landenberger, 1968

25. Search Technique; page 6.

Contributory Literature:
Kerfoot, 1978
Murdoch, 1977
Strickler, 1975a
Williamson, 1981

Pertinent Literature:

Akre and Johnson, 1979
Dixon, 1959
Fleshner, 1950
Hassell and May, 1974
Johnson and Crowley, 1980
Kerfoot, 1977
Laing, 1938
Murdie and Hassell, 1973
Readshaw, 1973
Treisman, 1975a
Ware, 1972

26. Prey Congregation; page 7.

Fleshner, 1951

27. Congregational Effections; page 7.

Contributory Literature:

Boulding and Hay, 1984
Eggers, 1977
Landenberger, 1968
Rogers, 1972

Pertinent Literature:

Alcock, 1974
Dixon, 1959
Dixon, 1970
Goss-Custard, 1970
Hassell and May, 1974
Landenberger, 1966
Macan, 1977
Smith and Dawkins, 1971

28. Decreased Handling Time; page 7.

Real, 1979

29. Breaking Congregational Contact; page 8.

Kiltie, 1980
Lazarus, 1972
Treisman, 1975a
Vine, 1975a
Wilkinson and English-loeb, 1982

30. Ambush Predators; page 8.

Taylor, 1976

31. Vigilence; page 8.

Contributory Literature:

Abramson, 1979
Dimond and Lazarus, 1974
Treisman, 1975b

Pertinent Literature:

Banard, 1980
Bertram, 1980
Brown, 1982
Caraco, 1979a
Lazarus, 1972
Lipetz and Bekoff, 1982
MacMillen and Carpenter, 1980

Caraco, 1979b
Crook et al, 1976
Dunbar and Dunbar, 1980
Elgar and Catterall, 1981
Hoogland, 1979
Inglis and Isaacson, 1978
Jennings and Evans, 1980
Metcalfe, 1984
Nelson and Mech, 1981
Powell, 1974
Sherman, 1977
Siegfried and Underhill, 1975
Sullivan, 1984
Treisman, 1975a
Underwood, 1982

32. Predator Confusion; page 8.

Milinski, 1977
Sandness and Murtry, 1970

33. Early Predator Identification; page 8.

Murdoch and Oaten, 1975

34. Spatial Heterogeneity; page 8.

Gerritsen, 1980
Gerritsen and Strickler, 1977
Ware, 1972

35. Small Refuges; page 9.

Contributory Literature:
Hildrew and Townsend, 1977
Johnson and Crowley, 1980
Macan, 1977

Pertinent Literature:
Benke, 1976
Benke, 1978
Connell, 1961
Holling, 1961
Sandness and Murtry, 1970

36. Large Refuges; page 9.

Contributory Literature:
Connell, 1970
Threlkeld et al., 1980

Pertinent Literature:
Caswell, 1978
Hardman and Turnbull, 1974
Macan, 1965
Paine, 1969

37. Different Predator Populations; page 9.

Paine, 1974

38. Temperature; page 9.

Anderson, 1970
Hebert and Loaring, 1980

Cooper and Goldman, 1982
Gophen, 1977
Messenger, 1968

39. Size Selective Predation; page 9.

Contributory Literature:
Brambilla, 1980
Byron, 1982
Giguere, 1979
Pastorok, 1980b
Pastorok, 1981
Smyly, 1980
Swift and Forward, 1981

Pertinent Literature:
Aquatic Invertebrates:
Allan, 1973
Ambler and Frost, 1974
Anderson, 1970
Brandl and Fernando, 1974
Brandl and Fernando, 1978
Confer, 1971
Cooper and Goldman, 1980
Federenko, 1975b
James, 1957
Jamieson, 1980
Kerfoot, 1977
Landry, 1978
Lewis, 1977
Riessen, 1982
Swift and Federenko, 1975
Thompson, 1975
Williamson and Gilbert, 1980
Wong, 1981

Aquatic Vertebrates:
Bernardi and Guissani, 1975
Brooks and Dodson, 1965
Confer et al., 1978
Cramer and Marzolf, 1970
Culver, 1980
Drenner and McComas, 1980
Eggars, 1978
Galbraith, 1967
Hrbacek, 1969
Hutchinson, 1971
Jacobs, 1978a
Jacobs, 1978b
Janssen, 1976
Kettle and O'Brien, 1978
Lynch et al., 1981
Macan, 1977
Northcote and Clarotto, 1975
O'Brien et al., 1976
Vinyard and O'Brien, 1976
Ware, 1972
Ware, 1973
Werner and Hall, 1974

Aquatic Predation in General:
Confer and Blades, 1975
Davies and Reynoldson, 1969
Dodson, 1970
Dodson, 1974a
Hairston and Pastorok, 1975
Hall et al., 1976
Lynch, 1975
Lynch, 1980
Sprules, 1972
Taylor, 1980
Zaret, 1978

40. Predator Age Class; page 10.

Contributory Literature:
Cooper and Goldman, 1980
Riessen, 1982

Pertinent Literature:

Anderson, 1970
Johnson, 1973
Morris, 1963
Murdoch, 1973

41. Invulnerable Age Classes; page 10.

Contributory Literature:

Brambilla, 1980
Hairston and Pastorok, 1975
Pastorok, 1980a

Pertinent Literature:

Connell, 1961
Gerritsen, 1978
Landry, 1978
Maiorana, 1976
Menge, 1972
Murdoch and Oaten, 1975
Paine, 1974
Paine, 1976

42. Age Dependent Movement Behavior; page 10.

Connell, 1970

43. Chaoborus Migration; page 11.

Contributory Literature:

Carter and Kwik, 1977
Chaston, 1969a
LaRow, 1968
Pope et al., 1973

Pertinent Literature:

Green et al., 1973
Juday, 1921
LaRow, 1969
Northcote, 1964
Parma, 1969

44. Prey Exposure; page 11.

Contributory Literature:

Giguere and Dill, 1980
Lewis, 1977
Swift, 1975

Pertinent Literature:

Bohrer, 1980
Enright, 1977
Lewis, 1975
Pearre, 1973

45. Visual Recognition; page 11.

Contributory Literature:

Stenson, 1978
Swift, 1976
VonEnde, 1979
Zaret and Suffern, 1976

Pertinent:

Carter and Kwik, 1977
Confer et al., 1978
Eggers, 1978
O'Brien, 1979
Pastorok, 1980
Pearre, 1973

Juday, 1921
Kerfoot and Peterson, 1980
Lewis, 1975
Lewis, 1980
Ringleberg, 1980
Stenson, 1980
Wright et al., 1980
Zaret, 1975

46. Clear Larvae; page 12.

Dodson, 1970
Kettle and O'Brien, 1978
Kerfoot, 1980b
Stenson, 1980

47. Oxygen Debt; page 12.

LaRow, 1970
Myers, 1980

48. Anaerobic Conditions; page 12.

Hunt, 1958

49. Surface Migration; page 12.

LaRow, 1976
Lewis, 1975

50. Activity Resricted to Hunting; page 12.

Giguere, 1980
Pastorok, 1981

51. No Extended Pursuit; page 12.

Pastorok, 1981

52. Handling Time; page 12.

Havel and Dodson, 1984
James, 1957
Pastorok, 1981

53. Mastication; page 12.

Monchadskii, 1945
Smyly, 1980

54. No Invertebrate Learning; page 14.

Griffiths, 1973
Holling, 1965
Jamieson, 1980
Landry, 1978
Murdoch and Marks, 1973
Wong, 1981

55. Chaoborus Learning; page 14.

Pastorok, 1980b
Riessen et al., 1984

56. Ambush; page 14.

Contributory Literature:
Riessen et al., 1984
Smyly, 1980
Swift and Fedorenko, 1975

Pertinent Literature:
Gerritsen, 1980
Pastorok, 1980a
Giguere et al., 1982
Pastorok, 1980b
Nachtigall, 1974

57. Prey Congregation; page 14.

Prepas and Rigler, 1978
Smith and Baylor, 1953

58. Water Movement; page 14.

George and Edwards, 1973
Stavn, 1971
McNaught and Hasler, 1961
Wetzel, 1975

59. Mechanoreception; page 14.

Contributory Literature:
Giguere and Dill, 1979
Kerfoot, 1978

Pertinent Literature:
Strickler, 1975a
Strickler and Bal, 1973
Strickler, 1975b
Strickler and Twombly, 1975

60. No Mechano-disturbances Created by Chaoborus while Hunting; page 14.

Williamson, 1980

61. Chemoreception; page 14.

Friedman and Strickler, 1975
Strickler, 1975b
Strickler, 1975a
Strickler and Twombly, 1975

62. Tracking; page 14.

Hamner and Hamner, 1977
Kerfoot, 1978

63. Maneuvers; page 15.

Kerfoot, 1980
Kerfoot et al., 1980
Kerfoot and Peterson, 1980
Riessen et al., 1984

64. Chaoborus as a Major Predator; page 15.

Contributory Literature:

Lewis, 1980
Neill, 1981
Northcote and Clarotto, 1975

Pertinent Literature:

Allan, 1973
Brambilla, 1980
Dodson, 1972
Fedorenko, 1975
Giguere, 1979
Hairston and Pastorok, 1975
Hall, 1964
Hrbacek, 1977
Lewis, 1975
Lewis, 1977
Lynch, 1979
Neill, 1978
Neill and Peacock, 1980
Smyly, 1976
Smyly, 1980
Sprules, 1972
Swuste et al., 1973
Threlkeld, 1979b
Zaret, 1975

65. Unlikely Distortion of Recognition Volume; page 15.

Gerritsen and Strickler, 1977
Giguere et al., 1982

66. Small Refuge Preclusion; page 15.

Kerfoot, 1978
Macan, 1977
Vinyard and O'Brien, 1976
Zaret, 1975

67. No Escape; page 15.

Hebert, 1974
Kerfoot, 1980

68. Littoral Zone Avoidance; page 15.

Siebeck, 1980
Wetzel, 1975

69. Benthic Predation; page 16.

Chaston, 1969b
LaRow, 1968
Pastorok, 1980a
Swuste et al., 1973
Wood, 1956

70. No Seeking Refuge; page 16.

Hall, 1964
Kerfoot, 1975
Wright, 1965

71. Temperature Effects on Chaoborus; page 16.

Fedorenko, 1975a
Riessen, 1982
Smyly, 1980

72. Chaoborus Population Subunits; page 17.

LaRow and Marzolf, 1970

73. Planktivore Population Presence; page 17.

Lane, 1979

74. Isolated Chaoborus Populations; page 17.

Neill, 1978

75. Copepod Predation; page 17.

Contributory Literature:

Anderson, 1971
Confer, 1971
Kwik and Carter, 1975
Makrewicz and Likens, 1975

Pertinent Literature:

Confer and Cooley, 1977
Hutchinson, 1971
Kerfoot, 1975
Kerfoot, 1977
Lynch, 1979
Neill, 1981

76. Refutation of the Poisson Process; page 18.

Contributory Literature:

Pedorenko, 1975a
Pastorok, 1980a
Smyly, 1980
Spitze, 1985
Vinyard and Menger, 1980

Pertinent Literature:

Akre and Johnson, 1979
Charnov, 1976
Eggers, 1977
Eveleigh and Chant, 1981
Fox and Murdoch, 1978
Gresens et al., 1982
Hardman and Turnbill, 1974
Hassell and May, 1974
Hassell et al., 1977
Haynes and Sisojevic, 1966
Holling, 1959a
Johnson et al., 1975
Lawton et al., 1975
Messenger, 1968
Morris, 1963
Real, 1977
Real, 1979
Rogers, 1972
Thompson, 1975
Thompson, 1978
Timin, 1973
Testowaryk, 1972
Ware, 1972

77. Complete Satiation; page 18.

Holling, 1963
Holling, 1966
Johnson et al., 1975

78. Species Specific Conditional Probability Reduction; page 19.

Pastorok, 1980a
Pastorok, 1981
Spitze, 1985

APPENDIX B

METHODS

METHODS 1

Controls

There are two general avenues through which error could have been introduced to the data; counting mistakes and actual physical losses of individual prey. Mistakes in counting could have occurred initially or at the termination of the experiment. These mistakes could have resulted in negative or positive variation from the assumed initial density. The variation could have been actual if the mistake occurred in the initial count or apparent if occurring in the termination count. It was impossible to assign proportions of this variation to the specific counting procedure.

There are several ways in which prey could have been physically lost. They may have escaped transfer to the experimental chamber or been lost when the experiment was terminated. Individuals could have been cannibalized. Dead prey could have degraded sufficiently to allow their bodies to pass termination screens.

Control data were collected in several different seasons (see Table 1, Appendix D) and have been arranged in treatment groups (see Table 2, Appendix D). A total of 455 control groups, involving 8140 animals was examined. In no group were more than two organisms missing from the expected. Occasionally there was a single extra prey item but only once were there two extra prey. This occurrence appears as a single extra prey in the data presentation.

As was expected, there was an apparent increase in the number of missing prey when the transfer to and the screening from the 880ml chamber was included in the process. However, there was no indication that the length of time the animals remained in any size container increased the number missing. This would seem to have ruled out cannibalism and the degration of the dead. Furthermore, there did not seem to be much greater difficulty in counting large groups accurately. There was an indication that after the chamber contents were screened, the chambers should be rinsed through the screens. Practice with the procedure may have improved accuracy but not much.

Control data collected at the densities of five, ten, fifteen, and twenty prey per chamber were compared to data collected in 1984 at the respective densities using a G-test (see Table 3, Appendix D). In all four cases, the null hypothesis that the controls and the data were of the same population was rejected at a probability level less than 0.005.

METHODS 2

Predator Size

As was pointed out in the Introduction, the relative sizes of antagonists involved in a predator-prey encounter are important in determining the outcome of that encounter. Adult, female M. edax were so similar in body size that no differentiation could be made through visual inspection. However, one or two egg sacs were often carried by the copepods, apparently affecting their weight substantially. It is hoped that the effect of egg sacs was distributed randomly throughout the data or has no effect on the predation rates. It was frequently difficult to collect enough prey and the elimination of so many possible prey items would have seriously hampered the collection of data. Furthermore, through processing, many females originally carrying eggs lost them. This made testing for the influence of egg sacs virtually impossible.

Conversely, C. punctipennis varied greatly in size apparently even between individuals of the same instar. Due to the ease of measuring length as compared to determining instar, length was used throughout as the determining factor as to when during its life cycle a predator could handle the relatively large M. edax adult females.

A comparison was conducted between data collected June 14, 1979 and that of July 24, 1979 to determine what differences might be expected in the predation rates of predators of different size ranges. The predators collected on June 13th were 6mm to 7mm in length and

presumed to be of the same cohort collected July 24th of which the longest were then 7-9mm. Rarely were any C. punctipennis larvae longer than 8.5mm. Those much longer than 8mm frequently entered pupation prior to conclusion of the experiment. As the time of initiation of those pupations could not be determined, the results had to be discarded. Seldom were any larvae much longer than 8mm used. A G-test was conducted to compare the results of the 6-7mm predators to that of the 7mm to 8mm predators.

	Number of Prey Removed						
	0	1	2	3	4	5	
6-7mm (June 14)	28	36	16	14	4	0	Number of individual predators exhibiting a particular response
7-8mm (July 24)	15	32	28	13	6	4	

$G = 13.527$; $\chi^2_{0.025(5)} = 12.832$; $\chi^2_{0.01(5)} = 15.086$ (Rohlf and Soka, 1969)

The G-value is significant at $P = 0.0125$. The null hypothesis that the number of prey removed is independent of the predator size is rejected.

However, this conclusion should be viewed with some skepticism. Field environmental conditions varied somewhat between the two collections in both ambient temperature and day length but seemingly more important was the possibility of an environmentally induced behavioral change during the intervening 41 days. Furthermore, the groups were not only differently sized but of different instars. To ascribe the statistical difference solely as a result of size differences is not entirely warranted. Nevertheless, the results seemed adequate provocation to restrict larval size to greater than 7mm.

METHODS 3

Isolation Interval

A preliminary experiment was conducted May 9, 1977. It is unique among the other data in that it was conducted over a 24 hour period in small petri dishes containing approximately 50mm of water. The experiment was originally designed to determine if C. punctipennis larvae would eat in the laboratory. In order to gather enough predators, two collections were necessary. The first group were collected May 5, 1977 with the predators isolated and starved from that date and will be referred to as the Starved Group. The second collection was made May 8, 1977 with those predators in isolation less than 24 hours and will be referred to as the Not-Starved Group. Isolation and testing were conducted at 25° C, approximately that of the ambient lake surface temperatures.

	Number of Prey Removed									
	5	6	7	8	9	10	11	12	13	14
Starved (May 5)	2			1	1	3	1			
Not-Starved (May 8)	1	1	1				1	2	1	1

$F_S = 1.033$; $F_{0.5(1,14)} = 0.479$; $F_{0.25(1,14)} = 1.44$ (Rohlf and Sokal, 1969).

The F-value is not significant. The null hypothesis that the number of prey removed is independent of the isolation interval is accepted.

METHODS 4

Experimental Temperature

As was stated in the Introduction, environmental temperature can affect the feeding rates of some predators (page 8). However, this is believed to be less effective with Chaoborus (Riessen, 1982; Smyly, 1980), particularly the fourth larval instar (Fedorenko, 1975a). Chaoborus larvae undergo a daily migration (see Introduction, page 10) taking them through a temperature range which can be great if a thermocline is involved. The prey are likely to undergo a similar migration. Chaoborus larvae are known to feed at the extremes of that migration (Pastorok, 1980; Swuste et al., 1973). Though feeding may be affected somewhat by temperature, it is likely that the behavior assumes a similar form over a wide range of temperatures. From the present study, it was apparent that at least at certain times seasonality was more important than ambient temperature in establishing the feeding rate (see Seasonal Variation, Results 3, Appendix C).

The object of this study was to explore the feeding behavior and not to establish rates immediately comparable to field situations. So as to reduce stress immediately prior to experimentation, promote comparability among experimental groups, and since the establishment of optimum temperatures would have been costly compared to the unreliability of the organism source, it was decided to forego searching for optimum temperatures and arbitrarily set a constant temperature in which the organisms responded with the feeding behavior.

This same temperature was maintained throughout processing of organisms as much as possible (see Counting Apparatus, Methods 6, Appendix B).

METHODS 5

Experimental Chamber Size

So long as animal behavior is not disrupted, the size of the experimental chamber is important only if one wishes to compare the data with a natural situation. In that case, the effect of all variables excluded from further examination as presented in the Methods section would have to be examined in detail. This is far beyond the scope of this study.

The major emphasis of this study was to reveal the most basic feeding behavior. It is not certain that chamber size does not affect the natural behavior but direct observation of the feeding behavior of Chaoborus larvae has been previously conducted in much smaller volumes than employed here (Giguere et al., 1982; Pastorok, 1981; Riessen et al., 1984; Smyly, 1980; Swift and Forward, 1981; Wong, 1981). Dodson (1975) found no differences in feeding rates of the copepod Heterocope septentrionalis when contained in either 220ml or 900ml containers. Furthermore, rather than a suppression of the behavior, Giguere et al. (1982) were more concerned that the chamber walls would enhance the feeding rate:

> . . . the extent to which predator and prey aggregate near plexiglas walls in the arenas is nearly compensated for by the fact that a wall prevents prey from approaching a predator from a particular direction.

The use of larger chambers incorporates two difficulties. The total volume of water used in a large number of replications at one

time would cause logistic problems and the number of prey necessary to arrive at a comparable density is greater. This latter feature compounds counting problems in both setting-up and concluding experiments. The number of replications conducted at any one time would certainly have been reduced.

The final volume employed here, approximately 880ml, corresponded nicely to that of Riessen (1982) who worked with 1200ml and Smyly (1980) with 1000ml volumes. Smyly kept Chaoborus larvae feeding up to 100 days in his experiments. Pastorok (1980a) used somewhat larger volumes, two to three liters, while Neill (1981) used large field enclosures. The sacrifice of replications is evident in both works.

If the ultimate objective is the comparison of laboratory and field rates, then once the feeding behavior is adequately represented at a particular chamber size, the effect of chamber size could easily be determined at any one or several densities and applied to the entire range of field densities. The shape of the chamber may be just as important as the size and must also be analyzed before considering application to field problems.

METHODS 6

Counting Apparatus

Mesocyclops edax are quick, powerful swimmers which will swim against any current. In order to reduce the time involved counting large numbers of these individuals, an apparatus was designed. A pure stock of approximately 2000 prey in 250ml of water was sucked into a glass tube 8mm in diameter, 6m long, in a coil 20cm across with a volume of approximately 400ml (see A, Figure VII). The upper end of the coil was sealed with a clamp (see B) holding the prey suspension within the tubing of the coil. A plastic bag containing ice and water was placed in the center of the coil. This slowed the organisms without apparent damage (see Controls, Methods 1, Appendix B).

While stress associated with cooling was not evident in the survival rate, it could have certainly altered the predation rate. If normal prey activity was reduced, the rate of encounter could have been reduced. However, if the prey could not have escaped as easily, more could have been caught. As long as this effect were random, the mathematical representation of the behavior should change only in amplitude. As this method more than doubled the counting rate and improved precision, the risk of biasing results, stemming from non-random dispersion of the effect, was accepted.

After a cooling down period of about 15 minutes, air was injected at the top of the coil with a 60ml syringe (see C). A stopcock (see D) facilitated refilling the air syringe. Water and

stopcock (see D) facilitated refilling the air syringe. Water and animals, unable to resist the current, were forced through a 3mm by 30mm tube (see E) individually or in small groups. When the desired number passed the junction in the middle of this tube, water was injected from a second 60ml syringe (see F). This forced everything already past the junction to exit the assembly into a shell vial. It was found useful to insert a screen (see G) to prevent reviving copepods from escaping into the water reservoir.

METHODS 7

Experimental Interval

As was stated in the Introduction (page 4), maximum predation rates are necessary for the construction of any theoretically sound mathematical representation of a predator-prey interaction. Furthermore, it was discussed how the behavior of Chaoborus larvae might lead to the isolation of a diurnal period during which the animals maintain maximum predation rates (page 11). The diurnal period presented was that after the evening surface migration and prior to dawn interment.

There is information that the behavioral sequence is not as simple as first presented. Chaston (1969) and LaRow (1968) both observed the sequential diurnal periods of larval behavior. This activity was believed related to migration with the following inactive period being used by the predators as ambush hunting time. Both authors saw an active period beginning at dusk and continuing for two or three hours. LaRow and Marzolf (1970) and Lewis (1977) observed that by the end of this period, the fourth instar Chaoborus surface population had peaked. Beginning approximately two hours later, a second similar sequence was observed by the authors. Personal observation revealed that Chaoborus larvae do sink while inactive and it seems reasonable that in order to remain in the greatest prey density, the predator might have to undergo a second migration. It seems then, that in a natural situation, during the nocturnal period,

larvae might be employed in behavior not directly related to the consumption of individual prey items. This would greatly increase the difficulty of establishing maximum predation rates.

The following set of experiments was designed to discern variable predation rates through the nocturnal period if they exist. Chaoborus larvae were exposed to prey during subsets of the nocturnal period. Each subset was three and a half hours long. Shorter subsets may be desirable for better isolation of a maximum rate. However, it was felt that with a restricted number of observations the subset length would be increased to offset initial inherent variation.

Among the five subsets, beginning at 10:00PM, 10:30PM, 1:45AM, 3:00AM, and 3:15AM, the null hypothesis, that the number of prey removed was independent of the period tested, was accepted but the probability was less than 0.5 that they all came from the same population (see test 1, Table 4, Appendix D). However, inspection and individual comparisons revealed that it was likely that the predation rate of the subset beginning at 10:30PM was greater than that beginning at 10:00PM ($P < 0.1$) (see test 2). Since 10:30 was between two and three hours after sunset, corresponding nicely to theory, all experimentation was begun at that time.

The length of the experiment presented a further complication. It appeared from the data that the maximum predation rate does not continue through to 6:00AM and maybe not even through to 5:00AM (see tests 4 and 5). The maximum rate could have begun to taper off at any time. However, short experiments may incorporate so much inherent variability that differences may be hidden by error. The intent of

this work was to reveal the nature of the behavior rather than develop rates for modelling natural situations. Therefore, a period of six hours was arbitrarily adopted, hopefully eliminating much of the time when predation rates are low while increasing the chances of encounters in each observation.

APPENDIX C

RESULTS

RESULTS 1

Exponential Simulation

The Poisson probability distribution estimates the proportion of instances where any particular number of random events (x) occurs within a specific time interval (t). It can be derived from the Binomial probability distribution where the parameter of that distribution is determined by the number of possible independent events (n) and the probability of an event (p). The mean number of events (μ) within a specific time interval equals the product of (n) and (p). If (n) is large such that a reduction to (n-1) when an event occurs is inconsequential and (p) is small such that a significant reduction does not occur within an interval (t), the Poisson distribution may be employed. The parameter of that distribution (λ) equals the product of (n) and (p). As a point of interest, the mean of the distribution (μ) and the standard deviation equal the parameter (λ). In order to adapt the distribution to different time intervals, the parameter becomes (λ)(t).

The probability distribution from which the interval between random events can be predicted when (μ) is known is the exponential probability distribution. The parameter of this distribution is equivalent to that of the Poisson distribution with a time interval of one or (λ).

The relationship between the Poisson and exponential distributions is mathematically exposed when the probability of no

events during the interval is calculated. The proportion of the area under the exponential curve ($\lambda e^{-\lambda t}$) from t=0.0 to t=t represents the probability that an event will occur before time (t). The area from (t) to infinity represents the probability that no events will occur within the interval [0,t]:

$$\int_{t}^{\infty} \lambda e^{-\lambda t} = e^{-\lambda t}$$

When calculated through the Poisson distribution, the probability that the number of events (x) in the interval 0 to (t) equals zero is:

$$p(o;t) = (e^{-\lambda t}(\lambda t)^{0})/0! = e^{-\lambda t}$$

Here, (λt) is generally referred to as (μ).

Using the exponential distribution, a stochastic computer simulating program was constructed through which discrete frequency distributions could be compiled. A distribution recorded the frequency at which any particular number of "events" occurred within a group of simulations at any particular (λ). The following list is the loop within the exponential simulation program which determines the number of "prey items" eaten by an individual "predator":

```
1          DO 10 J=1,D
2          CALL GGUBS(DSEED,1,P)
3          HT=(-1/λ) * ALOG(1.0-P(1))
4          TSUM=TSUM + HT
5          IF(TSUM.GT.TOT) GO TO 11
```

```
6   10      CONTINUE
7   11      CONTINUE
8           I=J - 1.0
```

1. Between lines 1 and 6, a loop is created which determines the time intervals necessary for the capture of a series of "prey items" by a "predator." The loop may repeat D times which is the number of available "prey items" and their density. J becomes the number of repetitions before the loop is exited.
2. Line 2 generates through IMSL a random number from a distribution which is uniform on the interval from 0.0 to 1.0.
3. The formula of line 3 generates an interval from an exponential distribution described by (λ), representing the hunting time, HT, necessary for the capture of an individual "prey item." P, a uniform random variable, is generated in line 2. (λ) is calculated from data, is equal to MU of the Holling Disk formula if DP = 0.0, is the average of a Poisson process, and is introduced into the model before entrance into the loop. If P has a uniform distribution, then, from the distributional theory of random variables, it is known that solving P = 1 - exp(- λ* HT) for HT results in a random variable with an exponential distribution. Thus, HT, as described by line 3 is an exponential random number.
4. TSUM in line 4 is the total time expended hunting and is initially set at 0.0.

5. In line 5, TOT is the total time allocated for each "predator" to hunt.
6. If TOT of line 5 is not exceeded, line 6 reinitiates the loop.
7. If TOT of line 5 is exceeded, line 7 leaves the loop.
8. As the last time through the loop exceeds the allocated time, the last capture is not completed where I is the number of captures.

This model should produce distributions homogeneous with Poisson distributions of the same average number of "prey" captured. This homogeneity was tested at every density between 3 and 40 prey per 880ml where experimentation had been conducted. The capture rate used was calculated from a linear regression of density versus the observed average number of captures in experimental data. The upper 95% confidence limit from that regression was used since a large capture rate would make the test for homogeneity more sensitive. The total exposure time, TOT, was set at six units, corresponding to the hours of exposure allowed experimentally.

As the number of simulation replications or individual "predators" within a distribution is increased, the shape of the resultant distribution is less likely to be greatly affected by vagaries in the random process and differences between distributions less likely masked. It seemed desirable not only to expose any differences which might be expected at replication levels approximating those produced experimentally but more subtle differences which could only be exposed with larger replication groups. Therefore, the model

was tested at each density with both 1,000 replications, representing experimental levels, and 5,000 replications. At any density, the model results used in comparisons between distributions of 1,000 replications were included with 4,000 replications for the homogeneity tests of larger groups. It was hoped that this inclusion might enhance revelations, garnered through inspection, of the necessity to observe larger groups of animals.

Each developed distribution was compared via the G-transformation of the Chi Square test (Sokal and Rohlf, 1969) to an estimated Poisson distribution with the mean of each equal to that prescribed by the upper 95% confidence limits of the linear regression of pooled experimental data. Table 5 (Appendix D) lists the p-values for a test of homogeneity of the simulated distributions and Poisson distributions for each density along with the predicted upper 95% confidence limit means. No obvious differences are noted and the exponential model appears to replicate a Poisson process as expected.

RESULTS 2

Density Reduction Phenomenon

The process where density was reduced in the experimental confines can easily be replicated with exponential simulation (see Exponential Simulation, Results 1, Appendix C). Within the operational loop of that model, the parameter for the calculation of intervals between successful predator-prey interactions remains constant and equal to the expected mean number consumed (μ), regardless of the number of prey remaining. However, it was also stated that (μ) = (n)(p), where (n) is the number of possible events at the initial density and (p) constant.

The density reduction phenomenon is duplicated in the simulation if after each successful consumption by an individually simulated predator, (n) or (D) of the model is reduced by one. Therefore, the interval for the initial consumption is governed by the parameter (λ), equalling (μ), from which the constant (p) is calculated. Subsequently, (λ) equals (p) time the reduced (n) or (D).

```
3          (λ) = (p)(D)
4          HT = (-1/λ) - ALOG(1.0-P(1))
5          TSUM =  TSUM + HT
6          D = D - 1
```

The homogeneity between distributions of simulations in which the density reduction phenomenon was incorporated and estimated Poisson distributions is shown in Table 6 (Appendix D). The parameters (p)

used in simulation and (μ) used in Poisson estimation were derived again from mean predation rates prescribed by the upper 95% confidence limits of the linear regression of pooled experimental data.

From inspection of the p-values in Table 6, it seemed that with large numbers of observations in each distribution, homogeneity between generated distributions involving the density reduction factor and calculated Poisson distributions was less obvious, particularly at lower densities. The loss of homogeneity at lower densities can be expected as single unit reductions in density cause a proportionally greater density reduction than at higher initial densities. It was also obvious that in areas where density reduction should have greater effect, lower densities, greater numbers of observations mollify initial random error and finer differentiation is possible. However, it seems that the number of observations must be increased perhaps by an order of magnitude over that presently possible experimentally before any differentiation in homogeneity between experimental data and calculated Poisson distributions caused by density reduction in the former would become statistically evident.

While the density reduction phenomenon presents no apparent difficulty in distributional analysis, it may be of some interest as to how great an effect the phenomenon has on average predation rates across a range of initial prey densities. That is, does density reduction deflate the estimated predation rate below that expected under natural conditions, where density reduction does not occur at proportions experienced experimentally? This seems particularly

important if one attempts to apply laboratory rates to field situations.

Values representing the average number of prey taken by a predator involved in a simple interaction without density reduction were obtained from the initial testing of the model (see Exponential Simulation, Results 1, Appendix C). Each value was developed from either 1000 or 5000 individual observations. They were then compared to the appropriate similar values calculated form the data of the present section to determine if both populations are best represented by a common linear regression (see Tables 7 and 8, Appendix D).

A comparison of means derived from 1000 simulated observations through both the exponential and density reduction models showed that in only 19 of 26 comparisons was the effect of density reduction sufficient to produce a reduced mean value. This is close to what might be expected with absolutely no effect. The test of whether both populations were best represented by a common line was equivocal. With the present experimental technology then, there is no statistical imperative indicating that some adjustment of laboratory derived predation rates is necessary.

However, when the compensation of aberrance, discovered if one could provide 5000 observations for each mean derivation, was considered, statistical differences appeared. Twenty-four of 26 mean comparisons had a reduced predation rate with density reduction and the hypothesis that both populations are best represented by a single linear regression was rejected at a probability of less than 0.001. It

seemed then that while the effect of density reduction was real, its consideration for present purposes was unnecessary.

RESULTS 3

Seasonal Variation

In 1983, Chaoborus punctipennis larvae were available in lengths greater than 7mm from 1 May through 7 June. Then a major emergence occurred leaving only larvae smaller than 7mm. Larvae larger than 7mm were again available from 2-19 July.

It seemed reasonable to assume that the temporally separated groups were members of different cohorts. As no large emergences were noted prior to collection of these organisms, it seemed reasonable that the individuals of both groups over-wintered as larvae but at different instars. Observation indicated a quantitative difference between the feeding rates of the two groups and a comparison of those rates through analysis of covariance seemed appropriate. The results show an unequivocal difference with the common line hypothesis rejected at a probability less than 0.001 (see Table 9, Appendix D).

In 1984, a similar cohort succession of Chaoborus larvae seemed to occur but was not as delimited. Apparently, members of one cohort were larger than 7mm from 13 May through 10 June. The subsequent cohort appeared in lengths greater than 7mm from 1 June through 14 July. From 1-10 June, 7mm members of both cohorts were present and perhaps distinguishable by coloration. The elder organisms seemed more opaque and yellow (Fedorenko and Swift, 1972). It was, however, impracticable to separate the groups for testing. Neither could the color characteristic be used to absolutely indicate the presence of the

second cohort in lengths greater than 7mm. Color only corroborated the situation as indicated by predation rate differences. The supposition that elder organisms were colored was substantiated by colored organism absence after 10 June. Placing the beginning of the 7mm population adulteration as 1 June was more of an arbitrary decision based upon the observation of predation rates after the fact.

The data were placed in three groups: the first collected before 1 June, the second from 1-10 June, and the third after 10 June. All three groups were best represented by different regressions with the results highly significant (see Tables 10, 11, 12, Appendix D).

The pretense that predation rates of large C. punctipennis larvae were not constant throughout one season was strongly substantiated by this data. That the change was a result of cohort replacement seemed reasonable and had observational support.

RESULTS 4

Distributional Summation

Comparisons of individual consumption results from different years showed that by distributional analysis, statistically different distributions existed (see Table 16, Appendix D). This may have been a result of random chance but may also have been a result of differences in the process. The latter might seem probable as differences in the process were evident from one week to the next in certain circumstances (see Seasonal Variation, Results 3, Appendix C), not to mention when observations were several years apart. As will be seen later, distributional analysis of predation components required large data pools, unapproachable within one or even several seasons under the primitive conditions prevailing during the data collection for this attempt. However, for both the chance of exposing predation components, albeit with the pooling of highly divergent data groups, but also for fashioning an initial attempt at distributional analysis of predator-prey behavior, it was felt that pooling was justified.

Later the reader will be afforded the opportunity to choose between the analyses of variously pooled data sets, more or less divergent, from which to draw conclusions. However, since highly divergent poolings will still be presented, it seemed necessary to know what might be expected from the worst in terms of false representation.

If distributional divergency were a result of different digestive pause intervals, one might expect the resultant pooled

distribution to appear affected by a mean pause interval. However, if divergency were the result of different mean hunting times, a seemingly more plausible assumption, the resultant pooled distribution might not appear affected by a pause equal to that necessary for the production of the predecessor distributions. As the direction of distributional analysis here was an estimation of a digestive pause, analysis might have been compromised in this latter case.

Any possible aberration from a constant pause interval caused by summation might be revealed by simulation comparisons. The digestive pause was introduced into the model in the following manner:

```
4        HT = (-1/λ) * ALOG(1.0-P(1))
5        T = HT + DP
6        TSUM = TSUM + T
```

where DP is the digestive pause interval.

Two distributions were constructed through simulation having equal digestive pause intervals but differing in the parameter for the production of hunting times (λ). For each of these distributions, (λ) was chosen as that which produced a specific mean number of prey eaten. These distributions were summed, representing pooling.

Distributions, where the individual replication number equaled the sum above and where the hunting time parameter was adjusted such that the mean number of prey consumed was the average of those of the summed distributions, were constructed across a range of pause lengths. At each pause length in the range three such distributions were created.

At any particular pause length, the three distributions with an average number eaten equal to that of the summed distribution were each compared to that distribution via the G-test. The resultant p-values were averaged and compared to similarly obtained averages at different digestive pause intervals. The entire process, from the construction of distributions for summation through comparisons to the distributional sets of these across a pause interval range, was conducted three times for each specific set of circumstances; initial density, observation number, mean number eaten, and digestive pause interval of the summed distributions.

The most extreme departure from homogeneity in the data occurred when that collected in 1979 at an initial density of twenty was compared to the pooled data at that density from all other years (see Table 16, last entry, Appendix D). A similar situation was constructed for summation testing through simulation:

1. Density was initially set at 20,
2. Six hundred individual replications were run for each of two distributions to be summed,
3. A digestive of pause of three hours, similar to that suggested by non-linear regression of the data (see below) was incorporated into each individual simulation,
4. Hunting time parameter (λ) values were manipulated such that one of the distributions resulted in a mean number of prey consumed of 1.0 while the other had a mean of 1.5,
5. The resultant summed distribution was compared to distributions of 1200 replications each where the hunting

time parameter (λ) was adjusted such that the mean number consumed was 1.25, the mean of the summed distribution.

Subsequently, the sensitivity of the distributions to the number of individual replications and the length of the digestive pause was analyzed. For the former case, the analysis was conducted with only 200 total individual replications. The digestive pause was halved to 1.5 hours in the latter case, corresponding well to the lower 95% confidence limits as suggested by non-linear regression (see below).

Results showed that in seven of nine cases, summed distributions more closely resembled distributions constructed with a digestive pause less than that used in their construction (see Table 17, Appendix D). It appeared that a reduction in the digestive pause of 15% might attain the best fit. Therefore, if a digestive pause was indeed in effect in the predation process, pooling of highly divergent data in terms of the average number of prey eaten might actually have concealed part of hat pause. Nevertheless, one would never expect that the absolute presence of a pause could be concealed in distributional analysis from the pooling of divergent data.

RESULTS 5

Digestive Pause and Poisson Distributional Comparisons

The ultimate distributional analysis will consist of comparisons of data to both distributions estimated by the Poisson formula, representing a process having no digestive pause, and distributions derived through simulation incorporating such a pause. It was felt that prior to this analysis, those data distributions enjoying the parametric levels which would allow statistical differentiation between them and either Poisson or simulated distributions, depending on whether a pause as suggested by regression exists or not, should be identified. If the mean number of prey eaten is low,such as at low densities, fewer digestive pauses would be experienced by the population constructing the distribution, the effect smaller, and less recognizable statistically. If the number of observations is low, the compensation of possible aberrance is less likely along with statistical differentiation. For this identification process, Poisson distributions with means and numbers of observations identical to data were compared to simulations incorporating pauses.

Data was organized into three groups for analysis. This was done so that any real or imagined problems arising from the pooling of disparate data might be avoided by one accepting the analysis of only that data pooled from sources showing close homogeneity to each other. Here, parameters for distribution construction were taken from those three groups. They were pooled 1983 and 1984 data; pooled 1980, 1981,

1983, and 1984 data; pooled 1979, 1980, 1981, 1982, 1983, and 1984 data.

For any particular pooled data set, a non-linear regression was conducted with a constant digestive pause which provided an estimate of the hunting time parameter (λ). This parameter (λ) and the digestive pause were introduced into the exponential simulation incorporating a digestive pause as described in the discussion of distributional summation (see Distributional Summation, Results 4, Appendix C). At any particular initial density, the number of simulations contained in a distribution equaled the number of data observations. As the hunting time parameter (λ) was derived from an entire data set consisting of many distributions, the mean number eaten in simulation was only approximately that of the corresponding data distribution.

The resultant distribution from simulation was compared to a Poisson distribution of the same mean. This comparison would show less of a difference than a comparison to a Poisson distribution with a mean suggested by regression. There, the difference in means would contribute to the total identifiable differences. As the objective of this exercise was to identify differences, this conservative approach seemed appropriate. The resultant p-value was averaged with two others derived from simulated distributions of the same parameters but created from different random number sets.

The pooled 1983 and 1984 data consisted of 21 distributions in a range of initial densities from three prey through 23 prey per 880ml chamber. The number of observations in each distribution varied from 101 to 233. As indicated earlier, non-linear regression suggested that

a pause of 3.2 hours for each prey item would produce the observed curvature in the average number of prey consumed across the density range for this data set. With this pause and the appropriate hunting time parameter (λ), derived from a separate non-linear regression with the pause held constant at 3.2 hours, three different distributions were created through simulation at each density, incorporating the appropriate number of replications. Each of the three distributions was compared to a Poisson distribution with an identical mean. From each comparison, a probability of homogeneity was derived through the G-test and averaged with the other two comparisons (see Table 20, Appendix D). An average probability less than 0.05 indicated that a statistical difference was likely to exist between a Poisson distribution and a simulation distribution affected by a pause of 3.2 hours. If empirical distributions were actually affected by a pause of that interval, they should then appear statistically different from Poisson distributions. Likewise, if empirically there was no pause, the distribution should appear significantly different from simulation distributions incorporating a 3.2 hour pause. This average probability of less than 0.05 occurred in 16 of 21 cases. In each of these 16 cases, the process was repeated at a shorter digestive pause interval.

In the repetition of these 16 cases, which either had a higher density, subsequently a higher feeding rate, or more observations than those not likely to show significant differences, the digestive pause was lowered to 2.5 hours. Here, comparisons showed that in only 7 combinations of density and observation number would significance likely appear.

The process was repeated by lowering the digestive pause until a pause was established for each set of circumstances at which significance would be unlikely. In only one case of 21, did the parameters of initial density (23) and number of observations (229) allow the likelihood of significant differences at a digestive pause below the 95% confidence interval suggested by regression (1.8 hours). This was a two-tailed test, so from this data set, only 2.5% of the time would one expect a lower digestive pause to occur by chance.

Further pooling revealed five more sets of conditions where the incorporation of a pause below the 95% confidence intervals would likely produce statistically different distributions than if no pause were involved (see Table 20, Appendix D). As two of these six circumstances represent only incompletely pooled data, four completely isolated sets of circumstances in the data remain where regressional and distributional analysis might be rigorously compared.

RESULTS 6

Digestive Pause and Empirical Distributional Comparisons

As stated earlier, the comparisons of empirical distributions to Poisson distributions of identical means revealed quite close homogeneity. Of the 26 isolated empirical distributions of the final pooling, the average probability of homogeneity with Poisson distributions approached 0.7 (see Table 21, Appendix D). Tests on lesser volumes of data showed similar results. However, it was also discussed earlier, that not all of these empirical distributions, even if having identity with Poisson distributions, could be expected to be statistically different from distributions involving a digestive pause as suggested by regression (see Digestive Pause and Poisson Distributional Comparisons, Results 5, Appendix C). In fact, those four isolated data sets of the final pooling (densities 15, 16, 20, and 23) producing distributions which, if identical to Poisson distributions, could be expected statistically different from distributions affected by a pause shorter than the smallest allowed by regression, had an average probability of homogeneity to Poisson distributions below 0.5 (see Table 21). It seemed possible then, that the empirical distributions still may not have been statistically different from distributions expected if a digestive pause is operating.

A similar testing method was employed as before (see Results 5). Here, three different distributions were created through simulation at

each density and digestive pause interval, having as their mean that of the appropriate empirical distribution. To arrive at that mean, the hunting time or exponential parameter (λ) was varied while the digestive pause remained constant. The appropriate empirical distributions were then compared to the simulations via the G-test.

A total of 17 empirical distributions was tested. Included among these were the four isolated cases mentioned above (density 23 with data from 1983 and 1984 and densities 15, 16, and 20 with data from all six collection years). Eleven of the other 13 cases involved distributions with parameters (density, average number of prey eaten, and number of observations) which, if used in comparisons of Poisson distributions to distributions affected by a digestive pause would not allow differentiation at pause levels below the 95% confidence limits for that pause as determined by the regression of the empirical data associated with and included within those distributions. However, the pauses at which Poisson and simulated distributions would be significantly different for these empirical conditions were nevertheless far below that suggested by regression (see Results 5). It was hoped that these inclusions would substantiate or refute any trends seen from the analysis of the best four cases.

Of these 11 distributions, four (densities 15, 16, and 20 of 1983 and 1984 collections and density 10 with 1980, 1981, 1983, and 1984 data) were subsequently pooled with 1979 and 1982 data for testing. The analysis of these four cases and also densities 15 and 20 collected in 1980, 1981, 1983, and 1984 with which the crucial

digestive pause was below the 95 percentile, were included to allay suspicion of pooling problems.

In synopsis, 11 distributions of isolated data were accepted for testing. Additionally, tests on six groups of data, subsequently pooled and included with those 11, were provided for those with difficulties accepting the pooling procedure.

For each of these 17 sets of conditions provided from empirical data (initial density, mean number of prey eaten, and number of observations) distributions were constructed through simulation incorporating a digestive pause. The digestive pause at which simulations were conducted was that determined as crucial or the greatest pause at which statistical differences were unlikely between Poisson distributions and digestive pause simulations for each specific set of conditions (see Results 5).

Three simulated distributions were constructed for each specific set of conditions including digestive pause. These were compared to the appropriate empirical distribution via the G-test. The derived probability of homogeneity was averaged with the other two constructed at each specific set of conditions and compared to the same empirical data (see Table 22, Appendix D).

In 9 of 11 isolated sets of conditions and in all six subsets tested, empirical distributions were significantly different than simulation distributions at digestive pauses where one would not expect simulated and Poisson distributional comparisons to show significance at the 0.05 probability level. This indicated that empirical

distributions resemble distributions incorporating digestive pauses even less than Poisson distributions.

In one of two cases where unexpected significance was not revealed (density 13 with data from all years), correspondence between the comparisons of both the empirical and Poisson distributions to simulations was to be expected as the empirical data was homogenetic to Poisson estimations at a probability level approaching 0.95 (see Table 21, Appendix D). The other case (density 40 from data collected in 1981) had the fewest number of observations included in any of the distributions tested.

Further testing was conducted with the four empirical distributions providing those sets of conditions where Poisson and simulation comparisons revealed a lack of homogeneity at a digestive pause below the regressional 95% confidence limits (densities 15, 16, 20, 23 of the final pooling). These tests revealed that the digestive pause must be lowered an average of 45% from that where Poisson and simulated distributions were unlikely to show significant differences, such that empirical and simulated distributions were likewise unlikely to show significant differences (see Tables 20 and 22).

The conclusions of this section were:

1. that empirical distributions did not resemble distributions incorporating a pause at anywhere near the magnitude of that pause suggested by regression,
2. that some agent was affecting the assumed underlying Poisson process in a fashion completely unlike that expected from a digestive process, here in the form of a pause.

It becomes necessary to describe that agent. If, as might be expected, that agent can be assumed an experimental artifact, then the comparisons of Poisson and simulated distributions should be most representative of the differentiation potential of the experimental data volume. Those comparisons indicated:

1. that a pause no greater and probably far less than 35% of that suggested by regression was actually operating (see Table 20, density 20, total pooling),
2. that regressional analysis, as its lowest estimate was higher than the greatest possible under distributional analysis, was inappropriate to measure the digestive effect,
3. that some other process must have been operating to construct the curvature observed in regressional analysis.

RESULTS 7

Refusal to Eat

Six empirical distributions were examined in connection with a possible refusal to eat by some predator individuals. These included those four isolated distributions whose parameters, when applied to Poisson and simulated distributions, were likely to produce significant differences between those distributions even if the digestive pause incorporated in simulation was below the 95% confidence limits suggested by regression (densities 15, 16, 20, and 23 of the final pooling). Also included were two distributions subsequently pooled with those above but whose parameters were also likely to produce similar results when applied to Poisson estimations and simulations (densities 15 and 20 with 1980, 1981, 1983, and 1984 data).

The initial comparisons of empirical data with Poisson estimations revealed an excess of non-consuming predators for all six distributions (see Table 21, Appendix D). When this excess was removed, the resultant adjusted distributions had higher means. Comparisons with Poisson estimations based on these higher means revealed yet more excess of non-consuming predators. The excess was once again removed. The process was repeated for each distribution until no more than one additional excess non-consuming individual could be identified. Initially, the average probability of homogeneity of the four isolated empirical distributions to Poisson estimations was

less than 0.5. After adjustment, the average was greater than 0.9 with all four comparisons improving (see Table 23, Appendix D).

It seemed then, that the process which created empirical distributions might very well be complicated by an experimental artifact or natural condition where a certain percentage of predators were not participating. This circumstance might create problems when laboratory derived predation rates are applied to natural ecosystems but that was not the objective of this study. However, before dismissing the refusal to eat circumstance, it should first be determined that this in itself cannot create the curvature observed in regressional analysis of means.

RESULTS 8

Refusal to Eat Regression Analysis

It seemed reasonable that a substantial proportion of predators refused to eat under laboratory conditions (see Refusal to Eat, Results 7, Appendix C). If extant, this proportion was shown to substantially change the maximum digestive pause possible as provided by distributional analysis (see Results 7). The proportion may also have altered the pause estimated by regression.

For the set where all data was pooled, the proportion of predators refusing to eat was incrementally identified for the 23 of 26 distributions within the set where an excess of the zero category was indicated. The process revealed an average of almost 15% of the individuals could be placed in the category of refusing to eat (see Table 24, Appendix D).

The means resulting from the removal category from the empirical distributions were then regressed. The quadratic expression still removed a significant amount of variation (see Table 24). However, the pause estimated through non-linear regression and the pause at the lower 95% confidence interval were both somewhat reduced but only by about a quarter hour (see Table 25, Appendix D). There certainly need be no undue concern that in this case the pause estimated by regression was the result of something so simple as mishandling of organisms or the experimental procedure.

APPENDIX D

TABLES

Table 1. Control runs.

Date	Prey per Replicate	Number of Replicates	Volume in Millimeters
11-7-78	20	4	880
14-7-78	20	4	880
26-6-79	30	51	880
21-3-80	20	9	30[a]
21-3-80	20	11	880
6-4-80	20	71	30[a]
6-4-80	20	55	880
8-4-81	20	33	880[b]
14-4-81	10	10	880
17-4-81	20	28	880
10-8-81	20	41	880
14-7-84	5	40	880
	10	40	880
	15	72	880
	20	39	880

[a]Thirty millimeters is not accurate but represents the volume of water necessary for the initial count which would vary but was never greater than 30 millimeters.

[b]Here chamber contents were poured through the termination screens but the chambers were not rinsed.

Table 2. Control treatment groups.

	No. Expected Prey	Recovered Minus Expected (-2)	(-1)	Even	(+1)	Proportion of Replications Showing Loss[1]	Expected Loss[1]
30 millimeters							
Immediately screened	20	0	3	44	3	0.064	0.003
Held 24 hours	20	0	1	28	1	0.036	0.002
880 millimeters							
Immediately screened	20	1	5	28	1	0.176	0.010
Held 24 hours	20	0	4	28	3	0.125	0.006
Held 6 hours	20	2	10	91	9	0.117	0.007
	5	0	1	38	1	0.026	0.005
	10	0	4	46	0	0.080	0.008
	15	1	6	64	1	0.098	0.007
	30	0	5	43	3	0.104	0.003
Not rinsed	20	2	4	25	2	0.194	0.013
17-4-81	20	1	2	21	4	0.125	0.008
10-8-81	20	0	5	31	5	0.139	0.007
14-7-84	20	1	3	35	0	0.103	0.006

[1]Calculations were made ignoring entirely any groups where an excess of prey was discovered, a procedure continued in the handling of all data.

Table 3. Control data versus 1984 data.

		Number Removed per Replication					G-test Probability
		0	1	2	3	4	
Density 5 880 mls	Control data	38	1				P < 0.005
	1984 data	93	34	11			
Density 10 880 mls	Control data	46	4				P < 0.005
	1984 data	73	34	22	6	1	
Density 15 880 mls	Control data	64	6	1			P < 0.005
	1984 data	73	35	18	8	1	
Density 20 880 mls	Control data	91	10	2			P < 0.005
	1984 data	56	27	18	5	4	

Table 4. Nocturnal period subset comparison.

Time Period	Number Removed per Replication 0	1	2	3	4	Date
10:00PM-1:30AM	13	15	16	3	0	2-8-79
10:30PM-2:00AM	14	15	8	4	4	27-7-79
1:45AM-5:15AM	20	29	21	3	1	11-8-79
3:00AM-6:30AM	17	12	12	5	0	3-8-79
3:15AM-6:45AM	20	14	8	2	1	28-7-79

1.	G-test among all five groups.	G = 20.638	$X^2_{0.5(16)}$ = 20.465
2.	G-test 10:00-1:30 to 10:30-2:00.	G = 8.400	$X^2_{0.1(4)}$ = 7.779
3.	G-test 3:00-6:30 to 3:15-6:45.	G = 1.697	$X^2_{0.7(3)}$ = 1.424
4.	G-test 10:30-2:00 to 3:00-6:30 + 3:15-6:45.	G = 10.092	$X^2_{0.05(4)}$ = 9.488
5.	G-test 10:30-2:00 to 1:45-5:15	G = 6.570	$X^2_{0.2(4)}$ = 5.989

Table 5. P-values from tests of homogeneity between exponentially simulated distributions and Poisson distributions.

Density	Mean Upper 95% C.L	P-values of Homogeneity between Distributions of 1000 Observations	P-values of homogeneity between Distributions of 5000 Observations
3	0.175	0.839	0.924
4	0.233	0.972	0.862
5	0.291	0.708	0.917
6	0.349	0.771	0.764
7	0.407	0.812	0.605
8	0.466	0.806	0.885
9	0.524	0.971	0.950
10	0.582	0.520	0.585
11	0.640	0.996	0.984
12	0.699	0.958	0.728
13	0.757	0.943	0.990
14	0.815	0.998	0.977
15	0.873	0.975	0.994
16	0.931	0.734	0.952
17	0.990	0.970	0.895
18	1.048	0.880	0.969
19	1.106	0.990	0.987
20	1.164	0.967	0.979
21	1.222	0.946	0.986
22	1.281	0.977	0.888
23	1.339	0.834	0.999
24	1.397	0.995	0.991
25	1.455	0.911	0.916
30	1.746	0.990	0.995
35	2.037	0.988	0.970
40	2.328	0.985	0.981
		$\bar{X}$ 0.901	0.911

Table 6. P-values from tests of homogeneity between exponentially simulated distributions incorporating density reduction and Poisson distributions.

Initial Density	Mean Upper 95% C.L.	P-values of Homogeneity between Distributions of 1000 Observations	P-values of homogeneity between Distributions of 5000 Observations
3	0.175	0.770	0.295
4	0.233	0.842	0.706
5	0.291	0.771	0.157
6	0.349	0.809	0.283
7	0.407	0.847	0.290
8	0.466	0.806	0.658
9	0.524	0.845	0.304
10	0.582	0.906	0.608
11	0.604	0.946	0.806
12	0.699	0.779	0.913
13	0.757	0.992	0.769
14	0.815	0.986	0.472
15	0.873	0.989	0.829
16	0.931	0.724	0.460
17	0.990	0.675	0.721
18	1.048	0.959	0.895
19	1.106	0.946	0.286
20	1.164	0.721	0.465
21	1.222	0.865	0.988
22	1.281	0.680	0.843
23	1.339	0.970	0.335
24	1.397	0.980	0.475
25	1.455	0.886	0.599
30	1.746	0.833	0.500
35	2.037	0.986	0.826
40	2.328	0.971	0.510
		$\bar{X}$ 0.866	0.577

Table 7. Analysis of covariance between means from 1000 exponentially simulated observations at each density and means from 1000 exponentially simulated observations incorporating density reduction at each density.

Density	Exponential Mean	Density Reduction Mean
3	0.188	0.166
4	0.229	0.218
5	0.255	0.285
6	0.353	0.366
7	0.444	0.412
8	0.477	0.452
9	0.510	0.487
10	0.620	0.575
11	0.649	0.659
12	0.678	0.658
13	0.799	0.786
14	0.787	0.799
15	0.892	0.873
16	0.874	0.899
17	1.036	0.933
18	1.037	1.027
19	1.108	1.119
20	1.148	1.127
21	1.141	1.222
22	1.351	1.264
23	1.331	1.275
24	1.366	1.415
25	1.493	1.398
30	1.743	1.646
35	2.064	1.974
40	2.319	2.260
Slope	0.058	0.056

Analysis of covariance

Source	Degrees of Freedom	Sum of Squares	Mean Squares	F-value
Total	50	0.129		
Total minus error	2	0.011	0.006	3.0
Error	48	0.118	0.002	

$P_{0.05(2,40)} = 3.23$

Table 8. Analysis of covariance between means from 5000 exponentially simulated observations at each density and means from 5000 exponentially simulated observations incorporating density reduction at each density.

Density	Exponential Mean	Density Reduction Mean
3	0.1818	0.1734
4	0.2224	0.2210
5	0.2848	0.2840
6	0.3398	0.3266
7	0.4254	0.3988
8	0.4670	0.4620
9	0.5256	0.5120
10	0.5978	0.5684
11	0.6368	0.6362
12	0.6910	0.6964
13	0.7652	0.7558
14	0.8124	0.7960
15	0.8648	0.8528
16	0.9408	0.9070
17	0.9788	0.9548
18	1.0264	1.0188
19	1.1056	1.0996
20	1.1662	1.1408
21	1.1926	1.2106
22	1.2986	1.2450
23	1.3380	1.2668
24	1.4184	1.3472
25	1.4662	1.4038
30	1.4662	1.4038
35	2.0556	2.0042
40	2.3246	2.2524
Slope	0.0583	0.0563

Analysis of covariance

Source	Degrees of Freedom	Sum of Squares	Mean Squares	F-value
Total	50	0.0300		
Total minus error	2	0.0127	0.0064	16
Error	48	0.0174	0.0004	

$P_{0.001(2,40)} = 8.25$

Table 9. Seasonal covariance 1983.

Initial Density		Predation Rates 5/1-6/7	Predation Rates 7/2-7/19
3		0.127	
4		0.194	0.374
5		0.280	0.351
6			
7		0.348	0.495
8			
9		0.390	0.970
10			0.847
11		0.505	
12		0.533	0.822
13		0.511	0.769
14		0.711	
15			0.685
16		0.452	0.766
17			1.176
18		0.993	0.684
19		0.711	
20			1.117
21		0.722	1.261
22			
23		0.722	1.126
	Slope	0.033	0.038

Analysis of covariance

Source	Degrees of Freedom	Sum of Squares	Mean Squares	F-value
ST	26	1.121		
ST-SE	2	0.530	0.265	10.765
SE	24	0.591	0.025	

$P_{0.001(2,24)} = 9.34$

Table 10. Seasonal covariance 1984, 5/13-5/31 X 6/11-7/14.

Initial Density	Predation Rates 5/13-5/31	Predation Rates 6/11-7/14
3	0.016	
4	0.091	0.228
5	0.138	0.406
6	0.129	0.573
7	0.248	0.500
8	0.221	0.615
9	0.275	0.765
10	0.324	0.735
11	0.373	0.705
12	0.340	0.644
13	0.323	0.530
14	0.464	0.775
15	0.376	0.733
16	0.406	0.625
17	0.541	0.986
18	0.478	0.800
19	0.520	0.911
20	0.469	0.940
21	0.636	1.175
22	0.615	1.098
23	0.567	1.037
Slope	0.027	0.038

Analysis of covariance

Source	Degrees of Freedom	Sum of Squares	Mean Squares	F-value
ST	40	1.652		
ST-SE	2	1.329	0.665	73.889
SE	38	0.323	0.009	

$P_{0.001(2,40)} = 8.25$

Table 11. Seasonal covariance 1984, 5/13-5/31 X 6/1-6/10.

Initial Density	Predation Rates 5/13-5/31	Predation Rates 6/1-6/10
3	0.016	0.114
4	0.091	0.206
5	0.138	0.294
6	0.129	0.299
7	0.248	
8	0.221	0.514
9	0.275	0.588
10	0.324	0.514
11	0.373	0.453
12	0.340	0.394
13	0.323	0.657
14	0.464	0.582
15	0.376	
16	0.406	0.829
17	0.541	0.486
18	0.478	0.438
19	0.520	0.471
20	0.469	1.057
21	0.636	0.765
22	0.615	0.545
23	0.567	0.638
Slope	0.027	0.024

Analysis of covariance

Source	Degrees of Freedom	Sum of Squares	Mean Squares	F-value
ST	38	0.746		
ST-SE	2	0.232	0.116	8.125
SE	36	0.514	0.014	

$P_{0.001(2,30)} = 8.77$

$P_{0.005(2,30)} = 6.35$

Table 12. Seasonal covariance 1984, 6/1-6/10 X 6/11-7/14.

Initial Density		Predation Rates 6/1-6/10	Predation Rates 6/11-7/14
3		0.114	0.184
4		0.206	0.228
5		0.294	0.406
6		0.299	0.573
7			
8		0.514	0.615
9		0.588	0.765
10		0.514	0.735
11		0.453	0.705
12		0.394	0.644
13		0.657	0.530
14		0.582	0.775
15			
16		0.829	0.625
17		0.486	0.986
18		0.438	0.800
19		0.471	0.911
20		1.057	0.940
21		0.765	1.175
22		0.545	1.098
23		0.638	1.037
	Slope	0.024	0.038

Analysis of covariance

Source	Degrees of Freedom	Sum of Squares	Mean Squares	F-value
ST	36	1.193		
ST-SE	2	0.464	0.232	11.048
SE	34	0.729	0.021	

$P_{0.001(2,30)} = 8.77$

Table 13. Yearly distribution data.

Date	No. of Observations	Mean Removed	Number Removed 0	1	2	3	4	5	6	7
1979										
Initial density 15										
8/15	96	0.706	51	28	11	6				
Initial density 20										
5/20	23	1.913	4	4	8	4	3			
6/7	21	1.095	10	7	0	2	0	2		
6/14	98	1.296	28	36	16	14	3	1		
6/21	82	1.683	23	21	11	15	10	2		
7/24	98	1.755	15	32	28	13	6	3	1	
7/30	90	1.511	19	33	20	11	6	0	1	
	P-value from test of homogeneity = 0.742									
Initial density 30										
7/8	93	1.441	22	36	15	13	6	1		
1980										
Initial density 10										
7/21	42	0.405	28	11	3					
8/15	45	0.533	29	10	4	2				
	P-value from test of homogeneity = 0.697									
Initial density 15										
4/25	46	0.674	25	12	8	1				
8/9	40	0.525	25	11	2	2				
8/15	43	0.791	16	21	5	1				
8/28	41	1.220	13	13	8	7				
	P-value from test of homogeneity = 0.088									
Initial density 20										
4/25	43	1.140	13	16	9	5				
5/11	47	0.936	16	20	9	2				
7/19	47	1.426	11	16	12	5	3			
9/4	40	1.100	13	7	6	2	1	1		
	P-value from test of homogeneity = 0.909									
Initial density 25										
8/9	40	1.125	14	17	3	2	4			
8/28	40	0.950	15	15	8	1	1			
9/4	31	0.935	15	6	8	1	1			
	P-value from test of homogeneity = 0.420									

Table 13 (continued).

Date	No. of Observations	Mean Removed	Number Removed 0	1	2	3	4	5	6	7
Initial density 30	45	1.578	13	10	9	9	4			
Initial density 35										
8/1	53	1.321	18	15	9	8	2	1		
Initial density 40										
7/21	40	1.150	9	17	13	1				
7/30	38	1.211	12	10	13	2	1			
	P-value from test of homogeneity = 0.371									
1981										
Initial density 5										
8/5	44	0.545	28	9	6	1				
8/22	17	0.176	14	3						
8/17	48	0.458	29	16	3					
	P-value from test of homogeneity = 0.397									
Initial density 10										
4/22	89	0.730	41	34	11	3				
5/9	92	0.630	50	27	14	1				
5/25	58	0.638	31	19	6	2				
	P-value from test of homogeneity = 0.698									
Initial density 15										
4/21	89	1.045	29	36	17	6	0	1		
5/3	89	0.933	36	32	13	7	1			
5/20	86	0.814	41	25	15	5				
	P-value from test of homogeneity = 0.847									
Initial density 20										
4/28	93	1.140	34	27	24	5	1	1	0	1
5/12	93	1.097	31	33	19	9	1			
5/16	90	1.289	26	30	24	4	5	0	1	
8/10	39	1.359	9	15	9	5	0	1		
8/28	17	1.000	6	7	3	0	1			
	P-value from test of homogeneity = 0.653									
Initial density 25										
7/26	44	1.591	9	11	15	7	2			
8/1	36	1.972	4	9	12	9	0	1	1	
	P-value from test of homogeneity = 0.912									

Table 13 (continued).

Date	No. of Observations	Mean Removed	Number Removed 0	1	2	3	4	5	6	7
1982										
Initial density 3										
7/16	95	0.137	83	11	1					
Initial density 4										
7/1	96	0.219	76	19	1					
Initial density 5										
7/6	89	0.213	70	19						
Initial density 6										
7/25	98	0.255	78	16	3	1				
Initial density 9										
7/7	95	0.526	60	25	6	3	1			
Initial density 10										
7/2	38	1.026	14	4	5	5				
Initial density 13										
7/20	73	0.507	47	18	5	3				
Initial density 16										
7/21	58	0.431	37	17	4					
7/29	95	0.632	57	24	9	2	3			
8/4	62	0.525	36	23	1	1	1			
	P-value from test of homogeneity = 0.680									
Initial density 20										
7/3	92	1.293	36	20	18	12	4	1	1	
Initial density 24										
7/8	95	1.463	32	26	15	11	7	3	0	1
1983										
Initial density 4										
7/8	91	0.374	64	20	7					
Initial density 5										
7/16	94	0.351	68	20	5	1				

Table 13 (continued).

Date	No. of Observations	Mean Removed	Number Removed 0	1	2	3	4	5	6	7
Initial density 7										
7/11	95	0.495	62	22	8	3				
Initial density 9	97	0.969	43	25	20	7	2			
Initial density 10										
7/11	85	0.848	38	29	11	7				
Initial density 12										
7/19	45	0.822	19	16	9	1				
Initial density 13										
7/10	52	0.769	21	24	5	2				
Initial density 15										
7/4	92	0.685	47	29	14	2				
Initial density 16										
7/7	94	0.766	48	26	14	6				
Initial density 17										
7/18	51	1.176	19	14	10	6	2			
Initial density 18										
7/12	95	0.684	54	25	12	0	4			
Initial density 20										
7/3	94	1.117	35	33	11	11	3	1		
Initial density 21										
7/15	92	1.261	30	27	21	10	3	1		
Initial density 23										
7/6	95	1.126	36	25	23	8	3			
1984										
Initial density 3										
6/11	33	0.182	27	6						
6/15	35	0.200	28	7						
6/26	35	0.171	30	4	1					
	P-value from test of homogeneity = 0.900									

Table 13 (continued).

Date	No. of Observations	Mean Removed	Number Removed 0	1	2	3	4	5	6	7
Initial density 4										
6/16	35	0.143	30	5						
6/25	35	0.114	31	4						
6/30	35	0.171	30	4	1					
7/5	35	0.486	23	8	3	1				
	P-value from test of homogeneity = 0.315									
Initial density 5										
6/12	34	0.471	21	10	3					
6/21	35	0.400	24	8	3					
7/1	35	0.429	24	7	4					
7/9	34	0.324	24	9	1					
	P-value from test of homogeneity = 0.963									
Initial density 6										
6/20	33	0.515	21	8	3	1				
6/24	34	0.529	21	9	3	1				
6/29	35	0.571	23	7	2	3				
7/14	34	0.676	16	14	3	1				
	P-value from test of homogeneity = 0.960									
Initial density 7										
6/13	35	0.429	23	9	3					
6/22	34	0.412	21	12	1					
7/2	34	0.676	18	11	3	2				
7/9	35	0.486	21	11	3					
	P-value from test of homogeneity = 0.910									
Initial density 8										
6/14	35	0.600	19	11	5					
6/23	34	0.706	17	12	3	2				
6/29	32	0.531	22	5	3	2				
7/4	34	0.618	18	11	5					
	P-value from test of homogeneity = 0.801									
Initial density 9										
6/18	34	0.794	18	8	5	3				
6/27	35	0.829	18	8	7	1	1			
7/3	35	0.800	16	10	9					
7/14	32	0.625	16	13	2	1				
	P-value from test of homogeneity = 0.769									
Initial density 10										
6/20	33	0.424	24	6	1	2				
6/24	35	0.743	20	7	6	1	1			
6/28	34	1.029	12	11	9	2				
7/5	34	0.736	17	10	6	1				
	P-value from test of homogeneity = 0.620									

Table 13 (continued).

Date	No. of Observations	Mean Removed	Number Removed 0	1	2	3	4	5	6	7
Initial density 11										
6/13	35	0.829	19	7	5	4				
6/27	35	0.457	24	7	3	1				
7/4	35	0.943	16	10	5	3	1			
7/10	34	0.588	21	7	5	1				
	P-value from test of homogeneity = 0.939									
Initial density 12										
6/14	34	0.529	19	12	3					
6/26	33	0.697	16	11	6					
6/30	35	0.800	20	6	5	4				
7/11	33	0.545	17	14	2					
	P-value from test of homogeneity = 0.451									
Initial density 13										
6/18	33	0.576	19	10	3	1				
6/21	33	0.576	19	9	5					
6/28	35	0.571	21	9	4	1				
7/7	33	0.394	23	8	1	1				
	P-value from test of homogeneity = 0.978									
Initial density 14										
6/12	34	0.647	20	7	6	1				
6/23	35	0.657	19	11	3	2				
7/3	34	1.118	15	7	8	2	1	1		
7/10	34	0.618	20	7	7	1				
	P-value from test of homogeneity = 0.936									
Initial density 15										
6/11	32	0.531	20	8	3	1				
6/16	34	0.412	23	8	3					
6/25	34	1.029	16	8	4	5	1			
7/5	35	0.943	14	11	8	2				
	P-value from test of homogeneity = 0.517									
Initial density 16										
6/18	34	0.735	18	11	2	2	1			
6/22	35	0.657	19	10	5	1				
7/1	35	0.714	18	10	6	1				
7/11	32	0.375	20	12						
	P-value from test of homogeneity = 0.621									
Initial density 17										
6/15	34	0.911	16	10	3	5				
6/25	35	0.857	16	12	4	2				
7/3	34	1.382	9	11	8	4	2			
7/10	35	0.800	16	13	3	3				
	P-value from test of homogeneity = 0.998									

Table 13 (continued).

Date	No. of Observations	Mean Removed	Number Removed 0	1	2	3	4	5	6	7
Initial density 18										
6/11	32	0.781	18	7	3	4				
6/16	35	0.714	19	11	2	2	1			
6/28	33	0.909	17	6	7	2	1			
	P-value from test of homogeneity = 0.858									
Initial density 19										
6/15	32	0.719	18	8	4	1	1			
6/22	34	1.000	15	9	6	3	1			
7/1	35	1.000	13	14	3	5				
	P-value from test of homogeneity = 0.867									
Initial density 20										
6/20	32	0.781	15	11	5	0	1			
6/24	34	0.971	14	9	9	2				
6/30	34	1.059	17	7	4	3	3			
	P-value from test of homogeneity = 0.653									
Initial density 21										
6/12	35	0.743	19	8	6	2				
6/23	34	1.118	12	13	4	3	2			
6/29	33	1.545	10	9	5	5	3	1		
7/4	35	1.086	15	9	4	7				
	P-value from test of homogeneity = 0.717									
Initial density 22										
6/14	34	1.000	13	10	9	2				
6/26	33	1.061	13	10	6	3	1			
7/2	34	1.118	15	9	5	1	4			
	P-value from test of homogeneity = 0.955									
Initial density 23										
6/13	33	0.939	16	7	7	2	1			
6/21	35	0.943	17	8	5	5				
6/27	33	1.333	13	8	5	3	3	1		
7/9	33	0.939	14	10	7	1	1			
	P-value from test of homogeneity = 0.934									

Table 14. Analysis of covariance between 1983 and 1984 data.

Density	1983 Data Mean	1984 Data Mean
3		0.184
4	0.374	0.228
5	0.351	0.406
6		0.573
7	0.495	0.500
8		0.615
9	0.970	0.765
10	0.847	0.735
11		0.705
12	0.822	0.644
13	0.769	0.530
14		0.755
15	0.685	0.733
16	0.766	0.625
17	1.176	0.986
18	0.684	0.800
19		0.911
20	1.117	0.940
21	1.261	1.175
22		1.098
23	1.126	1.037
Slope	0.038	0.038

Analysis of covariance

Source	Degrees of Freedom	Sum of Squares	Mean Squares	F-value
ST	33	0.714		
ST-SE	2	0.052	0.026	1.211
SE	31	0.662	0.021	

$P_{0.25(2,30)} = 1.38$

Table 15. Pooled distributional data.

Initial Density	Total Observations	Mean Removed	Number Removed 0	1	2	3	4	5	6	7
1983 plus 1984										
3	103	0.184	85	17	1					
4	231	0.286	178	41	11	1				
5	232	0.384	161	54	16	1				
6	136	0.573	81	38	11	6				
7	233	0.498	145	65	18	5				
8	135	0.615	76	39	16	4				
9	233	0.850	111	64	43	12	3			
10	221	0.778	111	63	33	13	1			
11	139	0.705	80	31	18	9	1			
12	180	0.689	91	59	25	5				
13	186	0.597	103	60	18	5				
14	138	0.775	74	32	24	6	1	1		
15	227	0.714	120	64	32	10	1			
16	230	0.683	123	69	27	10	1			
17	189	1.037	76	60	28	20	5			
18	195	0.744	108	49	24	8	6			
19	101	0.871	46	31	13	9	2			
20	194	1.026	81	60	29	16	7	1		
21	229	1.175	86	66	40	27	8	2		
22	102	1.098	41	29	20	5	1			
23	229	1.074	96	58	47	19	8	1		
1980 plus 1981 plus 1983 plus 1984										
5	341	0.405	232	82	25	2				
10	547	0.682	290	164	71	21	1			
15	661	0.823	305	214	100	39	2	1		
20	703	1.129	241	241	144	52	19	4	1	1
25	191	1.325	57	58	46	20	8	1	1	
30	45	1.578	13	10	9	9	4			
35	53	1.321	18	15	9	8	2	1		
40	78	1.179	21	27	26	3	1			
1979 plus 1980 plus 1981 plus 1982 plus 1983 plus 1984										
3	198	0.162	168	28	2					
4	327	0.266	254	60	12	1				
5	430	0.365	302	101	25	2				
6	234	0.440	159	54	14	7				
9	328	0.756	171	89	49	15	4			
10	585	0.704	304	178	76	26	1			
13	259	0.571	150	78	23	8				
15	757	0.808	356	242	111	45	2	1		
16	445	0.616	253	133	41	13	5			
20	1208	1.289	376	394	245	123	52	13	4	1
24	95	1.463	32	26	15	11	7	3	0	1
30	138	1.486	35	46	24	22	10	1		

Table 16. Homogeneity of empirical distributions between years.

Year	Number of Observations	Mean Removed	Number Removed 0	1	2	3	4	5	6	7
1979 : 1980										
Initial density 15										
1979	96	0.706	51	28	11	6				
1980	170	0.800	79	57	23	11				
		P-value from test of homogeneity = 0.860								
Initial density 20										
1979	413	1.470	99	133	83	59	29	8	2	
1980	177	1.152	53	69	36	14	4	1		
		P-value from test of homogeneity = 0.073								
Initial density 30										
1979	93	1.441	22	36	15	13	6	1		
1980	45	1.578	13	10	9	9	4			
		P-value from test of homogeneity = 0.782								
1979 : 1981										
Initial density 15										
1979	96	0.706	51	28	11	6				
1981	264	0.932	106	93	45	18	1	1		
		P-value from test of homogeneity = 0.473								
Initial density 20										
1979	413	1.470	99	133	83	59	29	8	2	
1981	332	1.187	106	112	79	23	8	2	1	1
		P-value from test of homogeneity = 0.042								
1979 : 1982										
Initial density 20										
1979	413	1.470	99	133	83	59	29	8	2	
1982	92	1.293	36	20	18	12	4	1	1	
		P-value from test of homogeneity = 0.256								

Table 16 (continued).

Year	Number of Observations	Mean Removed	Number Removed 0	1	2	3	4	5	6	7
1979 : 1983										
Initial density 15										
1979	96	0.706	51	28	11	6				
1983	92	0.685	47	29	14	2				
		P-value from test of homogeneity = 0.736								
Initial density 20										
1979	413	1.470	99	133	83	59	29	8	2	
1983	94	1.117	35	11	11	3	1			
		P-value from test of homogeneity = 0.240								
1979 : 1984										
Initial density 15										
1979	96	0.706	51	28	11	6				
1984	135	0.733	73	35	18	8	1			
		P-value from test of homogeneity = 0.978								
Initial density 20										
1979	413	1.470	99	133	83	59	29	8	2	
1984	100	0.940	46	27	18	5	4			
		P-value from test of homogeneity = 0.047								
1980 : 1981										
Initial density 10										
1980	87	0.471	57	21	7	2				
1981	239	0.669	122	80	31	6				
		P-value from test of homogeneity = 0.427								
Initial density 15										
1980	170	0.800	79	57	23	11				
1981	264	0.932	106	93	45	18	1	1		
		P-value from test of homogeneity = 0.857								

Table 16 (continued).

Year	Number of Observations	Mean Removed	Number Removed 0	1	2	3	4	5	6	7
1980 : 1981 (continued)										
Initial density 20										
1980	177	1.152	53	69	36	14	4	1		
1981	332	1.187	106	112	79	23	8	2	1	1
		P-value from test of homogeneity = 0.931								
Initial density 25										
1980	111	0.919	44	38	19	4	6			
1981	80	1.763	13	20	27	16	2	1	1	
		P-value from test of homogeneity = 0.789								
1980 : 1982										
Initial density 10										
1980	87	0.471	57	21	7	2				
1982	38	1.026	14	14	5	5				
		P-value from test of homogeneity = 0.138								
Initial density 20										
1980	177	1.152	53	69	36	14	4	1		
1982	92	1.293	36	20	18	12	4	1	1	
		P-value from test of homogeneity = 0.240								
1980 : 1983										
Initial density 10										
1980	87	0.471	57	21	7	2				
1983	85	0.848	38	29	11	7				
		P-value from test of homogeneity = 0.218								
Initial density 15										
1980	170	0.800	79	57	23	11				
1983	92	0.685	47	29	14	2				
		P-value from test of homogeneity = 0.815								
Initial density 20										
1980	177	1.152	53	69	36	14	4	1		
1983	94	1.117	35	33	11	11	3	1		
		P-value from test of homogeneity = 0.602								

Table 16 (continued).

Year	Number of Observations	Mean Removed	Number Removed 0	1	2	3	4	5	6	7
1980 : 1984										
Initial density 10										
1980	87	0.471	57	21	7	2				
1984	136	0.735	73	34	22	6	1			
		P-value from test of homogeneity = 0.455								
Initial density 15										
1980	170	0.800	79	57	23	11				
1984	135	0.733	73	35	18	8	1			
		P-value from test of homogeneity = 0.721								
Initial density 20										
1980	177	1.152	53	69	36	14	4	1		
1984	100	0.940	46	27	18	5	4			
		P-value from test of homogeneity = 0.424								
1981 : 1982										
Initial density 5										
1981	109	0.450	71	28	9	1				
1982	89	0.213	70	19						
		P-value from test of homogeneity = 0.037								
Initial density 10										
1981	239	0.669	122	80	31	6				
1982	38	1.026	14	14	5	5				
		P-value from test of homogeneity = 0.264								
Initial density 20										
1981	332	1.187	106	112	79	23	8	2	1	1
1982	92	1.293	36	20	18	12	4	1	1	
		P-value from test of homogeneity = 0.281								
1981 : 1983										
Initial density 5										
1981	109	0.450	71	28	9	1				
1983	94	0.351	68	20	5	1				
		P-value from test of homogeneity = 0.723								

Table 16 (continued).

Year	Number of Observations	Mean Removed	Number Removed 0	1	2	3	4	5	6	7
1981 : 1983 (continued)										
Initial density 10										
1981	239	0.669	122	80	31	6				
1983	85	0.848	38	29	11	7				
		P-value from test of homogeneity = 0.482								
Initial density 15										
1981	264	0.932	106	93	45	18	1	1		
1983	92	0.685	47	29	14	2				
		P-value from test of homogeneity = 0.386								
Initial density 20										
1981	332	1.187	106	112	79	23	8	2	1	1
1983	94	1.117	35	33	11	11	3	1		
		P-value from test of homogeneity = 0.375								
1981 : 1984										
Initial density 5										
1981	109	0.450	71	28	9	1				
1984	138	0.406	93	34	11					
		P-value from test of homogeneity = 0.957								
Initial density 10										
1981	239	0.669	122	80	31	6				
1984	136	0.735	73	34	22	6	1			
		P-value from test of homogeneity = 0.524								
Initial density 15										
1981	264	0.932	106	93	45	18	1	1		
1984	135	0.733	73	35	18	8	1			
		P-value from test of homogeneity = 0.314								
Initial density 20										
1981	332	1.187	106	112	79	23	8	2	1	1
1984	100	0.940	46	27	18	5	4			
		P-value from test of homogeneity = 0.437								

Table 16 (continued).

Year	Number of Observations	Mean Removed	Number Removed 0	1	2	3	4	5	6	7
1982 : 1983										
Initial density 4										
1982	96	0.219	76	19	1					
1983	91	0.374	64	20	7					
		P-value from test of homogeneity = 0.075								
Initial density 5										
1982	89	0.213	70	19						
1983	94	0.351	68	20	7					
		P-value from test of homogeneity = 0.135								
Initial density 9										
1982	95	0.526	60	25	6	3	1			
1983	97	0.969	43	25	20	7	2			
		P-value from test of homogeneity = 0.134								
Initial density 10										
1982	38	1.026	14	14	5	5				
1983	85	0.848	38	29	11	7				
		P-value from test of homogeneity = 0.911								
Initial density 13										
1982	73	0.507	47	18	5	3				
1983	52	0.769	21	24	5	2				
		P-value from test of homogeneity = 0.280								
Initial density 16										
1982	215	0.544	130	64	14	3	4			
1983	94	0.766	48	26	14	6				
		P-value from test of homogeneity = 0.860								
Initial density 20										
1982	92	1.293	36	20	18	12	4	1	1	
1983	94	1.117	35	33	11	11	3	1		
		P-value from test of homogeneity = 0.658								

Table 16 (continued).

Year	Number of Observations	Mean Removed	Number Removed 0	1	2	3	4	5	6	7
1982 : 1984										
Initial density 3										
1982	95	0.137	83	11	1					
1984	103	0.184	85	17	1					
		P-value from test of homogeneity = 0.500								
Initial density 4										
1982	96	0.219	76	19	1					
1984	140	0.229	114	21	4	1				
		P-value from test of homogeneity = 0.205								
Initial density 5										
1982	89	0.213	70	19						
1984	138	0.406	93	34	11					
		P-value from test of homogeneity = 0.049								
Initial density 6										
1982	98	0.255	78	16	3	1				
1984	136	0.574	81	38	11	6				
		P-value from test of homogeneity = 0.062								
Initial density 9										
1982	95	0.526	60	25	6	3	1			
1984	136	0.765	68	39	23	5	1			
		P-value from test of homogeneity = 0.302								
Initial density 10										
1982	38	1.026	14	14	5	5				
1984	136	0.735	73	34	22	6	1			
		P-value from test of homogeneity = 0.421								
Initial density 13										
1982	73	0.507	47	18	5	3				
1984	134	0.530	82	36	13	3				
		P-value from test of homogeneity = 0.913								

Table 16 (continued).

Year	Number of Observations	Mean Removed	Number Removed 0	1	2	3	4	5	6	7
1982 : 1984 (continued)										
Initial density 16										
1982	215	0.544	130	64	14	3	4			
1984	136	0.625	75	43	13	4	1			
		P-value from test of homogeneity = 0.465								
Initial density 20										
1982	92	1.293	36	20	18	12	4	1	1	
1984	100	0.940	46	27	18	5	4			
		P-value from test of homogeneity = 0.623								
1983 : 1984										
Initial density 4										
1983	91	0.374	64	20	7					
1984	140	0.228	114	21	4	1				
		P-value from test of homogeneity = 0.368								
Initial density 5										
1983	94	0.351	68	20	7					
1984	138	0.406	93	34	11					
		P-value from test of homogeneity = 0.848								
Initial density 7										
1983	95	0.495	62	22	8	3				
1984	138	0.500	83	43	10	2				
		P-value from test of homogeneity = 0.753								
Initial density 9										
1983	97	0.969	43	25	20	7	2			
1984	136	0.765	68	39	23	5	1			
		P-value from test of homogeneity = 0.625								
Initial density 10										
1983	85	0.848	38	29	11	7				
1984	136	0.735	73	34	22	6	1			
		P-value from test of homogeneity = 0.625								

Table 16 (continued).

Year	Number of Observations	Mean Removed	Number Removed 0	1	2	3	4	5	6	7
1983 : 1984 (continued)										
Initial density 12										
1983	45	0.822	19	16	9	1				
1984	135	0.644	72	43	16	4				
		P-value from test of homogeneity = 0.435								
Initial density 13										
1983	52	0.769	21	24	5	2				
1984	134	0.530	82	36	13	3				
		P-value from test of homogeneity = 0.284								
Initial density 15										
1983	92	0.685	47	29	14	2				
1984	135	0.733	73	35	18	8	1			
		P-value from test of homogeneity = 0.645								
Initial density 16										
1983	94	0.766	48	26	14	6				
1984	136	0.625	75	43	13	4	1			
		P-value from test of homogeneity = 0.727								
Initial density 17										
1983	51	1.176	19	14	10	6	2			
1984	138	0.986	57	46	18	14	3			
		P-value from test of homogeneity = 0.903								
Initial density 18										
1983	95	0.684	54	25	0.	4				
1984	100	0.800	54	24	12	8	2			
		P-value from test of homogeneity = 0.214								
Initial density 20										
1983	94	1.117	35	33	11	11	3	1		
1984	100	0.940	46	27	18	5	4			
		P-value from test of homogeneity = 0.568								

Table 16 (continued).

Year	Number of Observations	Mean Removed	Number Removed 0	1	2	3	4	5	6	7
1983 : 1984 (continued)										
Initial density 21										
1983	92	1.261	30	27	21	10	3	1		
1984	137	1.125	56	39	19	17	5	1		
		P-value from test of homogeneity = 0.771								
Initial density 23										
1983	95	1.126	36	25	23	8	3			
1984	134	1.037	60	33	24	11	5	1		
		P-value from test of homogeneity = 0.908								
1981 : 1983 : 1984										
Initial density 5										
1981	109	0.450	71	28	9	1				
1983	94	0.351	68	20	5	1				
1984	138	0.406	93	34	11					
		P-value from test of homogeneity = 0.954								
Initial density 10										
1981	239	0.669	122	80	31	6				
1983	85	0.848	38	29	11	7				
1984	136	0.735	73	34	22	6	1			
		P-value from test of homogeneity = 0.633								
Initial density 15										
1981	264	0.932	106	93	45	18	1	1		
1983	92	0.685	47	29	14	2				
1984	135	0.733	73	35	18	8	1			
		P-value from test of homogeneity = 0.447								
Initial density 20										
1981	332	1.187	106	112	79	23	8	2	1	1
1983	94	1.117	35	33	11	11	3	1		
1984	100	0.940	46	27	18	5	4			
		P-value from test of homogeneity = 0.530								

Table 16 (continued).

Year	Number of Observations	Mean Removed	Number Removed 0	1	2	3	4	5	6	7
1980 : 1983 : 1984										
Initial density 10										
1980	87	0.471	57	21	7	2				
1983	85	0.848	38	29	11	7				
1984	136	0.735	73	34	22	6	1			
		P-value from test of homogeneity = 0.467								
Initial density 15										
1980	170	0.800	79	57	23	11				
1983	92	0.685	47	29	14	2				
1984	135	0.733	73	35	18	8	1			
		P-value from test of homogeneity = 0.858								
Initial density 20										
1980	177	1.152	53	69	36	14	4	1		
1983	94	1.117	35	33	11	11	3	1		
1984	100	0.940	46	27	18	5	4			
		P-value from test of homogeneity = 0.707								
1980 : 1981 : 1983 : 1984										
Initial density 10										
1980	87	0.471	57	21	7	2				
1981	239	0.669	122	80	31	6				
1983	85	0.848	38	29	11	7				
1984	136	0.735	73	34	22	6	1			
		P-value from test of homogeneity = 0.542								
Initial density 15										
1980	170	0.800	79	57	23	11				
1981	264	0.932	106	93	45	18	1	1		
1982	92	0.685	47	29	14	2				
1984	135	0.733	73	35	18	8	1			
		P-value from test of homogeneity = 0.734								

Table 16 (continued).

Year	Number of Observations	Mean Removed	Number Removed 0	1	2	3	4	5	6	7
1980 : 1981 : 1983 : 1984 (continued)										
Initial density 20										
1980	177	1.152	53	69	36	14	4	1		
1981	332	1.187	106	112	79	23	8	2	1	1
1983	94	1.117	35	33	11	11	3	1		
1984	100	0.940	46	27	18	5	4			
		P-value from test of homogeneity = 0.887								
1980 : 1981 : 1982 : 1983 : 1984										
Initial density 20										
1980	177	1.152	53	69	36	14	4	1		
1981	332	1.187	106	112	79	23	8	2	1	1
1982	92	1.293	36	20	18	12	4	1	1	
1983	94	1.117	35	33	11	11	3	1		
1984	100	0.940	46	27	18	5	4			
		P-value from test of homogeneity = 0.790								
1979 : 1980 : 1981 : 1982 : 1983 : 1984										
Initial density 20										
1979	413	1.470	99	133	83	59	29	8	2	
1980	177	1.152	53	69	36	14	4	1		
1981	332	1.187	106	112	79	23	8	2	1	1
1982	92	1.293	36	20	18	12	4	1	1	
1983	94	1.117	35	33	11	11	3	1		
1984	100	0.940	46	27	18	5	4			
		P-value from test of homogeneity = 0.089								
1979 : Pooled data (1980 + 1981 + 1982 + 1983 + 1984)										
Initial density 20										
1979	413	1.470	99	133	83	59	29	8	2	
Pooled	795	1.152	276	261	162	65	23	5	2	1
		P-value from test of homogeneity = 0.009								

Table 17. Distributional summation.

Distributions Used for Summation

Number of Observations	Digestive Pause Interval in Hours	Mean Removed
600	3.00	1.00
600	3.00	1.50

Distributions for Comparisons to Summed Distribution

Number of Observations	Digestive Pause Interval in Hours	Mean Removed	Mean P-values from Three Tests of Homogeneity/Group		
			Group A	Group B	Group C
1200	3.00	1.25	0.244	0.163	0.038
1200	2.75	1.25	0.409	0.314	0.053
1200	2.65	1.25	0.467	0.386	0.090
1200	2.50	1.25	0.106	0.102	0.060

Distributions Used for Summation

Number of Observations	Digestive Pause Interval in Hours	Mean Removed
100	3.00	1.00
100	3.00	1.50

Distributions for Comparisons to Summed Distribution

Number of Observations	Digestive Pause Interval in Hours	Mean Removed	Mean P-values from Three Tests of Homogeneity/Group		
			Group A	Group B	Group C
200	3.00	1.25	0.788	0.882	0.460
200	2.75	1.25	0.796	0.847	0.551
200	2.50	1.25	0.835	0.753	0.851
200	2.25	1.25	0.394	0.304	0.533
200	2.00	1.25	0.190	0.139	0.165

Table 17 (continued).

Distributions Used for Summation

Number of Observations	Digestive Pause Interval in Hours	Mean Removed
600	1.50	1.00
600	1.50	1.50

Distributions for Comparisons to Summed Distribution

Number of Observations	Digestive Pause Interval in Hours	Mean Removed	Mean P-values from Three Tests of Homogeneity/Group		
			Group A	Group B	Group C
1200	1.50	1.25	0.696	0.513	0.478
1200	1.30	1.25	0.660	0.913	0.890
1200	1.10	1.25	0.143	0.491	0.509
1200	0.90	1.25	0.033	0.185	0.179

Table 18. Quadratic regressions.

Initial Density	Mean Removed
Pooling Group 1983 + 1984	
3	0.184
4	0.286
5	0.384
6	0.573
7	0.498
8	0.615
9	0.850
10	0.778
11	0.705
12	0.689
13	0.597
14	0.775
15	0.714
16	0.683
17	1.037
18	0.744
19	0.871
20	1.026
21	1.175
22	1.098
23	1.074

Slope A = 0.0797
(Slope B) = 0.0015
squared density

Quadratic Regressional Analysis

Source	df	SS	MS	F-value	P-value
Total	21	227.310			
Model	2	220.964	110.482	330.77	0.0001
Error	19	6.346	0.334		

R-square = 0.972

Type III Sum of Squares

Source	df	SS	F-value	P-value
Slope A	1	30.947	92.65	0.0001
(Slope B) squared density	1	3.668	10.98	0.0037

Table 18 (continued).

Initial Density	Mean Removed
Pooling Group 1980 + 1981 + 1983 + 1984	
3	0.184
4	0.286
5	0.405
6	0.573
7	0.498
8	0.615
9	0.850
10	0.682
11	0.705
12	0.689
13	0.597
14	0.775
15	0.823
16	0.683
17	1.037
18	0.744
19	0.911
20	1.129
21	1.755
22	1.100
23	1.074
25	1.325
30	1.578
35	1.321
40	1.179

Slope A = 0.075
(Slope B) = 0.0012
squared density

Quadratic Regressional Analysis

Source	df	SS	MS	F-value	P-value
Total	25	406.104			
Model	2	398.769	199.384	625.21	0.001
Error	23	7.335	0.319		

R-square = 0.982

Type III Sum of Squares

Source	df	SS	F-value	P-value
Slope A	1	99.967	313.47	0.0001
(Slope B) squared density	1	10.369	32.51	0.0001

Table 18 (continued).

Initial Density	Mean Removed
Pooling Group 1979 + 1980 + 1981 + 1982+ 1983 + 1984	
3	0.162
4	0.266
5	0.365
6	0.440
7	0.498
8	0.615
9	0.756
10	0.704
11	0.705
12	0.689
13	0.571
14	0.775
15	0.808
16	0.616
17	1.037
18	0.744
19	0.911
20	1.289
21	1.175
22	1.100
23	1.074
24	1.463
25	1.325
30	1.486
35	1.321
40	1.179

Slope A = 0.0731
(Slope B) = 0.0001
squared density

Quadratic Regressional Analysis

Source	df	SS	MS	F-value	P-value
Total	26	537.523			
Model	2	522.531	261.266	418.27	0.0001
Error	24	14.911	0.625		

R-square = 0.972

Table 18 (continued).

Initial Density Mean Removed

Type III Sum of Squares

Source	df	SS	F-value	P-value
Slope A	1	111.746	178.90	0.0001
(Slope B) squared density	1	9.032	14.46	0.0009

Table 19. Non-linear regressions.

Initial Density Pooling Group 1983 + 1984	Mean Removed
3	0.184
4	0.286
5	0.384
6	0.573
7	0.498
8	0.615
9	0.850
10	0.778
11	0.705
12	0.689
13	0.597
14	0.775
15	0.714
16	0.683
17	1.037
18	0.744
19	0.871
20	1.026
21	1.175
22	1.098
23	1.074

Non-Linear Regressional Analysis

Source	df	SS	MS
Total	21	12.661	
Model	2	12.374	6.187
Error	19	0.286	0.015

Parameter	Estimate	Std. Error	95% Confidence Lower	Upper
Hunting time	0.017	0.003	0.011	0.023
Pause in hours	3.197	0.680	1.774	4.620

Table 19 (continued).

Initial Density	Mean Removed
Pooling Group 1980 + 1981 + 1983 + 1984	
3	0.184
4	0.286
5	0.405
6	0.573
7	0.498
8	0.615
9	0.850
10	0.682
11	0.705
12	0.689
13	0.597
14	0.775
15	0.823
16	0.683
17	1.037
19	0.911
20	1.129
21	1.175
22	1.100
23	1.074
25	1.325
30	1.578
35	1.321
40	1.179

Non-Linear Regressional Analysis

Source	df	SS	MS
Total	25	20.353	
Model	2	19.894	9.947
Error	23	0.459	0.020

Parameter	Estimate	Std. Error	95% Confidence Lower	Upper
Hunting time	0.016	0.002	0.011	0.020
Pause in hours	2.714	0.421	1.843	3.586

Table 19 (continued).

Initial Density	Mean Removed
Pooling Group 1979 + 1980 + 1981 + 1982 + 1983 + 1984	
3	0.162
4	0.266
5	0.365
6	0.440
7	0.498
8	0.615
9	0.756
10	0.704
11	0.705
12	0.689
13	0.571
14	0.775
15	0.808
16	0.616
17	1.037
18	0.744
19	0.911
20	1.289
21	1.175
22	1.100
23	1.074
24	1.463
25	1.325
30	1.486
35	1.321
40	1.179

Non-Linear Regressional Analysis

Source	df	SS	MS
Total	26	22.152	
Model	2	21.577	10.789
Error	24	0.574	0.024

Parameter	Estimate	Std. Error	95% Confidence Lower	95% Confidence Upper
Hunting time	0.015	0.002	0.011	0.019
Pause in hours	2.500	0.452	1.567	3.433

Table 20. Averages of three P-values from tests of homogeneity between simulated distributions incorporating a digestive pause and Poisson distributions of identical means.

Initial Density	No. of Replications	Digestive Pause in Hours																				
		3.2	2.5	2.4	2.3	2.2	2.1	2.0	1.9	1.8	1.7	1.6	1.5	1.4	1.3	1.2	1.1	1.0	0.9	0.8	0.7	0.6	0.5
Pooled 1983 + 1984																							
3	103	0.768																					
4	231	0.335																					
5	232	0.154																					
6	136	0.140																					
7	233	0.047	0.136																				
8	135	0.120																					
9	233	0.007	0.099																				
10	221	0.006	0.063																				
11	139	0.025	0.140																				
12	180	0.006	0.059																				
13	186		0.045	0.053																			
14	138	0.006	0.067																				
15	227					0.044	0.057																
16	230						0.046	0.075															
17	189				0.034	0.056																	
18	195					0.039	0.054																
19	101	0.009	0.090																				
20	194							0.030	0.063														
21	229								0.040	0.051													
22	102	0.003	0.059																				
23	229										0.038	0.056	0.120	0.130	0.198	0.304	0.414	0.495	0.578				

Table 20 (continued).

Initial Density	No. of Replications	Digestive Pause in Hours																				
		3.2	2.5	2.4	2.3	2.2	2.1	2.0	1.9	1.8	1.7	1.6	1.5	1.4	1.3	1.2	1.1	1.0	0.9	0.8	0.7	0.6	0.5
5	341		0.240																				
10	547								0.030	0.073													
15	661														0.040	0.111	0.201	0.357	0.464	0.622			
20	703													0.017	0.055	0.076	0.155	0.204	0.334	0.433	0.621		
25	191								0.016	0.050													
30	45		0.116																				
35	53		0.040	0.066																			
40	78						0.043	0.052															
Pooled 1979 + 1980 + 1981	1982 + 1983 + 1984																						
3	198		0.797																				
4	321		0.511																				
5	430		0.150																				
6	234		0.219																				
9	328		0.033	0.052																			
10	585								0.021	0.052													
13	259					0.034	0.059																
15	757													0.027	0.054	0.140	0.259	0.395	0.471	0.604			
16	445													0.043	0.110	0.187	0.301	0.363	0.457	0.624			
20	1208																	0.016	0.056	0.104	0.303	0.402	0.504
24	95		0.052																				
30	138		0.116																				

Table 21. P-values from tests of homogeneity between empirical distributions and Poisson distributions of identical means.

Initial Density	Mean Removed	Number of Observations	P-Value from Test of Homogeneity Original	After Zero Adjustment
Pooling Group 1983 + 1984				
3	0.184	103	0.706	
4	0.286	231	0.700	
5	0.384	232	0.795	
6	0.573	136	0.819	
7	0.498	233	0.959	0.969
8	0.615	135	0.951	0.962
9	0.850	233	0.708	
10	0.778	221	0.722	
11	0.705	139	0.446	0.976
12	0.689	180	0.975	
13	0.597	186	0.998	
14	0.775	138	0.559	0.987
15	0.714	227	0.756	
16	0.683	230	0.854	
17	1.037	189	0.722	0.869
18	0.744	195	0.170	0.934
19	0.871	101	0.698	0.969
20	1.026	194	0.746	
21	1.175	229	0.512	0.987
22	1.098	102	0.847	0.991
23	1.074	229	0.497	0.994
Pooling Group 1980 + 1981 + 1983 + 1984				
5	0.405	341	0.838	
10	0.682	547	0.693	
15	0.823	661	0.554	
20	1.129	703	0.957	
25	1.325	191	0.957	0.999
30	1.578	45	0.875	
35	1.321	53	0.895	0.996
40	1.179	78	0.708	

Table 21 (continued).

Initial Density	Mean Removed	Number of Observations	P-Value from Test of Homogeneity Original	After Zero Adjustment
Pooling Group 1979 + 1980 + 1981 + 1982 + 1983 + 1984				
3	0.162	198	0.991	
4	0.266	327	0.801	0.989
5	0.365	430	0.919	0.953
6	0.440	234	0.588	0.883
9	0.7565	328	0.576	0.983
10	0.704	585	0.591	0.855
13	0.571	259	0.938	0.911
15	0.808	757	0.421	0.750
16	0.616	445	0.375	0.948
20	1.289	1208	0.641	0.994
24	1.463	95	0.538	0.992
30	1.486	138	0.835	0.909

Table 22. Averages of three P-values from tests of homogeneity between simulated distributions incorporating a digestive pause and empirical distributions.

Initial Density	No. of Replications	Digestive Pause in Hours																					
		2.2	2.1	2.0	1.9	1.8	1.7	1.6	1.5	1.4	1.3	1.2	1.1	1.0	0.9	0.8	0.7	0.6	0.5	0.4	0.3	0.2	0.1	0.0
Pooled 1983 + 1984																								
15	227		0.018																					
16	230			0.033																				
17	189	0.000																						
18	195		0.002																					
20	194				0.001																			
21	229					0.000																		
23*	229							0.000		0.001		0.004		0.017		0.031	0.046	0.069		0.197		0.284		0.406
Pooled 1980 + 1981 + 1083 + 1984																								
10	547					0.000																		
15*	661											0.007		0.032	0.047	0.093		0.239		0.389		0.481		0.573
20*	703										0.002	0.007		0.035	0.063	0.155		0.311		0.594		0.814		0.852
25	191					0.004																		
40	78		0.570																					
Pooled 1979 + 1980 + 1982 + 1983 + 1984																								
10	585					0.000																		
13	259		0.060																					
15*	757										0.003	0.007		0.029	0.081	0.108		0.160		0.306		0.471		0.423
16*	445										0.021			0.043	0.054	0.110		0.146		0.338		0.463		0.578
20*	1208														0.000			0.001	0.010	0.058		0.283		0.642

Table 23. Refusal to eat.

Initial Density	Excess Zeros Identified	Remaining Observations	Remaining Mean Eaten	P-Values from Test of Homogeneity: Empirical to Poisson Original	Adjusted
Pooling Group 1983 + 1984					
23	49	180	1.367	0.497	0.994
Pooling Group 1980 + 1981 + 1983 + 1984					
15	65	596	0.913	0.554	0.842
20	41	662	1.199	0.957	0.997
Pooling Group 1979 + 1980 + 1981 + 1982 + 1983 + 1984					
15	83	674	0.908	0.421	0.750
16	77	368	0.744	0.375	0.948
20	108	1100	1.415	0.641	0.994

Table 24. Refusal to eat, quadratic regression.

Initial Density	% Identified Extra Zeros	Mean Removed
3	0	0.162
4	17.4	0.322
5	8.6	0.399
6	30.8	0.635
7	9.0	0.547
8	6.7	0.669
9	23.2	0.984
10	13.2	0.811
11	35.3	1.089
12	0	0.689
13	7.7	0.619
14	28.0	1.092
15	11.0	0.908
16	17.3	0.744
17	13.8	1.202
18	32.8	1.107
19	15.8	1.082
20	8.8	1.415
21	17.0	1.416
22	18.6	1.349
23	21.4	1.367
24	18.8	1.792
25	6.8	1.421
30	5.1	1.565
35	13.2	1.522
40	0	1.179

Slope a = 0.0883

(Slope B) = -0.0012
squared density

Quadratic Regressional Analysis

Source	df	SS	MS	F-value	P-value
Total	26	658.446			
Model	2	641.599	320.800	457.02	0.0001
Error	24	16.846	0.702		

R-square = 0.974

Type III Sum of Squares

Source	df	SS	F-value	P-value
Slope A	1	135.324	192.79	0.0001
(Slope B) squared density	1	13.046	18.59	0.0002

Table 25. Refusal to eat, non-linear regression.

Initial Density	Mean Removed
3	0.162
4	0.322
5	0.399
6	0.635
7	0.547
8	0.669
9	0.984
10	0.811
11	1.089
12	0.689
13	0.619
14	1.092
15	0.908
16	0.744
17	1.202
18	1.107
19	1.082
20	1.415
21	1.416
22	1.349
23	1.367
24	1.792
25	1.421
30	1.565
35	1.522
40	1.179

Non-Linear Regressional Analysis

Source	df	SS	MS
Total	26	30.602	
Model	2	29.592	14.796
Error	24	1.010	0.042

Parameter	Estimate	Std. Error	95% Confidence Lower	Upper
Hunting time	0.018	0.003	0.012	0.024
Pause in hours	2.179	0.429	1.294	3.065

Table 26. Cubic regression.

Initial Density	Mean Removed	Standard Deviation
3	0.182	0.015
	0.200	
	0.171	
4	0.374	0.164
	0.143	
	0.114	
	0.171	
	0.486	
5	0.351	0.059
	0.471	
	0.400	
	0.429	
	0.324	
6	0.515	0.073
	0.529	
	0.571	
	0.676	
7	0.495	0.105
	0.428	
	0.412	
	0.676	
	0.486	
8	0.600	0.079
	0.706	
	0.531	
	0.618	
9	0.969	0.122
	0.794	
	0.829	
	0.800	
	0.625	
10	0.847	0.220
	0.424	
	0.743	
	1.029	
	0.735	

Table 26 (continued).

Initial Density	Mean Removed	Standard Deviation
11	0.829	0.222
	0.457	
	0.943	
	0.588	
12	0.822	0.138
	0.529	
	0.697	
	0.800	
	0.545	
13	0.769	0.133
	0.575	
	0.576	
	0.571	
	0.394	
14	0.647	0.239
	0.657	
	1.118	
	0.618	
15	0.685	0.263
	0.531	
	0.412	
	1.029	
	0.943	
16	0.766	0.158
	0.735	
	0.657	
	0.714	
	0.375	
17	1.176	0.246
	0.912	
	0.857	
	1.382	
	0.800	
18	0.684	0.100
	0.781	
	0.714	
	0.909	

Table 26 (continued).

Initial Density	Mean Removed	Standard Deviation
19	0.718	0.163
	1.000	
	1.000	
20	1.117	0.147
	0.781	
	0.971	
	1.058	
21	1.261	0.291
	0.743	
	1.118	
	1.545	
	1.086	
22	1.000	0.059
	1.060	
	1.118	
23	1.126	0.174
	0.939	
	0.943	
	1.333	
	0.939	

Slope A = 0.1195
(Slope B) x D^2 = -0.0071
(Slope C) x D^3 = 0.0002

Cubic Regressional Analysis

Source	df	SS	MS	F-value	P-value
Total	93	2477.34			
Model	3	2339.61	779.87	509.61	0.0001
Error	90	137.73	1.53		

R-square = 0.944

Type III Sum of Squares

Source	df	SS	F-value	P-value
Slope A	1	109.147	71.32	0.0001
(Slope B) x D^2	1	22.637	14.79	0.0001
(Slope C) x D^3	1	14.648	9.57	0.0026

APPENDIX E

FIGURES

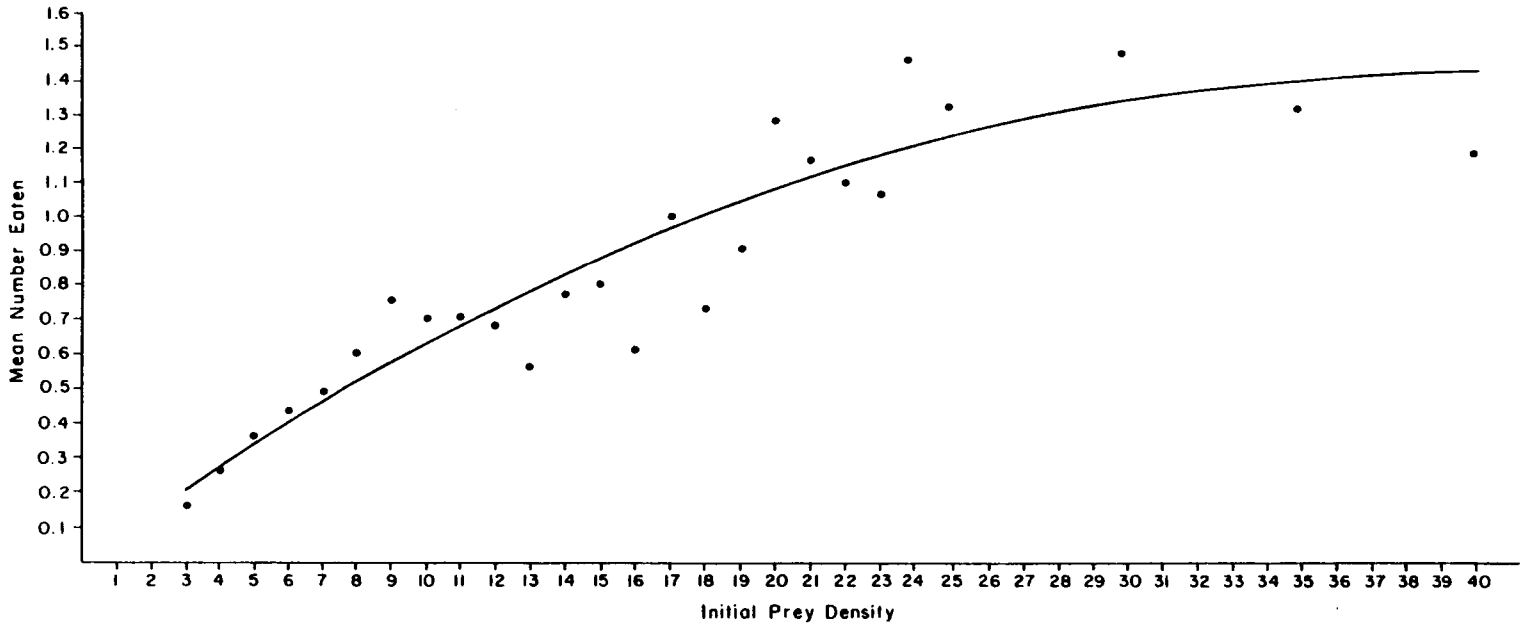

Figure I. Quadratic regression of pooled empirical data.

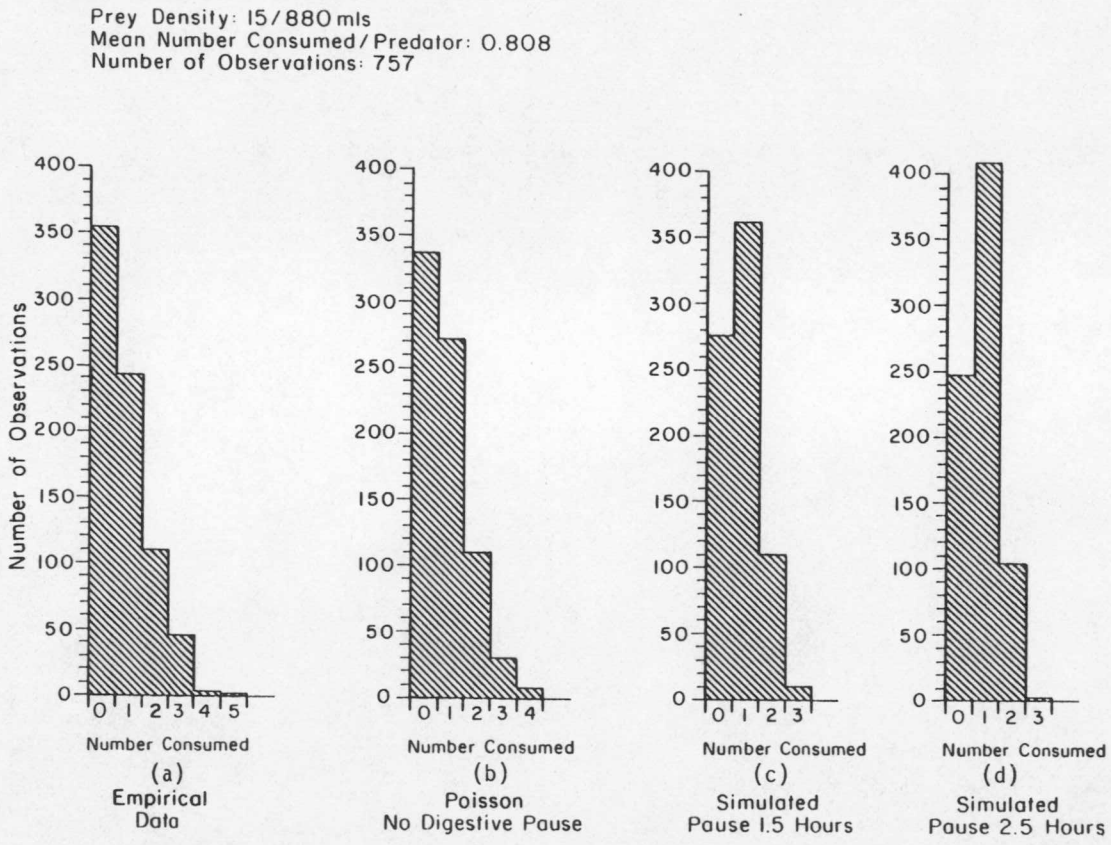

Figure II. Distributional comparisons at prey density: 15/880 mls.

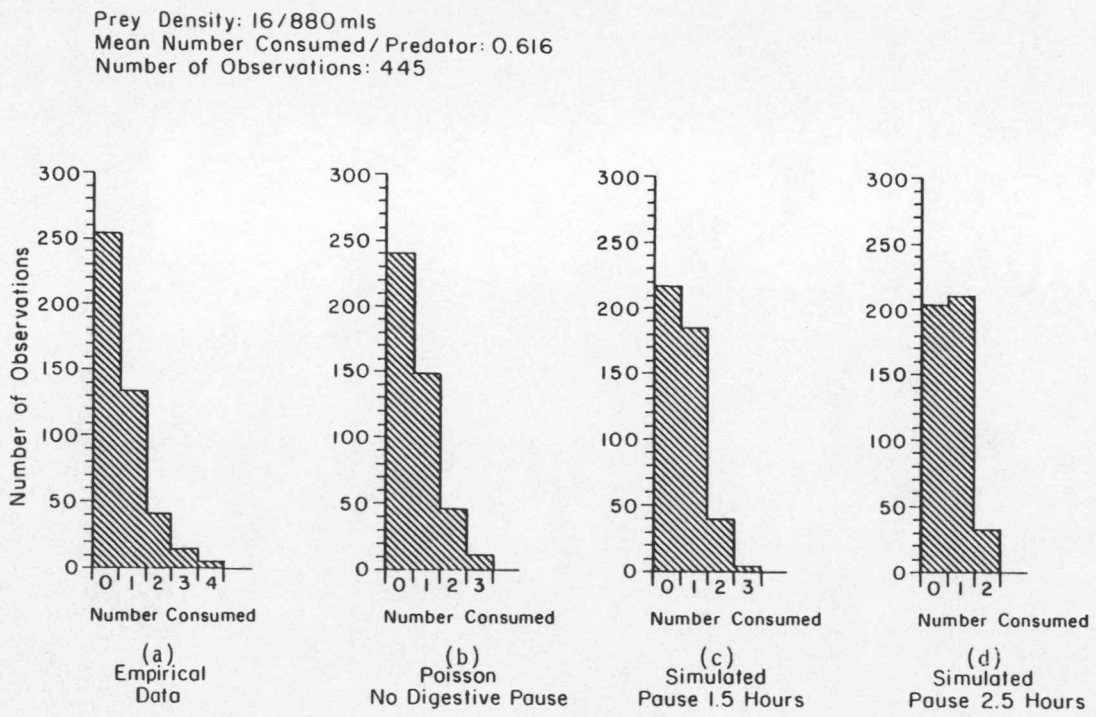

Figure III. Distributional comparisons at prey density: 16/880 mls.

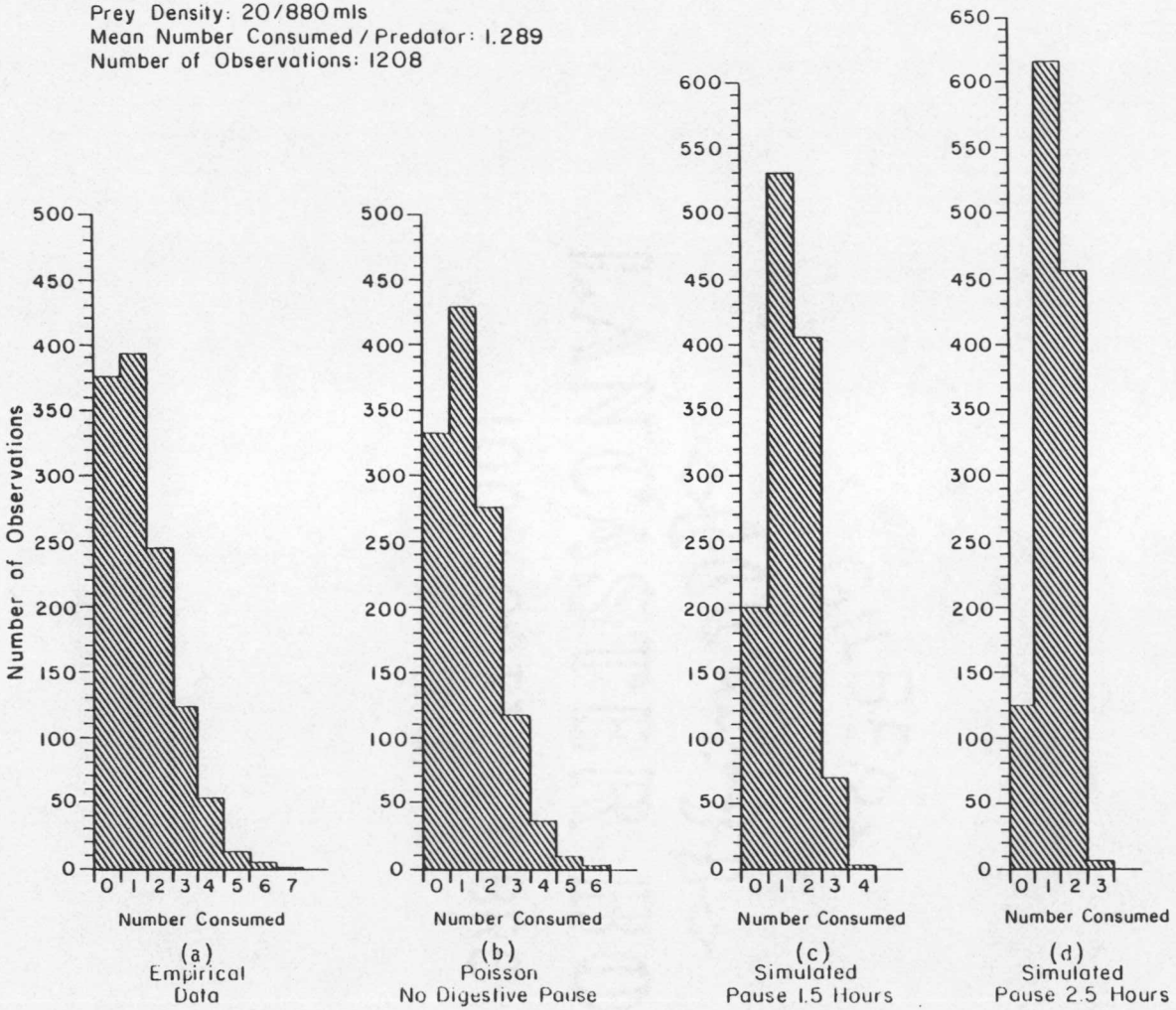

Figure IV. Distributional comparisons at prey density: 20/880 mls.

Prey Density: 23/880 mls
Mean Number Consumed/Predator: 1.074
Number of Observations: 229

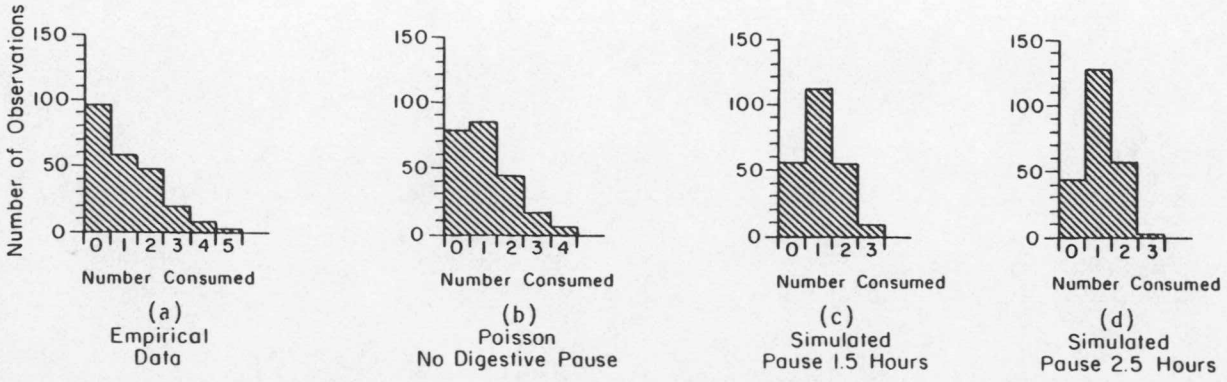

Figure V. Distributional comparisons at prey density: 23/880 mls.

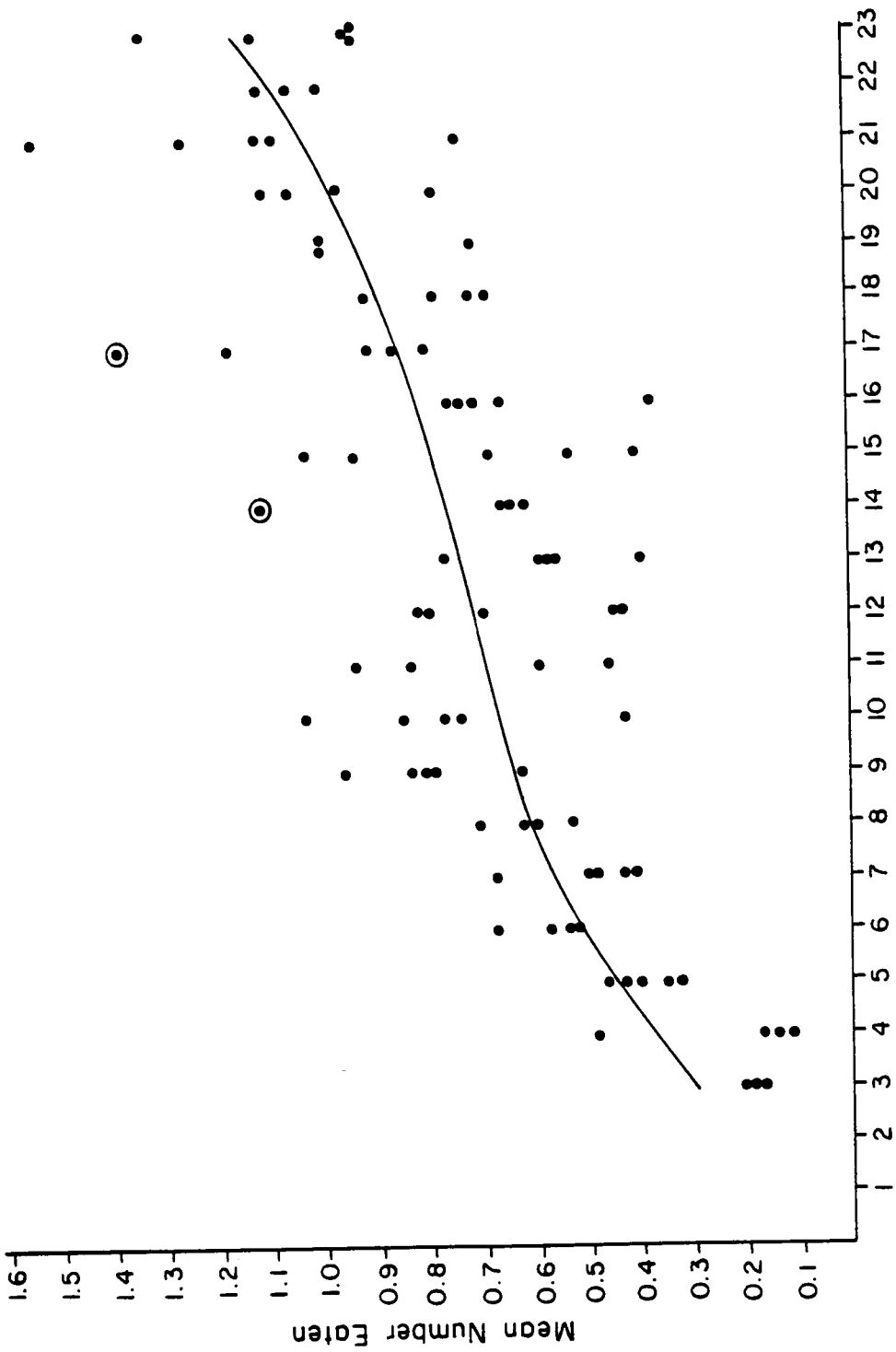

Figure VI. Cubic regression of 1983 and 1984 data.

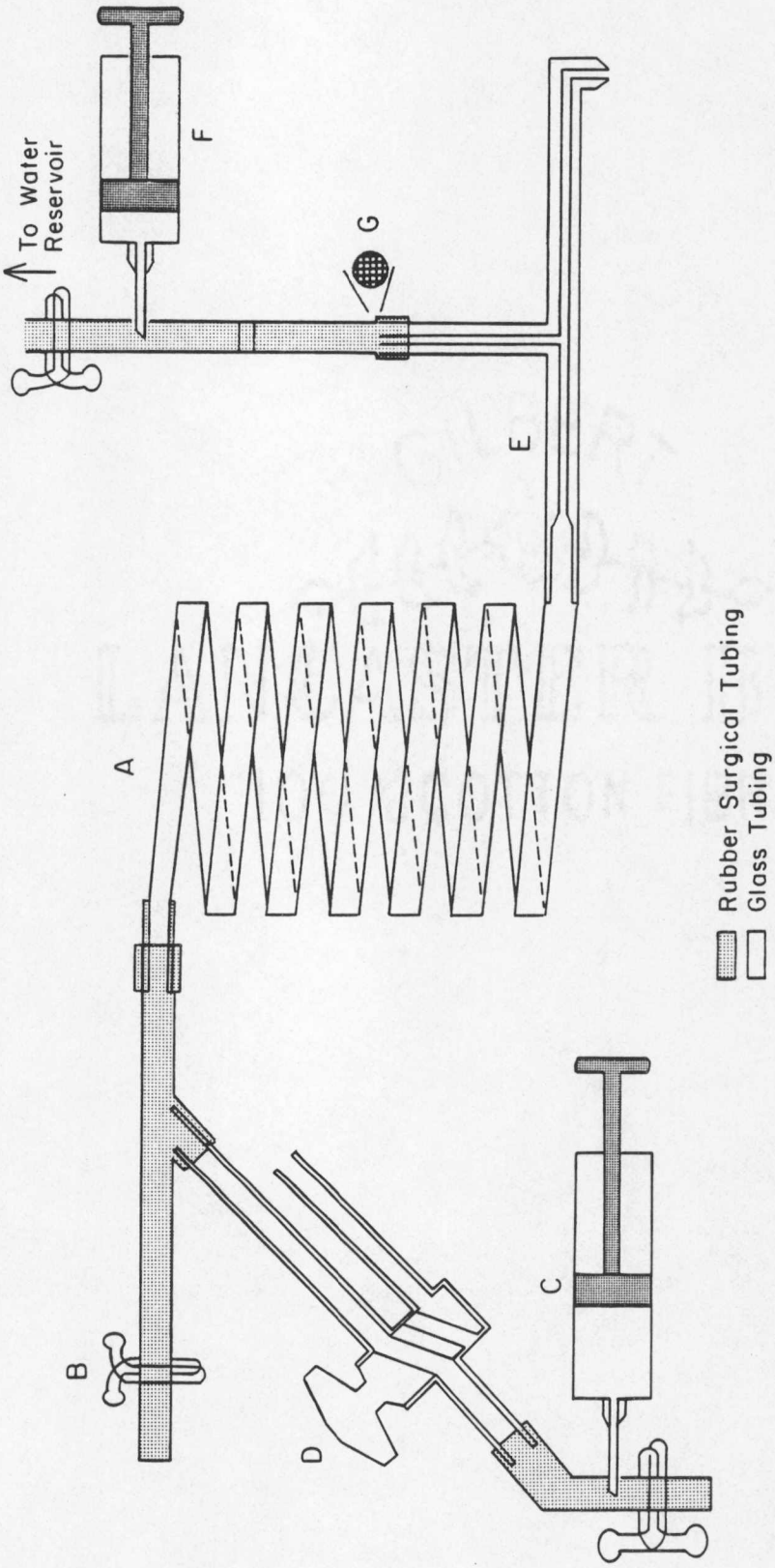

Figure VII. Counting apparatus.

VITA

Gregory Joseph Kauffman was born in Chambersburg, Pennsylvania on November 13, 1948. He attended elementary schools in that town and surrounding Franklin County. He was graduated from Chambersburg Area Senior High School in June 1966. The following September he entered Shippensburg University in Shippensburg, Pennsylvania, and in June 1970 he received a Bachelor of Arts degree in Biology.

After a three-year tour of duty with the United States Army, he entered graduate school at Shippensburg University in 1973 and received a Master of Science degree in June of 1975, with a thesis entitled, "The Cranial Musculature of the Common Shiner, Notropis cornutus." In September 1975 he entered The Graduate School of The University of Tennessee, Knoxville. He received the Doctor of Philosophy degree with a major in Ecology in March 1988.