NICHE ONTOGENY AND PROGRESSIVE DEVIATION

IN TWO CONGENERIC SUNFISHES, *ENNEACANTHUS OBESUS*

AND *E. GLORIOSUS* (CENTRARCHIDAE)

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ABSTRACT OF THE THESIS

Niche Ontogeny And Progressive Deviation In Two Congeneric Sunfishes, Enneacanthus obesus and E. gloriosus (Centrarchidae)

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The banded sunfish, *Enneacanthus obesus*, and the bluespotted sunfish, *E. gloriosus*, show progressive morphological deviation during development. Early developmental stages of the two species resemble one another more in general body dimensions than they resemble their own adults, and more than the adults resemble one another. Contrary to expectations, however, their food habits do not diverge concomitantly with morphology.

Niche relationships of *E. obesus* and *E. gloriosus* were inferred through dietary analysis. Dietary data are partly categorical and partly continuous. Detrended correspondence analysis, a multivariate technique designed specifically for categorical data, uncovers underlying resource gradients in the dietary data. It is more effective in discriminating among species on the basis of diet than factor analysis or principal components analysis, and it avoids the restrictive assumptions of discriminant analysis. In addition, the prey scores produced by

detrended correspondence analysis can be used to estimate components of niche width.

The larvae of both species feed most actively just before sunset. In E. gloriosus, the number of recently eaten prey in the stomach increases continuously from 0630 hours to 1830 hours, and then declines rapidly. Enneacanthus obesus shows a minor peak in the number of recently eaten prey at 0930 hours, and a major peak at 1830 hours. Early in the day, most food is in an undigested state and the volume of food in the intestine is low. Both species feed throughout the day, and the volume of food in both stomach and intestine increases gradually from dawn to dusk.

Dietary diversity is low for larvae of both species; it is highest in juveniles, and declines slightly with size. There are no significant differences in dietary diversity between the two species.

Enneacanthus obesus and E. gloriosus partition microhabitat rather than food or time. Both species live in dense littoral vegetation, but feed in different microhabitats. Enneacanthus obesus feeds to a greater extent on aquatic invertebrates that live on the leaves and stems of submerged macrophytes; E. gloriosus takes more free-swimming and benthic invertebrates. These differences remain throughout life.

PREFACE

Bonner (1965), in his engaging work "Size and Cycle", argued convincingly for the need to consider the entire life cycle as the central unit in biology. Nevertheless, many ecologists consider only adults of a species when framing their hypotheses. With respect to competitive interactions in ecological communities, this bias towards adults has led to a preponderance of theory that ignores other life-history stages. In higher vertebrates, such as birds and mammals, which feature extended parental care, this may be a valid simplification, but for lower vertebrates, most invertebrates, and plants this simplification may be invalid.

Gould (1977), and Raff and Kaufman (1983), recently heralded the long overdue incorporation of embryology into the evolutionary synthesis. This merger is sure to have repercussions in community ecology, and niche theory is likely to benefit most from an infusion of comparative embryology. A new view of the niche is emerging, and it is one of a niche that changes continuously throughout an organism's development.

In this dissertation, I examine ontogenetic shifts in the niches of two congeneric sunfishes, the banded sunfish

(*Enneacanthus obesus* Girard), and the bluespotted sunfish (*E. gloriosus* Holbrook). In preparing this study, I benefited by the advice and guidance of a number of faculty and fellow graduate students. I would like, foremost, to thank my major advisor, Robert C. Vrijenhoek, and the rest of my dissertation committee: Kenneth Able, Edmund Stiles, Thomas Whittam, and Peter Morin. In addition, Michael Friedman, of the Statistics Department, was a valuable aid in deciding which statistical techniques were appropriate for analysing the dietary data. Bori Olla, of the National Marine Fisheries Service, helped in the initial phase of the study, when I was still unsure of myself and looking for direction. Francesco Trama happily loaned me whatever limnological equipment and taxonomic keys I needed. Michael E. Douglas and James D. Felley both pushed me headlong into multivariate statistics. Catherine Chamberlin-Graham and Frank Donahue, seiners and kickers par excellence, assisted with the field work. Fellow students James Leslie, who spent patient hours teaching me gel electrophoresis, and Russell Schenck, with whom I spent many hours discussing the finer points of dietary analysis, were a great help. Russell Cookingham and Bruce Pyle, of the New Jersey Division of Fish and Game, went to great lengths to issue a special permit allowing me to snorkel in Collier's Mills Pond; Charles Menzer, and an unknown conservation officer at the Collier's Mills Wildlife Management Area, also helped.

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Finally, I especially thank my wife, Catherine Chamberlin-Graham, who has supported me, both financially and psychologically, in the face of an ever deteriorating academic job market. This dissertation is as much hers, as it is mine.

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CHAPTER I

As the species of the same genus . . . have
. . . much similarity in habits and constitution,
and always in structure, the struggle will . . .
be more severe between them if they come into
competition with each other, than between the
species of distinct genera.

Charles Darwin (1872a, page 116)

. . . the embryos of mammalia, of birds, lizards,
and snakes, and probably also of chelonia, are
in their earliest states exceedingly like one
another, both as a whole and in the mode of
development of their parts; so much so, in
fact, that we can often distinguish the embryos
only by their size. In my possession are two
little embryos . . ., whose names I have
omitted to attach, and at present I am quite
unable to say to what class they belong.

Karl Ernst von Baer (1828)
cited by Darwin (1872b, page 250)

INTRODUCTION

If morphologically similar species compete more often than dissimilar species, and if early developmental stages of related species "resemble one another more than they resemble [their own] adult stages, and more than the adult stages resemble one another" (de Beer 1940), then one must conclude that early stages of related species should compete more often than later stages. This conclusion proceeds from three related concepts: niche, competitive exclusion, and progressive deviation. Johnson (1910) first used the word 'niche' in an ecological sense, although the concept is much older (Gaffney 1973, Hutchinson 1978). It was Grinnell (1917), however, who popularized the term in his classic paper, "The niche-relationships of the California thrasher." For Grinnell (1924), the niche was a part of the habitat, the "ultimate unit . . . occupied by just one species or subspecies." In contrast to Grinnell's distributional concept of the niche, Elton (1927) used the word 'niche' to describe an organism's role within a community. Following Elton, Hutchinson (1957) introduced the multidimensional niche into ecology. Hutchinson's niche, which relied on Boolean algebra, included all environmental variables affecting a population. By his definition, a niche was that part of a hyperspace where a species could exist. The hyperspace was defined by the relevant environmental axes (e.g., temperature, food size, etc.). Hutchinson (1957) distinguished two kinds of niche:

a fundamental niche, occupied in the absence of competitors, and a realized niche, occupied in the presence of competitors. Then Maguire (1973) refined Hutchinson's model by adding an axis to show a population's response to the relevant environmental axes. For example, a population's intrinsic rate of increase may vary with temperature, food size, and predator density to define a population's response in 3-dimensional space. Finally, Whittaker, Levin, and Root (1973) suggested restricting the word 'niche' to the role of an organism within a community, and suggested restricting the word 'habitat' to the range of environments in which a species occurs.

Related to the concept of niche is the competitive exclusion principle. Hardin (1960) said it most succinctly: "complete competitors cannot coexist." Alternatively, species with identical niches cannot coexist. Many experiments support this principle (Gause 1934, Park 1948, 1954). Usually pitting two competitors against one another in a homogeneous environment, such experiments always result in one population becoming extinct. In a heterogeneous environment, however, rivals are no longer "complete competitors", and the outcome is uncertain. One or the other species may win, or both may coexist (Crombie 1947).

Because one can always find differences between any two species, the usefulness of the competitive exclusion principle has been questioned. In addition, both predation

(Paine 1966, Strong 1984) and environmental fluctuation (Armstrong and McGehee 1980, Levins 1979) may allow competitors to coexist. Less contentious, and more useful, than the competitive exclusion principle is the concept of limiting similarity, introduced by MacArthur and Levins (1967). Unlike the competitive exclusion principle, the concept of limiting similarity is nontautological, thus it can be the basis for testable hypotheses. Limiting similarity addresses the limits to the similarity of competing species (May 1976). How alike can two species be and still coexist?

An underlying assumption of limiting similarity, and of the competitive exclusion principle, is that species sharing a resource are more likely to compete than species not sharing a resource. But the priority of competition in structuring ecological communities is questionable (Strong et al. 1984). Resources rarely may be limiting, since predators, parasites, and environmental vagaries reduce the numbers of potential competitors (Connell 1975).

Despite the present confusion regarding the role of interspecific competition, closely related species must coexist in nature. It isn't the goal of this thesis to discriminate between differences evolved in situ and those that represent the "ghost of competition past" (Connell 1980). My goal is to address ontogenetic differences in morphology and resource use, and their interrelationships as they might effect resource overlap between closely related species. In addressing these concepts, one immediately confronts the idea of progressive deviation.

Karl Ernst von Baer, the leading embryologist of the 19th century, proposed four laws of development in his classic 1828 text, "Entwicklunsgeschichte der Thiere: Beobachtung und Reflexion." Paraphrasing Singer's (1959) translation.

1. General characters appear before special characters
2. Special characters develop from general characters
3. During development, related species diverge continuously from one another
4. Higher animals pass through stages resembling stages of lower animals

To describe Von Baer's third law, Fritz Muller (1864), the German-Brazilian naturalist, introduced the term progressive deviation. But recent evolutionary biologists have shown little interest in von Baer's laws. Gavin de Beer (1940) discussed them in "Embryos and Ancestors", Gould (1977) mentioned them briefly, and Mayr (1982) dismissed them as "largely descriptive and sterile from the explanatory point of view." Nevertheless, von Baer's laws validly describe development at the organismic level.

What is the evidence for closely related species diverging during development? Although quantitative evidence for deviation is rare, many embryologists have accepted the principle based on simple observation and comparison. Specialized larval adaptations, or caenogenesis, occur in some groups, notably insects, but most related species, as a rule, diverge in morphology.

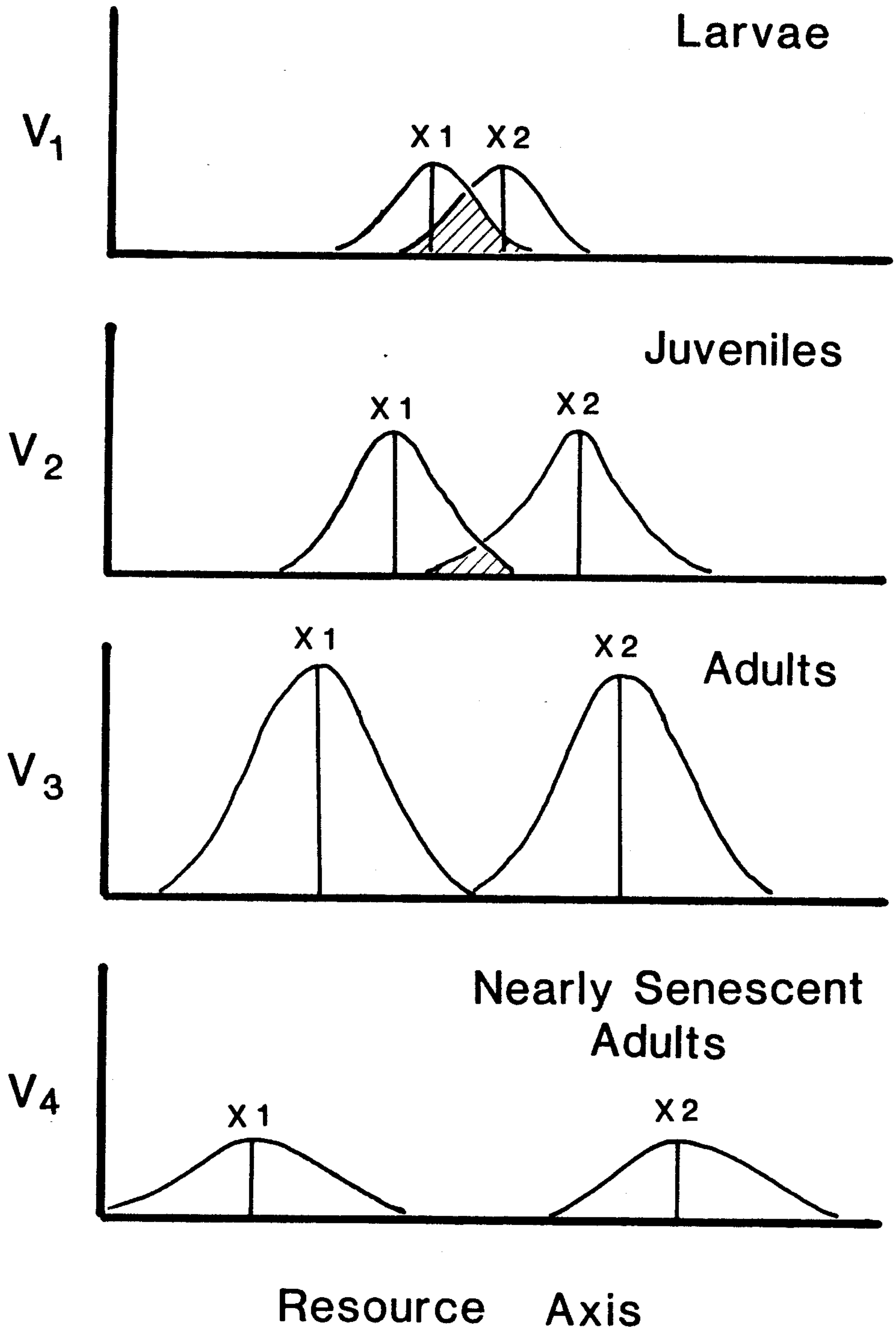
Progressive deviation occurs in many groups of organisms. For example, among the crustaceans, the group studied by Muller (1864), morphologically similar nauplii produce adults as disparate as ostracods, barnacles, and parasitic copepods. Deviation is also prevalent in the vertebrates, and is best illustrated by Haeckel's classic comparison of development in fish, salamander, tortoise, chick, hog, calf, rabbit, and man. Within the teleosts, Blaxter (1974) observed "a tendency for larvae to show smaller morphological distinctions than adults." Moreover, Hunter (1980) showed for six species of marine fishes that mouth sizes were more alike early than later in development. Brown and Colgan (1984) found ontogenetic divergence in mechanical feeding behaviors of four sunfishes, and Carey (1985) found divergence in photobehavioral responses of two charrs.

If morphological phenotypes diverge during development, and if morphology constrains the niche, one might expect niches to diverge during development. To answer this question, one must incorporate developmental concepts, such as progressive deviation, into a general theory of the niche. One can begin modifying Hutchinson's multidimensional niche by adding an axis to represent the life cycle. Thus one need not arbitrarily define two or more distinct niches, such as a larval niche and an adult niche. Fertilized egg, developing embryo, growing juvenile, reproductive adult, senescent adult, and all intermediates become incorporated into the niche. Following Maguire's (1973) example of adding an axis to indicate response to particular environmental conditions, the obvious measure of response is reproductive value (V_i), which is computed from age-specific survivorship and birth rates (Fisher 1958). Figure 1.1 shows a hypothetical model of progressive deviation of two species (species X_1 and X_2) on a resource axis. The heights of the curves reflect changing reproductive value: low at birth, highest when the two species start to reproduce, and zero at the end of their reproductive lives. This simple model demonstrates that total overlap (integrated over all ages) depends highly on reproductive value if niches diverge.

In this thesis, I examine niche ontogeny in two congeneric sunfishes (Centrarchidae), the banded sunfish (*Enneacanthus obesus* Baird) and the bluespotted sunfish (*E. gloriosus* Holbrook). These two species are ideal for testing hypotheses related to niche ontogeny. On casual examination, the adults, though morphologically alike, are easily distinguishable, whereas the larvae and juveniles are virtually indistinguishable. Moreover, the two species are sympatric over most of their range, and the embryos hatch at a small size. Finally, the adults breed at the same time in early spring, thus larvae, juveniles, and adults are of similar sizes.

I address the following specific questions: (1) Is morphological similarity between the two species related to size (Chapter V)? (2) How do food, space, or both change during development (Chapter IV)? (3) Do niches diverge during development concomitantly with morphology (Chapter V)? (4) How can one measure niche width and niche overlap from dietary data (Chapter III)?

Figure 1.1 Progressive deviation of two species on a hypothetical resource axis, e.g., prey size.


Larvae
V_1
X 1
X 2
Juveniles
V_2
X 1
X 2
X 1
X 2
Adults
V_3
Nearly Senescent Adults
V_4
X 1
X 2
Resource Axis

CHAPTER II

STUDY SITES

This study was conducted at two locations in southern New Jersey (Fig. 2.1). Success Lake, a highly acidic blackwater impoundment, lies within the the Pine Barrens, a region of nutrient-poor, sandy soils. Colliers Mills Pond, which is slightly acidic and lightly colored, lies just within the boundary of the Pine Barrens (as defined by McCormick 1973).

At the beginning of my study, on 7 June 1979, I measured methyl-orange alkalinity, phenolphthalein alkalinity, pH, and dissolved oxygen in both lakes. I measured pH with a portable Digisense pH-meter, and alkalinity and dissolved oxygen with Hach reagents (Hach Chemical Co.).

Success Lake

Success Lake (Fig. 2.1) is an 11.1 hectare impoundment on Shannae Brook, a tributary of the Ridgeway Branch of the Toms River, in Jackson Township, New Jersey (Cassville Quadrangle). Elevation of the lake is 30.5 m above sea level, and it lies within the Pine Barrens on the Cohansey Sand. The drainage is entirely wooded. Pitch pine (*Pinus* rigida) lowland (the vegetation types are from McCormick's (1973) classification) dominates the lake's northern and western shores; pine oak (Quercus spp.) forest dominates higher elevations on the southern shore. The Shannae Brook tributary drains hardwood forest and pitch pine lowland. A second tributary drains Collier's Mill Pond and Turnmill Pond and then flows through a cedar (Chamaecyparis thyoides) swamp before entering Success Lake. The substrate is primarily sand and gravel, but small coves and inlets may have shallow deposits of detritus. Unlike Collier's Mill Pond, submerged aquatic macrophytes are scant (Table 2.1). Shallow coves often have dense stands of floating macrophytes. Success Lake is a relatively pristine blackwater. Alkalinity and pH are low (Table 2.2). The water is highly colored, and usually clear. Strong winds, however, increase turbidity by mixing a flocculent material of complexed humic materials into the upper waters.

Collier's Mills Pond

Collier's Mills Pond (Fig. 2.1) is a 6.9 hectare impoundment on a tributary of the Ridgeway Branch of the Toms River in Ocean County, New Jersey (Cassville Quadrangle). The pond is at Collier's Mills within the Collier's Mills Wildlife Management Area. It lies just inside the western boundary of the Pine Barrens on the Cohansey Sand Formation at an elevation of 39.6 m. The drainage is surrounded by oak-pine and hardwood forest (McCormick 1973). The pond is shallow, with a mean depth of 0.9 m and a maximum depth of 1.8 m. The substrate along the shoreline is sand, gravel, and some detritus. In deeper water the substrate is mud and detritus. The entire basin is densely vegetated with submerged and floating aquatic macrophytes (Table 2.1). Chemically, Collier's Mills Pond is less acidic, and more alkaline, than Success Lake (Table 2.2). The water is lightly colored by dissolved humic substances.

Table 2.1 Aquatic macrophytes present in the two study sites. *

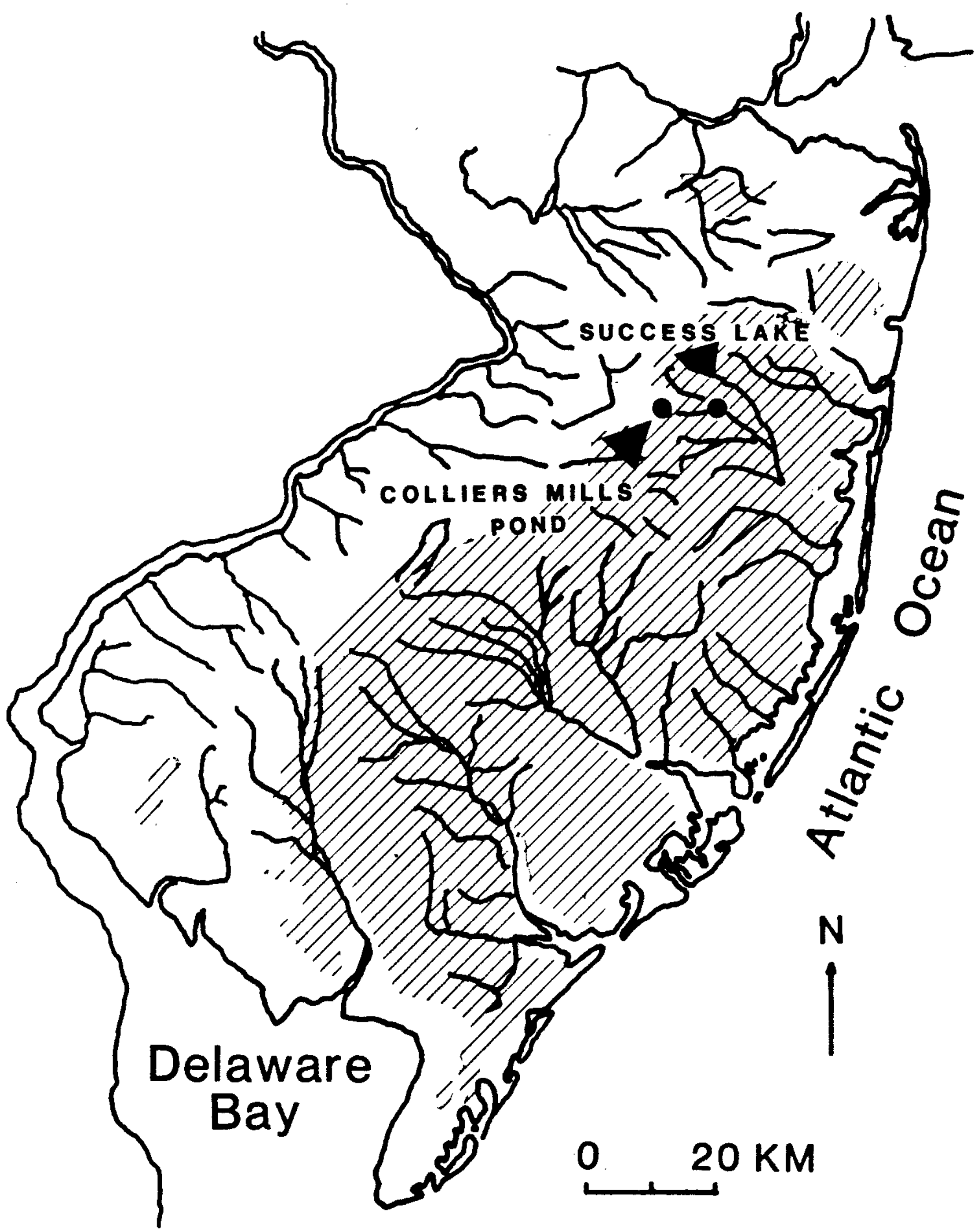
Species	Collier's Mill Pond	Success Lake
Sphagnum spp.	C	A
Myriophyllum spp.	A	
Utricularia spp.	A	C
Nuphar variegatum	C	P
Nymphaea odorata	C	C
Brasenia schreberi	C	
Decodon verticillatum	P	P

* Species abundance codes are:
A - abundant
C - common
P - present

Table 2.2 Physiochemical data for the two study sites, 7 June 1979.

Variable	Success Lake	Collier's Mill Pond
pH	4.3	5.7
Methyl-orange alkalinity (mg/l)	<4.0	6.0
Phenolphthalein alkalinity (mg/l)	0.0	0.0
Dissolved oxygen (mg/l)	7.0	10.0

Figure 2.1 Sampling localities in New Jersey.


SUCCESS LAKE
COLLIERS MILLS
POND
Atlantic Ocean
N
Delaware
Bay
0
20 KM

CHAPTER III

MULTIVARIATE ANALYSIS OF DIETARY DATA

Introduction

Diet is commonly used to compare the niches of co-occurring species. But diet confounds many niche dimensions, being influenced by the size and kind of prey, and by the microhabitat and time of activity of the interacting predators. For example, the kind of prey eaten might depend on the preferred microhabitat of the predator. The reverse is also possible, a predator may use a microhabitat because its preferred prey is there. In addition to confounding at least four niche dimensions, diet has both continuous and categorical attributes. Prey size and the predator's time of activity are continuous attributes. But habitat may be continuous or categorical, and prey type is a categorical attribute. In response to these problems, several multivariate techniques, including discriminant analysis, principal components analysis (PCA), and factor analysis, have been used with dietary data to compare the niches of co-occurring species (Desselle et al. 1978, Findley and Black 1983, Humphrey et al. 1983, Hughes 1985). Discriminant analysis, when applied to dietary data, combines dietary variables in a linear equation maximally discriminating among species. Factor analysis and PCA serve to reduce the number of dietary variables. These multivariate techniques, however, may have serious disadvantages when applied to dietary data.

Dietary data rarely satisfy the assumptions underlying discriminant analysis, factor analysis, and PCA. For discriminant analysis, those assumptions are multivariate normality and homogeneous covariance matrices (Williams 1983). Factor analysis has many of the same disadvantages. In particular, dietary data easily violate the assumption of multivariate normality. PCA has fewer restrictive assumptions than factor analysis, but still performs poorly on categorical data (Aitchison 1983).

Detrended correspondence analysis (DCA) is a multivariate eigenvector technique designed specifically for categorical data (Hill and Gauch 1980, Gauch 1983). It has been used by Sabo and Holmes (1983) to study foraging patterns (not diet) in birds. In this chapter, I demonstrate DCA's superiority to PCA, factor analysis, and canonical discriminant analysis when one's goal is to infer continuous niche axes from multivariate categorical dietary data. With DCA, one can estimate niche position, niche width, and niche overlap from dietary data. Furthermore, DCA discriminates between species better than factor analysis and PCA, and discriminates as well as discriminant analysis. And DCA has fewer restrictive assumptions than the other techniques. Finally, unlike the traditional multivariate techniques, the DCA scores can be used in a hierarchical analysis of variance to estimate within- and between-phenotype components of niche width (Van Valen 1965, Roughgarden 1972).

The within-phenotype component of niche width is the average variance in resources taken by individuals; the between-phenotype component of niche width is the variance due to differences among individuals. Partitioning components of niche width in this manner is only possible with DCA or reciprocal averaging, a related technique. In DCA the predator scores and prey scores are reciprocal averages of one another. Predator scores and prey loadings are not reciprocal averages of one another in PCA, factor analysis, or discriminant analysis.

In applying DCA to dietary data, the contents of each predator's stomach constitutes a sample. Since a foraging animal samples selectively, the ordering of food items along a DCA axis integrates the prey's spatial distribution and the predator's behavior. Dietary categories should behave like species do along an underlying ecological gradient, the model for which DCA was developed. That is, prey composition should turn over at regular intervals along a resource gradient.

Methods

To compare the performances of DCA, discriminant analysis, PCA, and factor analysis on actual dietary data, I introduce a small part of a data set that is considered in greater detail in Chapter IV. The data are the stomach contents of larval, juvenile, and adult banded sunfish (Enneacanthus obesus) and bluespotted sunfish (E. gloriosus) collected from Success Lake, NJ on 13 August 1980. I identified food items to the lowest feasible taxon, and for each fish, the counts of each kind of food were recorded. Statistical analyses were performed on the counts.

The DCA algorithm, DECORANA, was written by Hill (1979). It is available from Cornell University Ecology Programs (program CEP-40). DECORANA requires data in a condensed format, with the zero counts omitted. A fortran program called CONVERT, which was written by T. Whittam and myself, changed uncondensed dietary data to the condensed format. (A similar program called CONDENSE is available from Cornell University Ecology Programs.) Beginning with an arbitrary score for each category of prey (prey score), DECORANA calculates a score for each individual predator (sample score). The sample scores are the averages of the prey scores within each sample. Then, the prey scores are recalculated from the new sample scores. The new prey scores are the averages of the sample scores within each kind of prey. Both prey and sample scores are reciprocal averages of one another. The process continues, iteratively, until both prey and sample scores stabilize. The first axis is then rescaled so prey appear at regular intervals. Each consecutive axis is calculated similarly, but is constrained to have no systematic relation to the next lowermost axis. The criterion of independence is more stringent than the criterion of being uncorrelated; DECORANA detrends the sample scores with each iteration. Gauch (1983) discusses the technique in greater detail.

For exploratory factor analysis, I performed a PCA on the combined correlation matrix of food variables, and followed it by a varimax rotation of factors having eigenvalues greater than or equal to one (Kaiser 1958). PCA accounts for all of the variance in each variable; factor analysis accounts for the correlations among the variables. Ideally, the analysis will uncover relationships among dietary variables. For example, it might uncover meaningful groupings of prey (i.e. benthic prey, planktonic prey, etc.).

To find those foods maximally discriminating between the two sunfishes, I performed a canonical discriminant analysis on the covariance matrices of food variables. Canonical discriminant analysis is a canonical correlation analysis in which one set of variables (i.e. the two species of sunfish) are each dichotomous variables, with 0 or 1 denoting group membership. Canonical correlation and discriminant analysis give identical results (Tatsuoka 1953). Canonical discriminant analysis, however, is used more frequently for exploratory analysis.

Since rare foods may distort all of these analyses, I decreased the effects of rare prey by downweighting, an option of DECORANA that reduces the abundance of rare prey in proportion to their frequency (Hill 1979). Rare prey are those with less than one fifth the frequency of the most common prey. DECORANA automatically omits prey with weights less than 0.01. To make DCA, PCA, factor analysis, and canonical discriminant analysis comparable, I applied the downweightings from DECORANA to the other three analyses as well.

For PCA, factor analysis, and DCA, I combined individuals of the two species of Enneacanthus. Alternatively, one could perform a separate analysis for each species, but the disadvantage here is that no comparisons between species can be made. A consequence of combining species in PCA and factor analysis is that the correlation of one prey variable to another may change if the two species of predators have different means on one or both of the prey variables (Lindeman et al. 1980). For example, within each species two prey may be positively correlated, but in the composite group they may be uncorrelated, or even negatively correlated. With the Enneacanthus data, a preliminary comparison of the combined and uncombined correlation matrices showed only minor changes in most correlation coefficients, and no drastic changes of sign.

For each species, and for each statistical technique, I plotted 50 and 95 percent frequency ellipses on the first two reduced axes. If only one axis was found, as frequently happens with discriminant analysis, I plotted frequency polygons. A 50 percent frequency ellipse contains 50 percent of the observations in a distribution; a 95 percent frequency ellipse contains 95 percent of the observations. The center of these ellipses is the bivariate mean (Sokal and Rohlf 1981). A frequency ellipse's advantage over a confidence ellipse is that it is less influenced by sample size. This is important when the object is to compare distributions rather than bivariate means. Green's (1971) classic paper on the multidimensional niche is a precedent for its use.

To estimate the variance in resources taken by a species (i.e. its niche width), I used DCA to extract the relevant niche axes. This could also be done with the other multivariate techniques. The standard deviation of predator scores on an axis is a measure of niche width. Moreover, by using prey scores from DCA in a hierarchical analysis of variance, I partitioned niche width into two variance components: a within-phenotype component and a between-phenotype component.

To partition components of niche width, I wrote a fortran program, SAMPLE, that randomly sampled two or more food items from each stomach. The program also identified each food item, and assigned DCA scores based on the previous analysis. For example, if 5 prey were sampled from a stomach, and identified as two cyclopoid copepods, an oribatid mite, a *Ferrissia*, and a *Monostyla*, then that fish would be assigned these scores on the first DCA axis: 82, 82, 351, 224, and 174 (see Table 3.5). By sampling two or more prey from each fish, I partitioned the variance in the DCA scores into two components: among individuals (phenotypes) and within individuals (phenotypes). To demonstrate this technique, I sampled two prey at random from each of 101 *E. gloriosus* (12 to 13 mm standard length) that I collected on 13 August 1980 in Success Lake.

Results

PCA of the correlation matrix resulted in 13 components with eigenvalues greater than 1 (Table 3.1). These 13 components accounted for 63 percent of the total variance in the data. An orthogonal rotation of these 13 components produced little improvement (Table 3.2). Correlations among dietary variables were low (only 13.9 percent were significant at the 0.05 level), and nearly all were positive. Kaiser's (1970) measure of sampling adequacy (MSA) averaged a poor 0.55, which indicated that the dietary variables insufficiently defined the common factors. An MSA of 0.8 or better is considered good; one less than 0.50 is unacceptable (Kaiser and Rice 1974, Cerny and Kaiser 1977). Ten of the dietary variables had MSA's less than 0.5. Moreover, the average communality, which measures the degree to which the common factors account for each variable's variance (Lindeman et al. 1980), was merely 0.59.

Those loadings with absolute values of 0.4 or more define the common factors (Lindeman et al. 1980). On all but factor 8, the loadings defining the factors were positive. Factor 1 represented a oribatid-Alonella factor, factor 2 a planktonic rotifer factor, and factor 3 a hydracarina-tendiped factor, and so on. (See Appendix 7.3 for a taxonomic listing of prey.) Factor 8 contrasted cyclopoid copepods and Bosmina longirostris (Cladocera) with Caenis, a mayfly (Ephemeroptera) nymph. Thus, the common factors, except factor 8, seem to measure discrete niches; an individual used a resource (e.g., oribatid mites and Alonella), or it did not. Enneacanthus obesus and E. gloriosus had significant differences in their mean scores on 7 of the first 13 principal components, and on 5 of the first 13 common factors (Table 3.3).

The pattern of PCA scores resembles a crude ellipse (Fig. 3.1), which is what one would expect if the distribution of points were multivariate normal. The univariate distributions, however, were skewed to the right on the first principal component, and towards the top on the second principal component. Those fish with high scores on the first component fed on Alonella excisa (Cladocera), tendiped larvae, Pentaneura (Tendipedidae), oribatid mites, hydracarina, Chydorus sphaericus

(Cladocera), and Sida crystallina (Cladocera). Fish with low scores on the first component did not feed on these prey. Fish with high scores on the second component fed on Keratella and an unidentified rotifer.

By rotating the PCA axes to simple structure, the roughly elliptic pattern of PCA scores becomes even more distorted (Fig. 3.2). Four fish (two of each species) had high scores on the first factor; the remaining fish were clustered at the opposite end of the axis. Thus the first factor is the product of only four fish that fed on Trichocerca and Keratella (Rotifera). Similarly, the second factor has few fish with high scores (stomachs containing Arcella and unicellular algae), and many fish with low scores.

Canonical discriminant analysis distinguished E. obesus from E. gloriosus (Fig. 3.3). But, in contrast to the 13 factors extracted by the minimum eigenvalue criterion, only one significant canonical variable was extracted (Table 3.4). This first canonical variable contrasts oribatid mites with cyclopoid copepods. Oribatid mites graze on aquatic plants; the cyclopoidea are benthic forms such as Cyclops bicolor and Eucyclops agilis. Thus this canonical variable seems to measure an underlying microhabitat gradient. Enneacanthus obesus had a mean score of 1.34 on the first canonical variable; E. gloriosus had a mean score of -0.65. The two covariance matrices used in this analysis were highly heterogeneous (Chi-Square = 1963.7, 528 degrees of freedom, $p < 0.0005$).

Detrended correspondence analysis produced continuous resource axes with both prey (Table 3.5) and predator (Fig. 3.4) scores for each. Although as many axes as dietary categories can be extracted, DECORANA produces scores for the first four axes only. The first two axes, which are shown in Figure 3.4, usually convey most of the information. The units of the prey scores are 100 times 1 standard deviation, which is about one quarter of a prey species's turnover on the axis (Hill 1979). Those prey with high scores on axis 1, such as oribatid mites, hydracarina, Caraphractus, and Sida crystallina live on aquatic vegetation. (See Appendix 7.3 for habitats of prey.) Those prey with low scores on axis 1, such as Keratella, and Bosmina longirostris swim freely or are planktonic. Thus axis 1 contrasts two microhabitats, or feeding strategies. Because the prey and predator scores are reciprocal averages of one another, individual fishes with high scores on axis 1 are gleaning prey off the surfaces of aquatic plants (Fig. 3.4). Similarly, those fish with low scores on axis 1 are taking most prey in the water column.

The four statistical techniques differed in their ability to discriminate between the two species of Enneacanthus. Factor analysis produced the least discrimination between the two species (Fig. 3.5).

Although the mean factor scores differed on the first factor (Table 3.3), E. gloriosus's frequency ellipses fell entirely within E. obesus's ellipses. PCA was only slightly better at discriminating between E. obesus and E. gloriosus (Fig. 3.6). The two species had significantly different means on both the first and second principal components (Table 3.3). The frequency ellipses, however, showed high overlap; the center of E. gloriosus's distribution fell almost entirely within the center of E. obesus's distribution. DCA, in contrast to PCA and factor analysis, showed better separation of the frequency ellipses (Fig. 3.7). Canonical discriminant analysis also produced satisfactory discrimination between the two species (Fig. 3.3).

Table 3.6 shows how I used a hierarchical analysis of variance to estimate variance components of the DCA scores. Twenty one percent of E. gloriosus's variance on the first DCA axis was attributable to the between-phenotype component; 79 percent was attributable to the within-phenotype component.

Discussion

Of the four techniques, DCA and canonical discriminant analysis provided the best discrimination between the two species on the basis of diet. Factor analysis and PCA, in contrast, discriminated least. In addition, factor analysis and PCA failed in their primary purpose: data reduction. Thirteen common factors were extracted, but they still accounted for only 63 percent of the total variance. And the first three principal axes accounted for only 21.9 percent of the total variance. Moreover, none of the axes had a clear biological interpretation, and the factor analysis was highly sensitive to outliers.

If prey species are distributed along underlying resource gradients, an assumption made earlier, the factor analysis showed otherwise. With the exception of factor 8, the factor analysis uncovered discrete groups of prey rather than continuous sequences of prey. In contrast, DCA and, to some extent, canonical discriminant analysis, uncovered apparently continuous resource gradients. What is the correct interpretation? Are the niche dimensions measured by dietary data continuous or discrete?

The correct interpretation can be deduced by considering the correlation matrix of the 32 dietary variables. If prey exhibit gaussian distributions along resource axes, and if individual predators sample random points along the axis, then only those prey whose distribution's lie close to one another will show strong positive correlations. As the distance between two species lying next to one another on a gradient increases, the correlation between the two species rapidly approaches zero. This will be true even when the two distributions still overlap. Negative correlations cannot occur.

If, on the other hand, the prey are treated as discrete resources, or if they inhabit discrete patches, and if the predator moves from patch to patch, both positive and negative correlations are possible. Those prey species found together in the same patch should be positively correlated in the predator's diet; those prey species living in different patches should be negatively correlated in the predator's diet. A predator cannot feed in two patches simultaneously. If it spends more time in one patch, it must spend less time in the others. Hence the negative correlations.

The pattern I observed in the original correlation matrix supports the assumption that prey are distributed along underlying resource gradients. Of 496 off-diagonal correlations, 71 were positive, 3 were negative. The three marginally significant negative correlations ($r=-0.16$, -0.16, and -0.17 at $p < 0.05$) are probably attributable to type I error.

Canonical discriminant analysis produced a single axis discriminating between the two species. This axis, like the first DCA axis and factor 8, measured an underlying habitat gradient. Nevertheless, one should be cautious in applying discriminant analysis to dietary data. Canonical discriminant analysis begins with two or more covariance matrices. If the prey have gaussian distributions along a continuous gradient, simple correlations or covariances will fail to summarize the underlying structure. Moreover, as the sunfish data show, the covariance matrices may be highly heterogeneous, thus violating an important assumption of the technique.

DCA produced clearly interpretable resource axes. The first axis, which the two sunfishes partitioned, reflected an underlying microhabitat gradient. This gradient contrasted planktonic and free-swimming species with those species living on aquatic plants. The first canonical variable and factor 8 also appeared to measure this resource axis.

Although DCA has many advantages over other techniques, several uncertainties are involved in using it to estimate niche width. The DCA algorithm rescales each axis so that prey fall at roughly equal intervals. The rescaling presumably remedies a distortion inherent to reciprocal averaging and PCA (Hill and Gauch 1980, Gauch et al. 1981, Gauch 1983). But any distortion of the niche axes, either before or after rescaling, would severely limit DCA's usefulness in comparative studies of niche width. An additional problem is that estimates of niche width on DCA axes are study dependent. But even if these problems prove insurmountable, DCA will still be valuable in finding niche dimensions that can be studied directly.

In spite of these reservations, DCA performs better on dietary data than PCA, factor analysis, and canonical discriminant analysis. Dietary data satisfy the assumptions underlying DCA, but fail to satisfy the assumptions underlying the other techniques. Austin (1985), in reviewing various methods of indirect ordination, concluded that there was little justification for using techniques having an underlying linear model in preference to DCA. In addition to these substantial benefits, DCA may finally allow one to estimate components of niche width from dietary data. A final advantage, and one that has always been a problem in niche analyses, is that no assumptions regarding niche dimensionality need to be made. Even when diet is an unimportant niche dimension, it often reflects other dimensions that are important.

Table 3.1. Principal components analysis showing the factor loadings greater than 0.3.

Eigenvalues	2.81	2.32	1.87	1.59	1.52	1.44	1.32	1.22	1.19	1.13
Percent of Variance	8.8	7.3	5.8	5.0	4.7	4.5	4.1	3.8	3.7	3.5
Cumulative Percent of Variance	8.8	16.1	21.9	26.9	31.6	36.1	40.2	44.1	47.8	51.4
<u>Difflugia</u>										
<u>Arcella</u>			0.33							
Cyclopoidea					0.33					
Nauplius						0.44				
<u>Alona rectangula</u>										
<u>Chydorus sphaericus</u>			0.35							
<u>C. bicornutus</u>				0.44						
<u>Alonella excisa</u>	0.35									
<u>Sida crystallina</u>			0.46							
<u>Bosmina longirostris</u>										0.43
<u>Ilyocryptus spinifer</u>									-0.49	0.35
<u>Streblocerus serricaudatus</u>						0.46				0.31
Cladoceran spp.	0.31				0.34					
<u>Orthocladius</u> spp.										
<u>Polypedilum</u> spp.	0.30									
<u>Calopsectra</u> spp.				0.34						
<u>Pentaneura</u> spp.	0.34									
Tendipedid spp.										
Oribatei spp.	0.31									
Hydracarina spp.	0.35							-0.35		
<u>Alluadomyia</u> spp.								0.33	0.35	
<u>Caenis</u> spp.									-0.48	

Table 3.1. Continued.

Eigenvalues	2.81	2.32	1.87	1.59	1.52	1.44	1.32	1.22	1.19	1.13
Caraphractus cinctus										
Oxyethira spp.							0.33			
Insecta spp.								0.44		-0.32
Trichocerca sp.		0.42		0.31						
Keratella cochlearis		0.47								
Monostyla sp.										
Rotifer spp.							0.37			
Ferrissia parallela										
Filamentous algae							0.32			
Unicellular algae			0.33							

Table 3.2. Varimax rotation of principal components showing factor loadings greater than 0.3.

	Uncorrelated Factors									
	1	2	3	4	5	6	7	8	9	10
Eigenvalues	2.1	2.0	1.9	1.5	1.5	1.4	1.4	1.4	1.3	1.3
Difflugia							0.65			
Arcella				0.66						
Cyclopoidea								0.74		
Nauplius						0.81				
Alona rectangula			0.43		0.51					
Chydorus sphaericus				0.66						
C. bicornutus							0.70			
Alonella excisa	0.73									
Sida crystallina				0.34	0.71					
Bosmina longirostris								0.58		
Ilyocryptus spinifer										
Streblocerus serricaudatus									0.76	
Cladoceran spp.	0.69									
Orthocladius spp.										
Polypedilum spp.			0.46							
Calopsectra spp.										0.77
Pentaneura spp.		0.33	0.44							
Tendipedid spp.			0.62							
Oribatei spp.	0.73									
Hydracarina spp.			0.70							
Alluadomyia spp.									0.66	
Caenis spp.								-0.44		

Table 3.2. <u>Continued</u>.

	Uncorrelated Factors									
	1	2	3	4	5	6	7	8	9	10
Eigenvalues	2.1	2.0	1.9	1.5	1.5	1.4	1.4	1.4	1.3	1.3
Caraphractus cinctus			0.38						0.38	
Oxyethira sp.							-0.30			
Insecta spp.	0.41				0.41					
Trichocerca sp.		0.86								
Keratella cochlearis		0.92								
Monostyla sp.						0.63				
Rotifer spp.					0.61	0.45				
Ferrissia parallela										0.46
Filamentous algae										
Unicellular algae				0.58						

Table 3.3 Mean scores for *E. obesus* and *E. gloriosus* on derived PCA and factor analysis axes.

	PCA			Factor Analysis		
Axis	*E. gloriosus*	*E. obesus*		*E. gloriosus*	*E. obesus*	
1	-0.43	0.89	***	-0.25	0.52	***
2	0.16	-0.34	*	-0.07	0.14	
3	0.25	-0.52	***	-0.13	0.27	*
4	0.02	-0.05		0.03	-0.07	
5	0.03	-0.06		0.08	-0.16	*
6	0.16	-0.34	**	0.03	-0.06	
7	-0.12	0.34	**	0.19	-0.39	***
8	0.01	-0.03		0.20	-0.41	***
9	-0.03	0.06		-0.04	0.09	
10	0.13	-0.26	**	-0.07	0.15	
11	-0.02	0.04		0.08	-0.16	
12	0.12	-0.26	**	-0.03	0.05	
13	0.01	-0.03		-0.02	0.05	

* $p < 0.05$
** $p < 0.005$
*** $p < 0.0005$

Table 3.4 Standardized canonical coefficients.

Prey	Canonical Variable
Difflugia	-0.151
Arcella	0.011
Cyclopoidea	-0.447
Nauplius	-0.128
Alona rectangula	-0.310
Chydorus sphaericus	-0.131
Chydorus bicornutus	-0.166
Alonella excisa	-0.097
Sida crystallina	-0.033
Bosmina longirostris	-0.034
Ilyocryptus spinifera	-0.188
Streblocerus serricaudata	-0.145
Cladocera spp	0.195
Orthocladius spp	-0.057
Polypedilum spp	0.225
Calopsectra spp	0.041
Pentaneura spp	-0.237
Tendipedid spp	0.303
Orbitei spp	0.570
Hydracarina spp	0.328
Alluaduomyia spp	0.210
Caenis sp	0.244
Caraphractus cinctus	0.231
Oxyethira sp	0.184
Insecta spp	0.157
Tricocerca sp	0.036
Keratella cochlearis	0.175
Monostyla sp	0.046
Rotifera spp	-0.049
Ferrissia parallela	0.181
Filamentous algae	-0.036
Unicellular algae	-0.105

Canonical Correlation = 0.685
Canonical R = 0.469
Eigenvalue = 0.883
Likelihood Ratio = 0.531 ($p < 0.0001$)

Table 3.5 DCA prey scores.

Prey	Axis 1	2	3	4
Difflugia	-161	46	28	78
Arcella	217	149	41	40
Cyclopoidea	82	152	96	126
Nauplius	163	159	94	183
Alona rectangula	41	127	94	127
Chydorus sphaericus	201	55	-87	241
C. bicornutus	208	23	-9	162
Alonella excisa	214	58	-32	215
Sida crystallina	215	176	49	-74
Bosmina longirostris	-116	236	67	68
Ilyocryptus spinifer	-8	128	123	272
Streblocerus serricaudatus	147	220	107	193
Cladocera spp.	32	-60	-25	15
Orthocladius spp.	178	190	233	139
Polypedilum spp.	227	114	94	147
Calopsectra spp.	204	113	180	174
Pentaneura spp.	132	38	188	330
Tendipedid spp.	194	97	221	-27
Oribatei spp.	351	16	88	122
Hydracarina spp.	255	274	-33	116
Alluadomyia spp.	233	85	176	147
Caenis spp.	46	47	426	198
Caraphractus cinctus	233	84	157	184
Oxyethira sp.	144	158	169	126
Insecta spp.	225	60	115	117
Trichocerca spp.	110	244	133	-149
Keratella cochlearis	-151	440	186	46
Monostyla sp.	174	270	101	-132
Rotifera spp.	-132	436	84	94
Ferrissia parallela	224	8	289	186
Filamentous algae	-3	75	214	266
Unicellular algae	201	193	25	251
Eigenvalue	0.186	0.155	0.121	0.095

Table 3.6 Nested analysis of variance for within- and between-phenotype components of niche width, *E. gloriosus* (12 to 13 mm standard length).

Source	DF	Sum of Squares	Mean Square	Variance Component	Percent
Total	201	1.37×10^6	6.79×10^3	6.8×10^3	100.00
Among phenotypes	100	0.82×10^6	8.25×10^3	1.4×10^3	21.29
Within phenotypes	101	0.54×10^6	5.35×10^3	5.3×10^3	78.71

Figure 3.1 PCA scores on principal components 1 and 2.

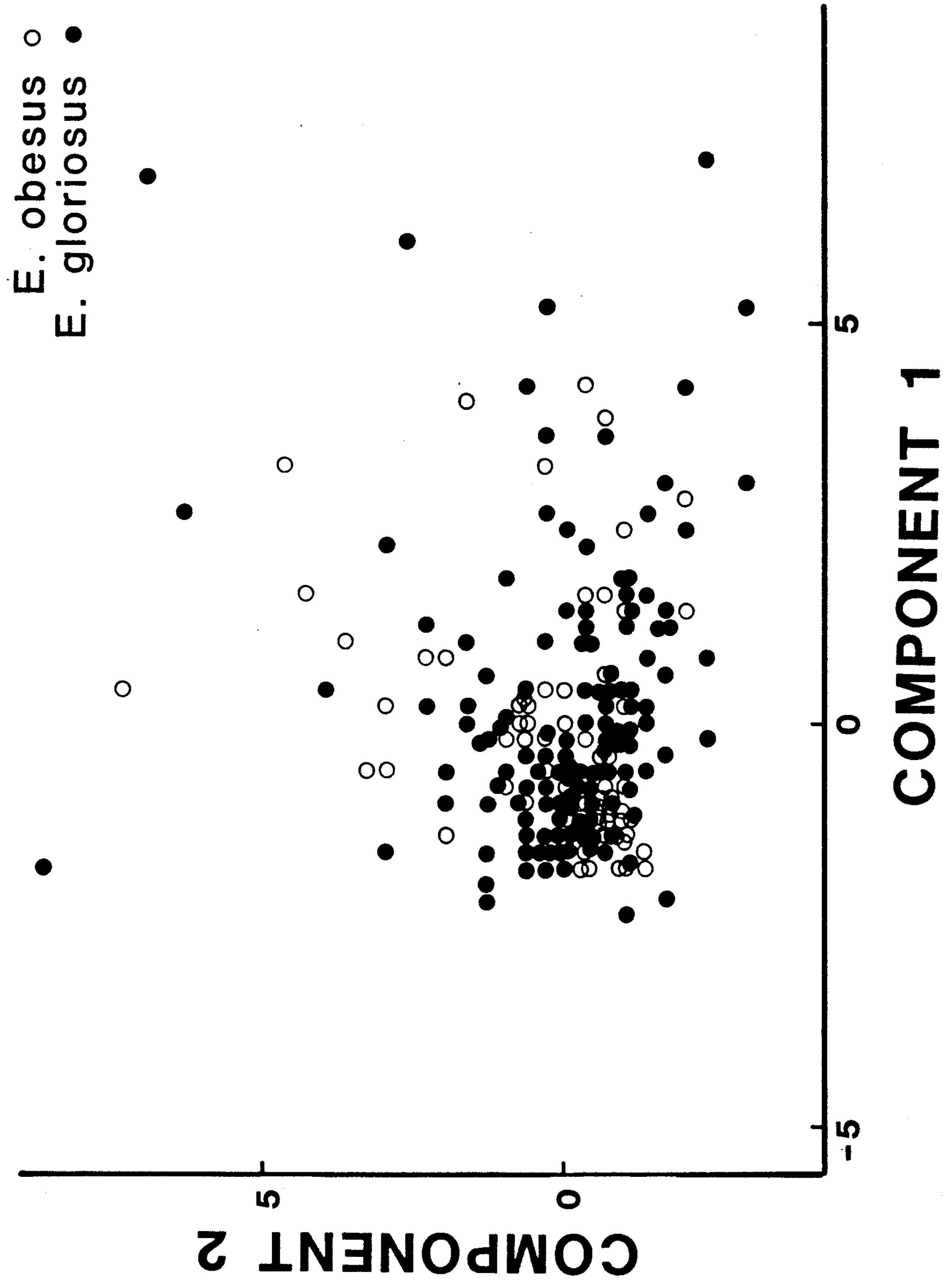

E. obesus ○
E. gloriosus ●
COMPONENT 1
COMPONENT 2
-5
0
5
0
5

Figure 3.2 Factor analysis scores on factors 1 and 2.

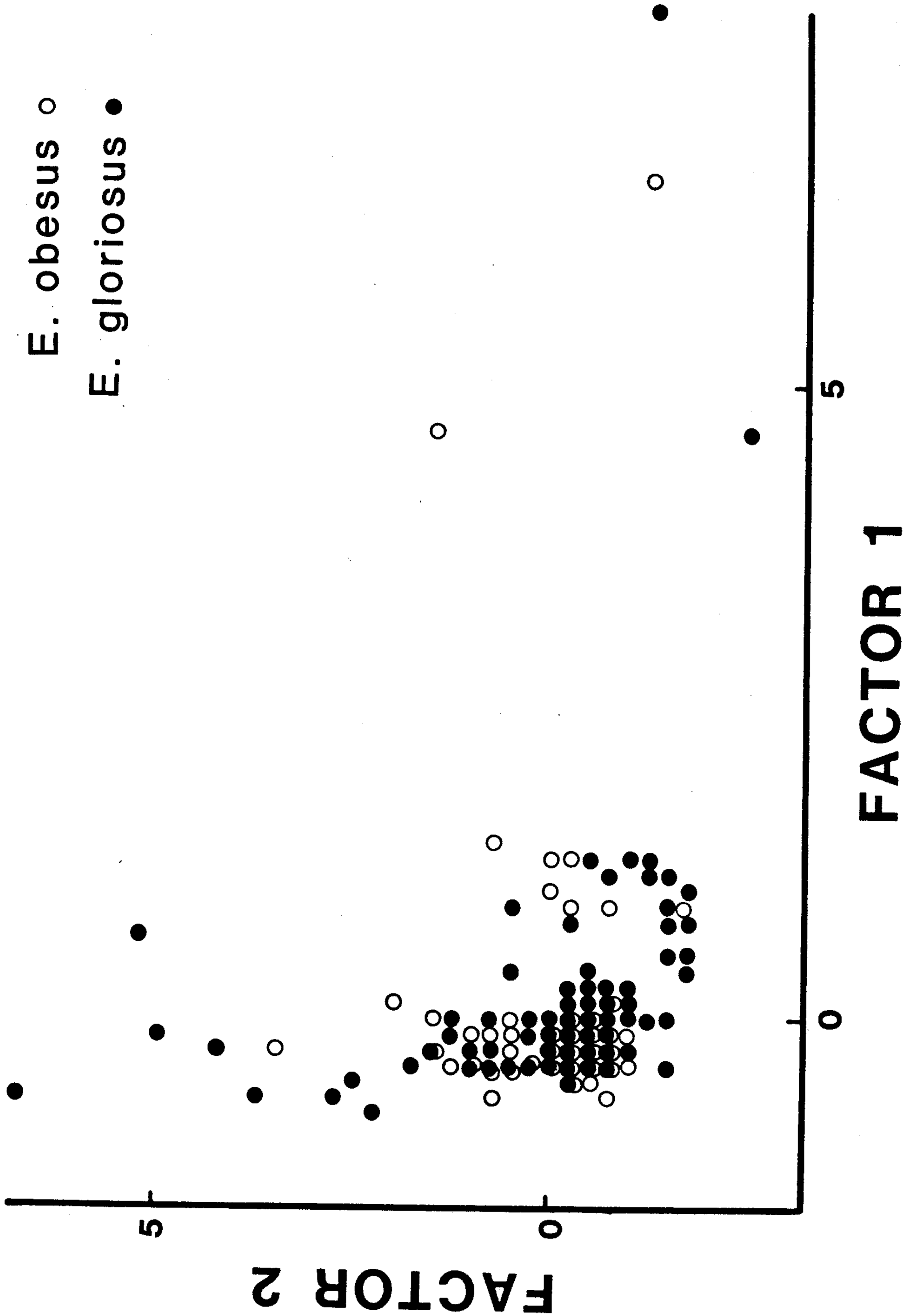

E. obesus
E. gloriosus
FACTOR 1
FACTOR 2
0
5
0
5

Figure 3.3 Frequency polygons of canonical scores.

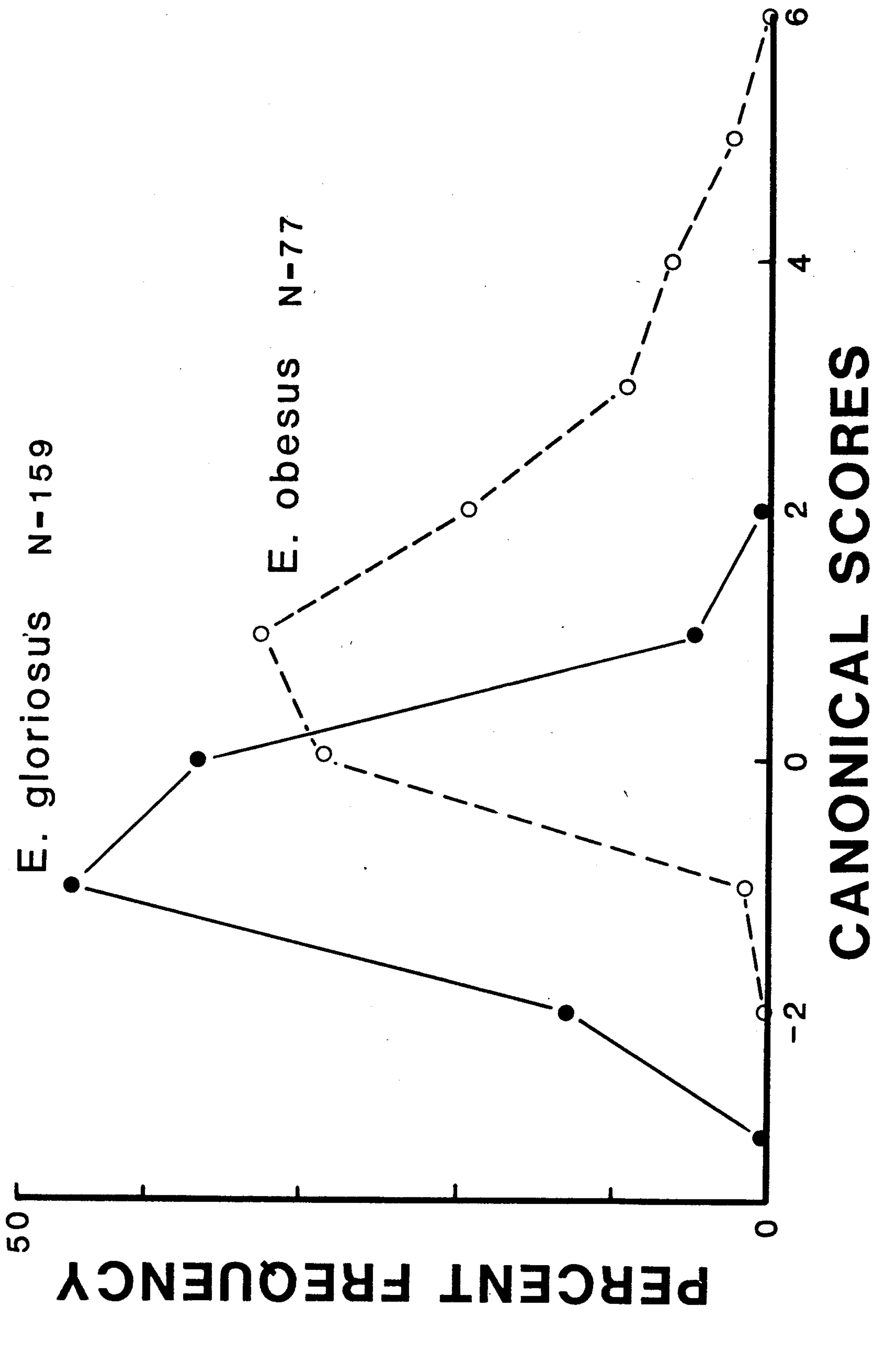

E. gloriosus N-159
E. obesus N-77
PERCENT FREQUENCY
50
0
CANONICAL SCORES
-2
0
2
4
6

Figure 3.4 DCA sample scores on axes 1 and 2.

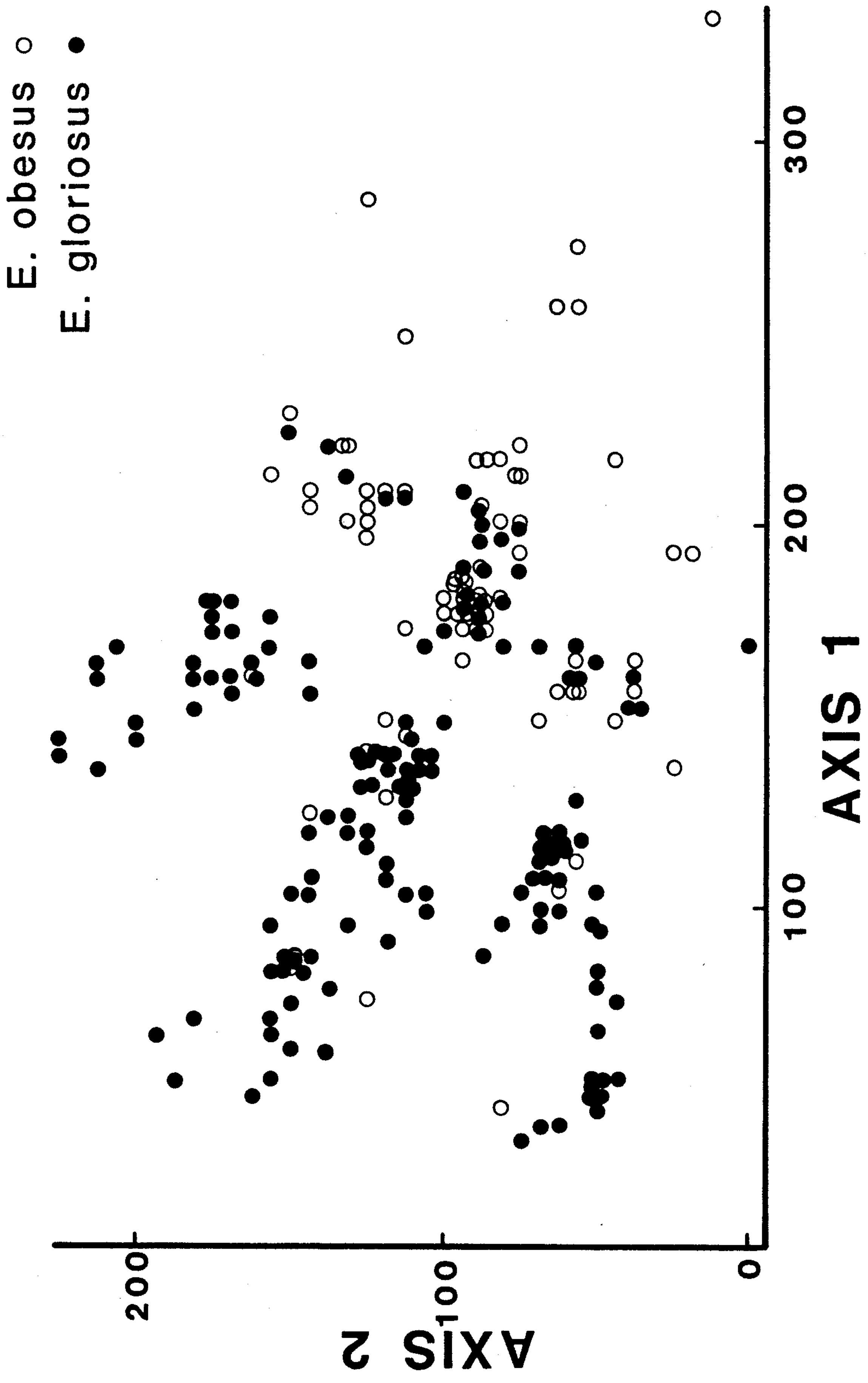
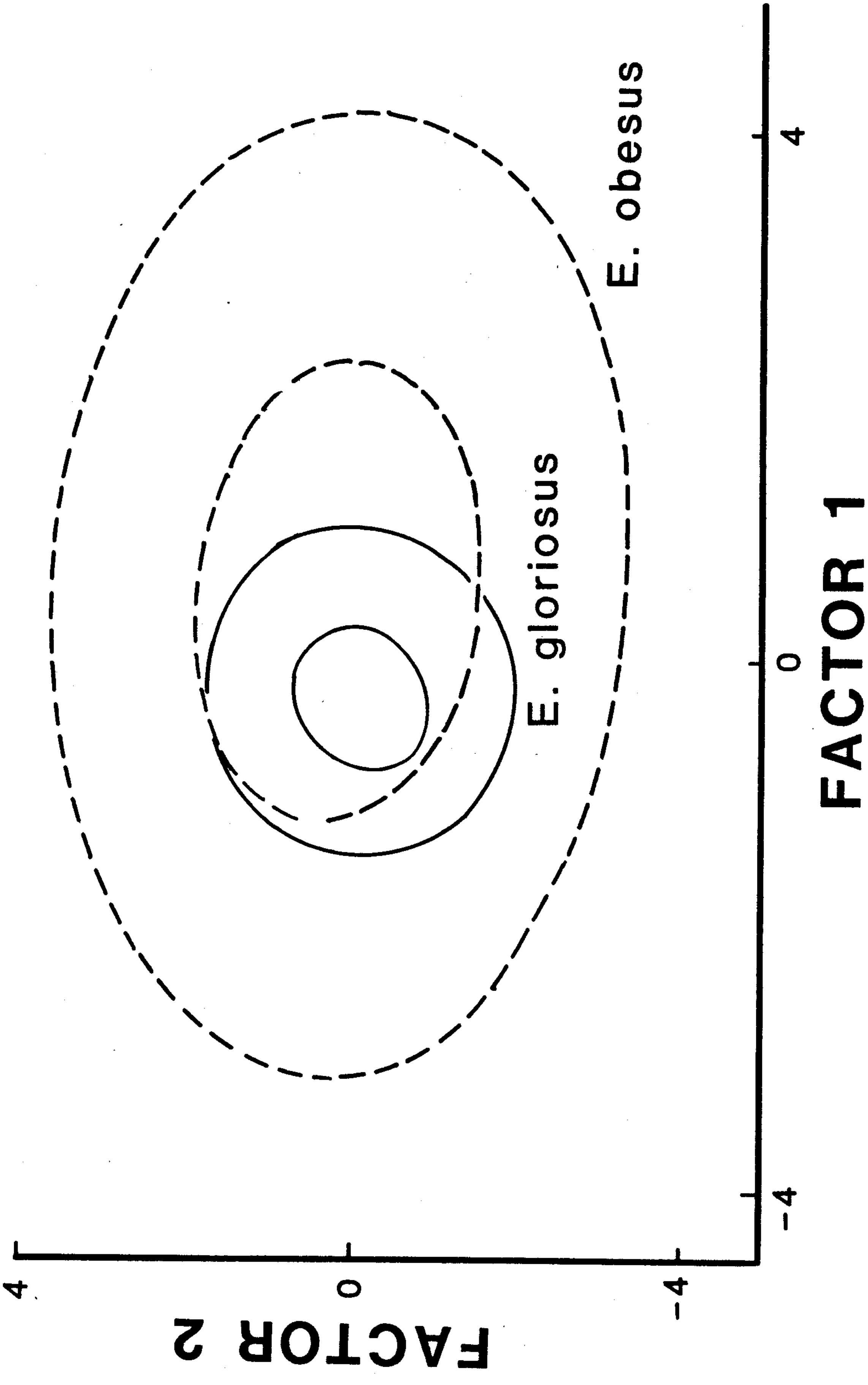

E. obesus
E. gloriosus
AXIS 1
AXIS 2
0
100
200
300
0
100
200

Figure 3.5 Fifty and 95 percent frequency ellipses for factor scores.



FACTOR 1
FACTOR 2
-4
0
4
E. obesus
E. gloriosus

Figure 3.6 Fifty and 95 percent frequency ellipses for PCA scores.

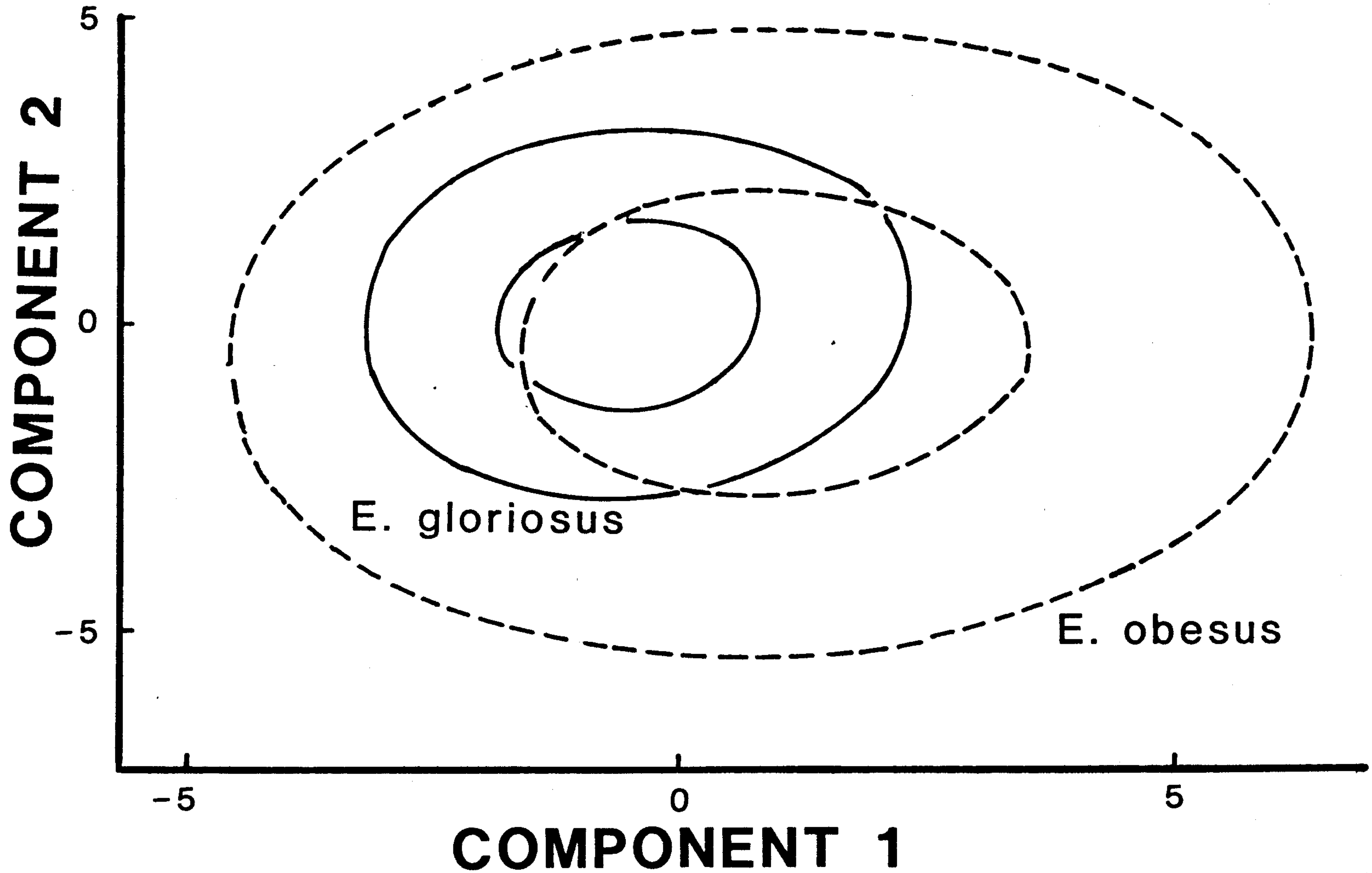
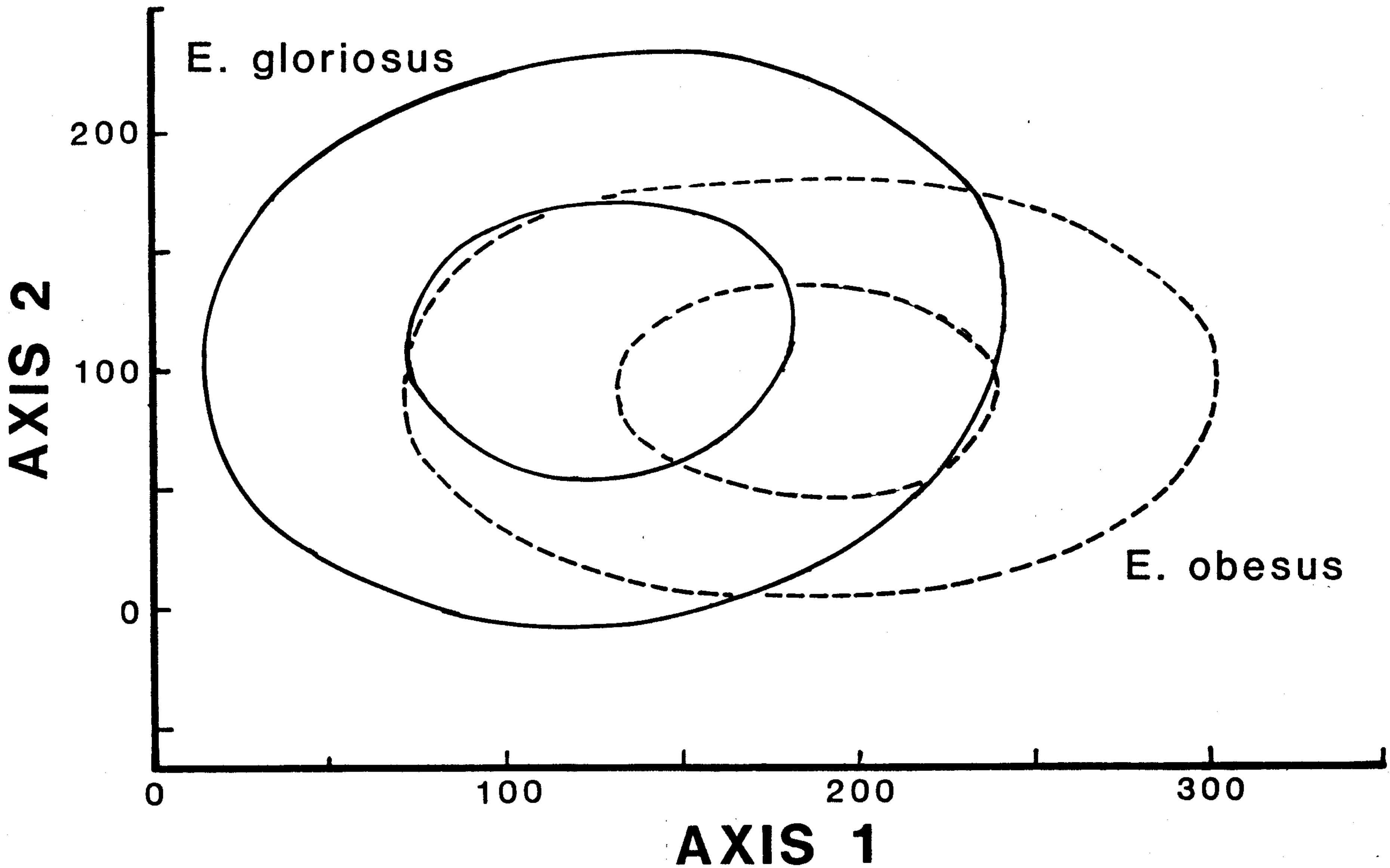

5
0
-5
COMPONENT 2
-5
0
5
COMPONENT 1
E. gloriosus
E. obesus

Figure 3.7 Fifty and 95 percent frequency ellipses for DCA scores.


E. gloriosus
E. obesus
200
100
0
AXIS 2
0
100
200
300
AXIS 1

CHAPTER IV

ONTOGENETIC NICHE SHIFTS

Introduction

Many animals undergo niche shifts during their lives. These shifts are usually related to body size or age. For example, differences in diet between juvenile and adult birds are associated with learning to forage efficiently, an effect related to age (Recher and Recher 1969, Orians 1969, Burger and Gochfeld 1983, Gochfeld and Burger 1984). In the lower vertebrates, many invertebrates, and in most plants, size drives ontogenetic shifts in diet or habitat use (Werner and Gilliam 1984, Peters 1983). Ontogenetic niche shifts can be gradual or precipitous, great or small. Amphibians and most aquatic insects show dramatic shifts associated with metamorphosis; larvae are aquatic, and adults are terrestrial or semiaquatic (Wilbur 1980). Most species of animals, however, change habitat or behavior more gradually. In fishes, for example, gradual ontogenetic shifts by individual species are well documented. Nevertheless, comparative studies (see Keast 1980 and Govoni et al. 1983) on fishes are scarce, and few have looked at the ontogeny of interactions among related species.

In this chapter, I look at ontogenetic niche shifts in two congeneric sunfishes, *Enneacanthus gloriosus* and *E. obesus*. By MacNally's (1983) criteria (i.e. taxonomic relationship, broad sympatry, and synchronous occurrence), they comprise a guild. Both species inhabit the littoral zone of quiet waters. They overlap broadly in breeding period and habitat, have similar daily periodicity, and are morphologically alike even as adults. I show that *E. obesus* and *E. gloriosus* partition microhabitat, and that larvae, juveniles, and adults of each species partition food by size.

Materials and Methods

Nesting Sites

I surveyed sunfish nests in Collier's Mill Pond on 19 June 1980, when both *E. obesus* and *E. gloriosus* were at their spawning peak. Neither *E. gloriosus* nor *E. obesus* constructed nests that I could observe underwater. Both species were nesting in extremely shallow and densely vegetated water. It was impossible to observe spawning fish from either above or below. Brushing the vegetation away, even delicately, invariably ruined the nest. Thus, I resorted to quantifying nest location by seining.

I located breeding males with short hauls (approximately a meter square) with a seine having 5 mm mesh. Breeding males were easily identified by their brilliant coloration. As evidence that these males were probably guarding nests or courting females, I often collected breeding males and gravid females in the same short seine hauls. I sampled nesting males in the upper pond, where both species were abundant.

Identifying Larval *Enneacanthus*

Poor keys to larval fishes are the greatest obstacle to studying resource partitioning in fishes. Many closely related species cannot be identified with certainty. By using electrophoretic isozyme markers, however, this difficulty can be surmounted (Morgan 1975).

Adult *E. obesus* and *E. gloriosus* from Collier's Mills Pond were examined electrophoretically for 32 enzymes. Eye, liver, caudal muscle, heart, and brain tissues were dissected from individual fish. Tissues were homogenized by hand in 1.5 volumes of cold (4 C), buffered (pH 7.0) grinding solution containing 0.001 M Tris, 0.001 M EDTA, and 0.005 mM NADP. Homogenized samples were immediately frozen at -80 C. After thawing, and prior to electrophoresis, the extracts were centrifuged at 5,000 x g for 5 minutes. The supernatant was electrophoresed at 23.1 volts per cm for 4 hours on horizontal, 12.5% (weight by volume) starch gels. Initially, Electrostarch Lot No. 307 (Electrostarch Inc., Madison, Wisconsin) was used, and later, when this lot was exhausted, a comparable 1:1 mixture of Electrostarch Lot No. 392 and Sigma Starch

(Sigma Co., St. Louis, Missouri) was used. Enzymatic staining procedures were Shaw and Prasad's (1970).

Buffering systems in the initial screening included:

1. 0.189 M Tris and 0.083 M Citrate, pH 6.0. The buffer was diluted 1:10 for making the gel, and is undiluted for the electrodes.
2. 0.188 M Tris and 0.065 M Citrate, pH 6.8. The buffer was diluted 1:19 for making the gel, and was undiluted for the electrodes (Shaw and Prasad 1970).
3. 0.04 M Citrate was adjusted to pH 6.0 with N-(3-Aminopropyl)-morpholine. The buffer is diluted 1:19 for making the gel, and is undiluted for the electrodes (Clayton and Tretiak 1972).
4. 0.04 M Citrate, 0.2 M EDTA, and 0.65 M Borate, pH 8.0. The buffer was diluted 1:10 for making the gel, and was undiluted for the electrodes (Shaw and Prasad 1970).

The electrophoretic techniques required several modifications to accomodate small larvae. A filter-paper wick, which I used in various sizes, worked better than preformed slots in the starch. I used 1.5 x 6.5 mm wicks for the smallest larvae, and 3.5 x 6.5 mm wicks for the largest larvae. To ensure a concentrated enzyme, less than a half drop of grinding solution was required for the smallest larvae. In addition, I often modified the staining recipes to increase their sensitivity.

Twenty seven presumptive gene loci were indentified. Of these, 6 loci expressed fixed allelic differences (diagnostic markers) between the two species. An allele was considered fixed if its frequency in a population was 0.95 or greater. The diagnostic loci were malate dehydrogenase-2 (Mdh-2), peptidase-2 (Pep-2), phosphoglucose isomerase-1 (Pgi-1), phosphoglucose isomerase-2 (Pgi-2), glyceraldehyde-3-phosphate dehydrogenase-2 (Gap-1), and alpha-glycerophosphate dehydrogenase-2 (Gpd-2). All 6 loci were expressed predominantly in muscle, and all but Pgi-2 migrated anodally. Leucylglycylglycine was a substrate for detecting peptidase. Best resolution was achieved in the following buffering systems: aminopropylmorpholine pH 6.0 (Clayton and Tretiak 1972) for Mdh, Pgi, and Gap, tris-versene-borate pH 8.0 (Shaw and Prasad 1970) for Pep, and tris-citrate pH 6.0 (Shaw and Prasad 1970) for Gpd. (See Appendix 7.1 for a listing of all enzymes and buffers, and Table 4.1 for the proportional electrophoretic mobilities of the diagnostic alleles.)

Additional unscored bands were from Pep-1, Mdh-1, and Mdh-3 (in muscle tissue), Gpd-1 (in liver), and Gap-2 (in eye); all these additional loci but Mdh-3 were fixed for the same alleles in both species. Mdh-3, presumably mitochondrial Mdh, was difficult to score. All other enzymes and loci were either monomorphic or difficult to score.

When more than one locus encoded an enzyme, the loci were numbered by decreasing anodal mobility. Allozymes were named by their proportional electrophoretic mobilities, relative to the common allele at a locus in populations of pure *E. gloriosus*.

Because they unambigously differentiated the two species, and because they could be identified from single small fish on a single gel, I chose Mdh-2, Pgi-1, and Pgi-2 as diagnostic markers for larval *E. gloriosus* and *E. obesus*. Graham and Felley (1985) showed that three populations of *E. obesus* in New Jersey were fixed for $Mdh\text{-}2^{28}$, $Pgi\text{-}1^{112}$, and $Pgi\text{-}2^{87}$. In three populations of pure *E. gloriosus* in New Jersey, the alternate alleles were fixed. Appendix 7.2 presents the electrophoretic phenotypes for the 3 markers.

In Success Lake, occasional fish were heterozygous for one or more of the diagnostic markers. Indeed three fish were heterozygous at all three loci, and may have been F_1 hybrids. Because the numbers of these fish of potentially mixed ancestry were small, all heterozygotes or mixed homozygotes were omitted from consideration in this study.

Dietary Analysis

I collected fish for dietary analysis from Success Lake, Ocean Co., New Jersey on 4 dates in 1979 and 1980. My first collection in each year was timed to the appearance of larval *Enneacanthus*, and a second collection followed a month later in 1979 and two weeks later in 1980. On each date, I sampled continuously throughout the day, and in various habitats. Fish were immediately placed on ice, which prevents regurgitation (Doxtater 1963). They were frozen at -60 C on returning to the laboratory. After thawing, I measured each fish's standard length, removed the stomach (or the entire gut if the pyloric caecae were undeveloped), and mounted the stomach contents in Kaizer's medium, and saved the bodies for electrophoresis. The fish species were identified electrophoretically by using the three diagnostic markers. Each fish's diet was quantified by counting the items in each food category. Food items were identified to the lowest possible taxon using Roback (1957), Ward and Whipple (1959), and Pennak (1978).

Dietary Periodicity

To study daily feeding periodicity, I collected young-of-the-year *Enneacanthus* on 13 August 1980 from Success Lake during six periods (0630, 0930, 1230, 1530, 1830, and 2000 hours EST, daylight savings time). These collections began at sunrise, and ended after sunset. I collected fish with a long-handled dip-net along a homogeneous section of shoreline. The habitats sampled in this study included submerged *Sphagnum*, emergent *Eleocharis*, floating-leaved *Nymphaea odorata*, and open water. During any one sampling period I subsampled widely spaced, previously undisturbed, sites, so as to randomize my sampling with respect to location. Fish were immediately placed on ice. At day's end all specimens were frozen at -60 C.

After thawing the fish, I measured their standard lengths, removed their stomach contents, and disrupted their tissues in grinding solution prior to electrophoretic analysis. The stomach contents were mounted in Kaizer's medium on a glass slide and examined with a binocular scope. Food items were identified to the lowest feasible taxon (usually genus). Each food item was classified by its digestive state:

1. Item undigested. Recently consumed.
2. Slight digestion. Some antennae or appendages missing.
3. Advanced digestion. Tissue a formless mass within the exoskeleton. All, or most, appendages missing.
4. Digested. Only the exoskeleton remaining.

Food items that lack an exoskeleton and are easily digested (annelids) and those extremely resistant to digestion (nematodes, algae, etc) were left unclassified.

Daily changes in stomach and intestinal fullness were studied. Stomach fullness was estimated visually. Stomachs were given scores ranging from 0, for empty stomachs, to 100, for distended stomachs. The scores were assigned in increments of 10 (i. e. 0, 10, 20, etc.), but those stomachs with only a trace of food were scored as 1.

I estimated intestinal fullness by measuring the length of intestine containing food.

To compare the effects of time and species identity on stomach and intestinal fullness, I used an unbalanced 6 Times by 2 Species Factorial Design. Percentage stomach fullness, which has an underlying binomial distribution, required an arcsine transformation (x' = arcsine $x^{-1/2}$) to produce an approximately normal distribution (Zar 1974). The analysis was performed using SAS's General Linear Models procedure (SAS Institute Inc. 1985).

Since both stomach and intestinal fullness were correlated with standard length, I analysed the data by analysis of covariance, with standard length as the covariate. Individual fish are assumed to be randomly allocated to a time category; the same assumption is invalid with respect to species. Using analysis of covariance in non-experimental research risks specification error, which occurs when intact groups (i.e. species) are equated on a given variable (i.e. standard length) (Pedhazur 1982). The risk is that the two species may also differ on some other variables, say intestinal length, intestinal width, or stomach size; by equating species on standard length, their differences on intestinal length, intestinal width, and stomach size may be accentuated. Although the two species may differ, all that can be said with confidence is that the species differ in some aspect of diet or dietary morphology.

Statistical Analysis of Dietary Data

I used detrended correspondence analysis (DCA) to study the resource gradients underlying the foraging behavior of _E_. _obesus_ and _E_. _gloriosus_. In this application, each fish's stomach contents constitutes a sample containing many food items. If a foraging animal is selective in its 'sampling', ordinated food items represent a resource gradient, integrating the prey's spatial distribution and the predator's behavior. DCA was performed on the counts of each food within each stomach. The algorithm employed, DECORANA, was written by Hill (1979). Since rare food items may distort the analysis, I used DECORANA's downweighting option. Sample scores obtained with DCA were subjected to further statistical analysis using SAS.

Results

Nesting Sites

Adult _E_. _obesus_ and _E_. _gloriosus_ used similar habitats during their spawning period. During May and June, adults were in shallow, densely vegetated water close to shore. Reproductive male _E_. _obesus_ and _E_. _gloriosus_ in Collier's Mills Pond were captured at the same average depth ($t=1.10$, $df=28$, $.50 > p > .20$, see Table 4.2). Breeding male _E_. _obesus_ and _E_. _gloriosus_ were independently associated among seine hauls ($X^2=0.685$, Yates correction for continuity, $df = 1$, $0.25 < p < 0.50$, Table 4.3).

Sizes of Young-of-the-Year

In Success Lake, young-of-the-year E. obesus were longer, on average, than young-of-the-year E. gloriosus in 1979 and 1980 (Table 4.4). Species, month, and year all had significant effects on standard length (Table 4.5). In addition, species and year had an interactive effect on mean standard length; E. obesus were, on the average, 2 mm longer than E. gloriosus in 1979 and 4.5 mm longer in 1980.

Dietary Periodicity

Enneacanthus obesus and E. gloriosus in Success Lake had similar daily changes in stomach fullness (Fig. 4.1). Both time and species had significant effects on stomach fullness (Table 4.6). Stomachs were nearly empty early in the day, filled rapidly between 0630 and 0930 hours, and continued to fill from 1830 hours until darkness. Although E. gloriosus had a greater average fullness, there was no interactaction between time and species.

All sources of variation (i.e. species, time, and the species by time interaction) had significant effects on intestinal fullness (Table 4.6). The highly significant interaction between time and species suggests that E. obesus and E. gloriosus processed their food differently. Enneacanthus obesus accumulated more food in its intestine late in the day (Fig. 4.2).

Recently eaten food items (digestive states 1 and 2), showed that the two species differed in feeding periodicity. Enneacanthus obesus fed actively in the early morning (0930 hrs), was relatively inactive during midday (1230), and fed most actively just before sunset (1830 hrs) (Fig. 4.3). In contrast, E. gloriosus showed no midday decline in feeding.

Diet

The diets of larval E. gloriosus in July of 1979 and 1980 were dominated by Bosmina longirostris, a planktonic cladoceran, and cyclopoid copepods. (See Appendix 7.3 for taxonomy and habitat of all prey. Appendices 7.4 and 7.6 show mean numbers of prey per stomach and frequencies of occurrence for each kind of food.) Other important prey, based on number and percent occurrence, were cyclopoid copepods and cladocerans (Chydorus sphaericus, Eurycercus lamellatus, Diaphanosoma brachyurum, and Sida crystallina).

Larval E. gloriosus in August 1979 (Appendix 7.5) and 1980 (Appendices 7.7 and 7.9) fed mostly on cyclopoid copepods (Cyclops bicolor and Eucyclops agilis). Other common prey in August 1979 were cladocerans (Diaphanosoma brachyurum and Bosmina longirostris), rotifers (Keratella cochlearis), aquatic mites (hydracarina), and chironomid larvae (Pentaneura spp). Common items in the stomachs of fish sampled in 1980 were oligochaetes, cladocerans (Sida crystallina, Ilyocryptus spinifer, Alona guttata, and Chydorus shaericus), chironomid larvae (Pentaneura spp., Cricotopus slossonae, and Calopsecra sp. 1), filamentous algae, and sand grains.

Juvenile and adult *E. gloriosus* (Appendices 7.8 and 7.10) fed mostly on cyclopoid copepods, but these were less numerous in the stomachs of larger individuals than in the larvae. Ephemeropterans (*Caenis* sp.), chironomids (*Pentaneura* spp. and *Calopsectra* sp. 1), corixids, oribatid mites, trichoptera (*Oecetis* spp.), collembolans (*Podura aquatica*), aquatic hymenoptera (*Caraphractus cinctus*), and annelids were also common prey of juveniles and adults.

In contrast to the diet of *E. gloriosus* sampled in July of 1979 and 1980, *Bosmina longirostris* was an unimportant part of the diet of larval *E. obesus* (Appendices 7.4 and 7.6). *Sida crystallina*, a cladoceran, was the most important prey of larval *E. obesus*. Also important in the diet of larval *E. obesus* were cyclopoid copepods, and two cladocerans: *Acropreus harpae* and *Pleuroxus hastatus*.

As in larval *E. gloriosus*, the most important element in the diet of larval *E. obesus* during August of 1979 and 1980 was cyclopoid copepods (Appendix 7.5, 7.7, 7.9). There were, however, considerable differences between the secondary prey eaten by *E. obesus* and those eaten by *E. gloriosus*. Oribatid mites, such as *Hydrozetes* and *Trimalaconothrus*, and various hydracarina and halacaridae were important in the diet of *E. obesus*, but were rare in the diet of *E. gloriosus*. Several cladocerans, including *Scapholebris mucronata*, *Alonella excisa*, *Acroperus harpae*, and *Disparalona rostrata* were common in the diet of

E. obesus, but not in the diet of E. gloriosus. Additional prey that distinguished E. obesus from E. gloriosus were Polypedilum spp. (chironomidae) and Alluadomyia (heleidae).

As in E. gloriosus, juvenile and adult E. obesus (Appendices 7.8 and 7.10) included cyclopoid copepods, Calopsectra sp. 1, Caenis sp., and annelids as major components of their diet. The main distinguishing element in the diet of juvenile and adult E. obesus was the abundance of oribatid mites (mostly Hydrozetes) and hydracarina; both of these groups were rarely in the diet of E. gloriosus. In addition to the aquatic mites, E. obesus differed by occasionally taking prey from the surface. Several individuals had many adult chironomids in their stomachs, as well as the water striders Mesovelia and Microvelia. In addition, Ilyocryptus spinifer (cladocera), Ferrissia parallela (gastropoda), Oxyethira (trichoptera), and bdelloid rotifers were more frequent in the diet of juvenile and adult E. obesus.

Dietary Analysis

July 2, 1979

The first DCA axis contrasted Bosmina longirostris (a small open-water cladoceran), with unicellular algae, Pleuroxus hastatus (a littoral cladoceran), and Sida crystallina (a littoral cladoceran that attaches to aquatic plants) (Table 4.9). Enneacanthus gloriosus had significantly higher scores on this axis (Fig. 4.4). Even the smallest (5.45 to 10.0 mm) *E. obesus* and *E. gloriosus* were distinct.

August 16, 1979

Both *E. obesus* and *E. gloriosus* showed ontogenetic shifts on axis 1. This resource axis distinguished stomachs containing *Diaphanosoma brachyurum* (a benthic cladoceran) from stomachs containing *Polypedilum* sp 2 (Tendipedae), hydracarina (Arachnida), and copepod nauplii (Table 4.10). Over the size range of 10 to 17 mm, both species showed increasing scores with increasing size (Fig. 4.5).

August 13, 1980

The first axis distinguished *E. obesus* from *E. gloriosus*, and appears to represent a habitat gradient. Prey with high scores on axis 1 (Table 4.11) live on aquatic vegetation: Oribatei and Hydracarina (Arachnida), *Alluadomyia* (Diptera), *Caraphractus* (Hemiptera), *Ferrissia* (Gastropoda), and *Sida crystallina* (Cladocera). Those prey with low scores are open water forms: *Keratella* (Rotifera), and *Bosmina longirostris* (cladocera). *Difflugia* (Protozoa), which had the lowest score on this axis, is cosmopolitan in its habitat; it is found in the plankton, as well as the benthos and periphyton. There were no ontogenetic changes by either species on this axis. *Enneacanthus obesus* had the higher scores on DCA axis 1

(Fig. 4.6). Sample scores on DCA axes 2 through 4 shifted with increasing size, but there were no differences between the species on these axes.

August 27, 1980

Size had a significant effect on DCA scores on the first axis: DCA scores increased with increasing size of the predator. High scores on the first axis were associated with large aquatic insects, such as adult corixids, *Caraphractus* (a wasp), and dragonfly nymphs, and the large seeds of *Nymphaea* (Table 4.12). There were no significant differences in resource use by either species on this axis, but larger individuals used a greater variety of resources (i.e. they used both large and small prey) (Fig. 4.7)).

Dietary Diversity

Figure 4.8 presents dietary diversity for all fish collected in Success Lake during 1979 and 1980. For this analysis, individuals were placed into nine size classes: 1) less than 9 mm, 2) 9-11 mm, 3) 11-13 mm, 4) 13-15 mm, 5) 15-17 mm, 6) 17-19 mm, 7) 19-21 mm, 8) 21-29 mm, and 9) greater than 29 mm. Dietary diversity increased with size to a maximum in 17 to 21 mm fish, and then declined slightly in larger fish. There were no significant differences in dietary diversity between *E. obesus* and *E. gloriosus*.

Discussion

Enneacanthus obesus and *E. gloriosus* partition microhabitat and time of daily activity rather than nesting habitat. Different sized individuals within each species also partition resources: small fish take small foods; large fish take both large and small foods. Thus three important niche dimensions partitioned by *Enneacanthus* are microhabitat, food size, and time of daily activity.

Although spawning *E. obesus* and *E. gloriosus* showed high temporal overlap, *E. obesus* probably began spawning earlier than *E. gloriosus* in Success Lake. This accounted for the 2 to 4.5 mm difference in mean size between the two species. Nevertheless, the niche differences I observed between *E. obesus* and *E. gloriosus* were not attributable to their slight differences in average size, but were wholly attributable to differences in microhabitat.

The very smallest *E. gloriosus* (less than 10 mm SL) fed predominantly on *Bosmina longirostris*, which is a free-swimming cladoceran (Fairchild 1981). But they also included prey associated with vegetation or benthos, such as *Chydorus sphaericus*, *Eurycercus lamellatus*, and *Sida crystallina* (Whiteside et al. 1978, Fairchild 1981). *Sida crystallina*, which is an attached filter feeder (Hutchinson 1967), is an especially good indicator of occasional gleaning on the part of *E. gloriosus*.

In larvae larger than 10 mm SL, cyclopoid copepods, such as *Cyclops bicolor* and *Eucyclops agilis*, became the dominant prey. Most cyclopoid copepods, including

Eucyclops agilis, are littoral benthic species (Pennak 1978). In addition, Diaphanosoma brachyurum, a benthic cladoceran (Hutchinson 1967), is common in the diet of larger larval E. gloriosus. Pentaneura spp., a predatory chironomid, has species that are benthic and others that live on aquatic plants. Although benthic prey predominated in larger larvae, several planktonic species (Hutchinson 1967) were also present in the diet: Bosmina longirostris and Keratella cochlearis.

Juvenile and adult E. gloriosus continued to feed on strictly benthic prey, such as the cyclopoid copepods, oligochaetes, and Oecetis, and on prey that are both benthic and vegetational, such as Caenis sp. and Pentaneura. Divers (corixid beetles), swimmers (Caraphractus cinctus), neustonic forms (Podura aquatica), climbers on aquatic plants (oribatid mites), and Nymphaea seeds were also important prey, and attest to this species's diverse foraging behavior. Young larvae, then, fed predominantly on planktonic prey; above 10 mm they gradually switched to benthic prey, and fed mostly on benthic prey as juveniles and adults.

In contrast to E. gloriosus, which fed on planktonic cladocerans, young larval E. obesus fed mostly on Sida crystallina and Acroperus harpae, two cladocerans associated with aquatic vegetation (Fairchild 1981). Some cyclopoidea, which are indicative of benthic foraging, were also preyed upon. Larvae larger than 10 mm SL continued to feed on vegetational (orabatid mites, hydracarina, Alonella excisa) and benthic (cyclopoidea, Alluadomyia) prey. Pentaneura, another important prey genus, has both vegetational and benthic species. Dietary occurrence of Keratella cochlearis, a free-swimming rotifer, and Scapholebris mucronata, which swims just below the surface, suggests that larval E. obesus are not restricted to gleaning prey off of plants or probing the substrate. Juvenile and adult E. obesus still fed on predominantly vegetational (Ferrissia, oribatid mites, Oxyethira) and benthic (cyclopoidea and oligochaeta) prey. Many adults also foraged at the surface on water striders and adult midges.

Based on all the dietary data from both years, E. obesus probably feeds in shallow, densely vegetated water where individuals can easily move from benthic to vegetational to surface prey. Enneacanthus gloriosus, differs from E. obesus by taking fewer prey associated with vegetation or water surface. Perhaps E. gloriosus forage in deeper water on the edges of the weed beds, thus obtaining more benthic and free-swimming species. Both E. obesus and E. gloriosus share many of the same benthic prey, such as the cyclopoid copepods.

In contrast to Enneacanthus in Success Lake, young-of-the-year sunfishes and yellow perch in Lake Opinicon, Ontario partition food by its size (Keast 1980). In Lake Opinicon, the adults occur in different habitats.

Each species's larvae appear sequentially, since the adults breed at different times. Thus the larvae are different sizes; large, older larvae eat large prey. In contrast to Keast's study, Govoni et al. (1983) compared Brevoortia patronus (gulf menhaden), Leiostomus xanthurus (spot), and Micropogonius undulatus (Atlantic croaker) in the Gulf of Mexico. These three species are morphologically distinct as larvae and adults, and unsurprisingly, the larvae are dietarily distinct.

Ontogenetic microhabitat shifts by E. gloriosus may give a clue to its geographical distribution. Graham and Hastings (1984) suggested that the scarcity of strictly planktivorous fishes in blackwaters could be due to low planktonic productivity and reduced visibility. A prediction of this hypothesis is that E. gloriosus, which is less frequent in blackwaters than E. obesus, should be the more planktivorous species. Since E obesus is nearly restricted to blackwaters in New Jersey, it should be less planktivorous than E. gloriosus. Patterns of resource use in Success Lake support this hypothesis.

While niche partitioning itself gives no clue to competition among E. obesus and E. gloriosus, circumstantial evidence indicates they do compete. First, morphology, size, habitat (shallow, densely vegetated littoral zone), and diet (small aquatic invertebrates) are similar. Secondly, E. obesus occurs in different habitats in allopatry and sympatry. In drainages where the two species occur together, E. *obesus* is restricted to acidic blackwaters, but E. *gloriosus* is more frequent in less acidic clearwaters (Graham and Hastings 1984, Hastings 1984). In New England, however, where E. *obesus* occurs alone, it lives in extremely clear glacial lakes (Cohen 1977, Graham, in review and personal observation).

In conclusion, larval *Enneacanthus* partitioned resources at the smallest sizes I was able to sample. Although the average young-of-the-year E. *obesus* was slightly larger than young-of-the-year E. *gloriosus*, the differences in resources were not because of differences in size. Both species showed ontogenetic shifts in prey size; E. *gloriosus* alone shifted microhabitat.

Table 4.1 Proportional electrophoretic mobilities of the diagnostic alleles, relative to the common allele (100) in populations of E. *gloriosus*.

Enzyme	Locus	Allele
Malate dehydrogenase	Mdh-2	100
		28
Phosphoglucose isomerase	Pgi-1	100
		112
Peptidase	Pep-2	100
		135
Glyceraldehyde-3-phosphate	Gap-1	100
		85
Alpha-glycerophosphate dehydrogenase	Gpd-2	100
		149

Table 4.2 Mean depth of reproductive male *Enneacanthus* in Collier's Mills Pond on 19 June 1980.

Species	Mean Depth (m)	Std. Dev.	n
E. obesus	0.1767	0.0553	12
E. gloriosus	0.1528	0.0603	18

Table 4.3 Observed frequencies of breeding male *Enneacanthus* among square meter seine hauls in Collier's Mills Pond, 19 June 1980. Expected frequencies are in parentheses.

		E. gloriosus		
		Present	Absent	Totals
E. obesus	Present	5 (3.5)	5 (6.5)	10
	Absent	10 (11.6)	24 (22.4)	34
	Totals	15	29	44

Table 4.4 Mean standard lengths of young-of-the-year *E. obesus* and *E. gloriosus*.

Lake	Species	Date	N	Mean	SD	SE
Success						
	E. obesus	2 July 1979	37	9.057	2.759	0.454
		16 Aug 1979	13	13.822	3.053	0.847
		4 July 1980	2	13.475	1.534	1.085
		13 July 1980	62	14.479	2.792	0.355
		27 Aug 1980	37	18.914	2.745	0.451
	E. gloriosus	2 July 1979	12	7.017	0.955	0.276
		16 Aug 1979	14	11.649	2.081	0.556
		4 July 1980	12	7.896	2.045	0.590
		13 July 1980	152	12.474	1.365	0.111
		27 Aug 1980	54	13.901	1.723	0.234
Collier's Mills						
	E. obesus	20 Aug 1979	1	6.21	-	-
	E. gloriosus	6 July 1979	6	6.35	1.027	0.419
		10 July 1979	27	6.01	2.045	0.395
		20 Aug 1980	29	8.95	3.630	0.674
		23 July 1980	5	12.484	3.993	1.786
		30 July 1980	6	9.68	2.220	0.906
		29 Aug 1980	5	13.90	2.943	1.316

Table 4.5 Analysis of variance table for the effects of species, month, year, and their interactions on standard length of young-of-the-year Enneacanthus during July and August of 1979 and 1980 in Success Lake.

Source of Variation	DF	SS	F	P
Species	1	275.2	51.65	.0001
Month	1	724.6	136.00	.0001
Year	1	181.1	34.00	.0001
Species x Month	1	0.5	0.10	.7486
Species x Year	1	41.3	7.75	.0059
Month x Year	1	18.1	3.40	.0669
Species x Month x Year	1	0.2	0.03	.8555
Fish (S x M x Y)	182	969.7		

Table 4.6 Analysis of covariance for intestinal fullness and percent stomach fullness (arcsine transformation) as a function of time of day, species, and their interaction. Standard length is the covariate.

		Intestinal Fullness	Stomach Fullness
Source of Variation	DF	F	F
Time of Day	5	16.3 ****	12.5 ****
Species	1	15.3 ****	4.8 *
Standard Length	1	9.8 ***	4.8 *
Time x Species	5	6.4 ****	1.5 ns
Error	229		

* $p < 0.05$
*** $p < 0.001$
**** $p < 0.0005$

Table 4.7 DCA prey scores, 2 July 1979.

Prey	Axis 1	2	3	4
Unicellular algae	-190	238	233	13
Filamentous algae	160	217	620	-54
Cyclopoidea (intermediate)	170	137	204	213
Cyclopoidea (large)	66	326	107	238
<u>Sida crystallina</u>	19	176	197	92
<u>Bosmina longirostris</u>	396	219	-1	209
<u>Ophryoxus gracilis</u>	186	73	202	9
<u>Eurycercus lamellatus</u>	260	73	285	0
<u>Acroperus harpae</u>	206	-51	34	183
<u>Pleuroxus hastatus</u>	-26	152	267	297
<u>Pleuroxus striatus</u>	83	232	259	403
<u>Chydorus sphaericus</u>	269	248	443	199
Unidentified cladoceran	218	379	162	93
Orabitei	169	218	506	-70
<u>Pentaneura</u> spp.	161	202	512	169
Tendipedidae	185	362	331	341
<u>Alluaduomyia</u> spp.	163	426	21	168
Eigenvalue	0.492	0.292	0.202	0.100

Table 4.8 DCA prey scores, 16 August 1979.

Prey	Axis 1	2	3	4
Arcella	30	-126	-39	59
Keratella cochlearis	32	430	287	-70
Annelid setae	136	88	56	-87
Cyclopoidea (intermediate)	136	108	88	119
Nauplius spp.	-87	237	388	12
Sida crystallina	106	60	555	247
Diaphanosoma brachyurum	450	179	196	236
Alona guttata	184	8	-264	-116
Chydorus sphaericus	-50	-83	-341	107
Alonella excisa	-7	14	-205	88
Scapholebris mucronata	-38	-40	168	89
Unidentified cladoceran	201	084	-81	-62
Orabitei	-54	-18	146	189
Hydracarina	-71	131	-77	29
Pentaneura spp.	53	206	63	-18
Pseudochironomus spp.	119	163	190	186
Polypedilum sp. 1	-31	148	102	-112
Polypedilum sp. 2	-69	10	59	75
Calopsectra sp. 1	303	103	297	153
Tendipedidae	264	78	235	-128
Alluaduomyia spp.	85	-6	-208	147
Aquatic insect	-11	-170	77	-7
Ferrissia parallela	172	-57	467	311
Eigenvalue	0.259	0.153	0.074	0.058

Table 4.9 DCA prey scores, 13 August 1980.

Prey	Axis 1	Axis 2	Axis 3	Axis 4
Difflugia spp.	-161	46	28	78
Arcella spp.	217	149	41	40
Cyclopoidea	82	152	96	126
Nauplius	163	159	94	183
Alona rectangula	41	127	94	127
Chydorus sphaericus	201	55	-87	241
C. bicornutus	208	23	-9	162
Alonella excisa	214	58	-32	215
Sida crystallina	215	176	49	-74
Bosmina longirostris	-116	236	67	68
Ilyocryptus spinifer	-8	128	123	272
Streblocerus serricaudata	147	220	107	193
Cladocera	32	-60	-25	15
Orthocladius spp.	178	190	233	139
Polypedilum spp.	227	114	94	147
Calopsectra spp.	204	113	180	174
Pentaneura spp.	132	38	188	330
Tendipedidae	194	97	221	-27
Oribatei	351	16	88	122
Hydracarina	255	274	-33	116
Alluadomyia spp.	233	85	176	147
Caenis spp.	46	47	426	198
Caraphractus cinctus	233	84	157	184
Oxyethira sp.	144	158	169	126
Insecta	225	60	115	117
Trichocerca spp.	110	244	133	-149
Keratella cochlearis	-151	440	186	46
Monostyla spp.	174	270	101	-132
Rotifera	-132	436	84	94
Ferrissia parallela	224	8	289	186
Filamentous algae	-3	75	214	266
Unicellular algae	201	193	25	251
Eigenvalue	0.186	0.155	0.121	0.095

Table 4.10 DCA prey scores, 27 August 1980.

Prey	Axis 1	2	3	4
Unicellular algae	-5	321	121	177
Filamentous algae	56	261	55	187
Arcella spp.	46	132	25	178
Difflugia spp.	25	443	54	171
Keratella cochlearis	12	-96	89	197
Bdelloidea	5	312	85	191
Annelid setae	63	247	58	182
Cyclopoidea (small)	0	113	7	202
Cyclopoidea (intermediate)	67	63	95	190
Cyclopoidea (large)	16	198	7	204
Nauplius spp.	24	28	140	173
Sida crystallina	-14	156	55	178
Latona parviremis	10	162	33	180
Diaphanosoma brachyurum	30	46	93	169
Simocephalus serrulatus	11	421	103	178
Bosmina longirostris	44	-87	59	187
Macrothrix laticornis	10	-34	123	184
Ilyocryptus spinifer	0	177	85	187
Acroperus harpae	33	117	86	188
Alona guttata	-3	144	136	180
Chydorus sphaericus	24	108	103	181
Alonella excisa	31	111	134	215
Disparalona rostrata	3	160	132	187
Unidentified cladoceran	70	134	71	190
Orbitei	76	169	30	247
Hydracarina	97	127	111	219
Caenis sp.	84	443	39	187
Dragonfly nymph	434	142	95	262
Damselfly nymph	11	463	120	185
Corixid adult	482	35	0	0
Oxyethira sp.	20	173	123	173
Pentaneura spp.	7	203	77	177
Corynoneura taris	34	103	73	223
Cricotopus slossonae	51	26	399	190
Orthocladius spp.	10	25	-62	176
Polypedilum illinoense	2	156	21	217
Calopsectra sp. 1	6	350	95	180
Tendipedidae	48	28	-41	177
Tendipedid pupa	38	444	65	209

Table 4.10 Continued.

Prey	Axis 1	Axis 2	Axis 3	Axis 4
Tendipedid adult	285	131	75	261
Alluaduomyia spp.	35	138	20	217
Caraphractus cinctus	455	156	85	277
Ferrissia parallela	71	161	78	182
Sand grains	225	139	76	178
Pine pollen	36	210	15	195
Seed	588	141	100	251
Eigenvalue	0.379	0.219	0.139	0.106

Figure 4.1 Arcsine of mean stomach fullness versus time of day.

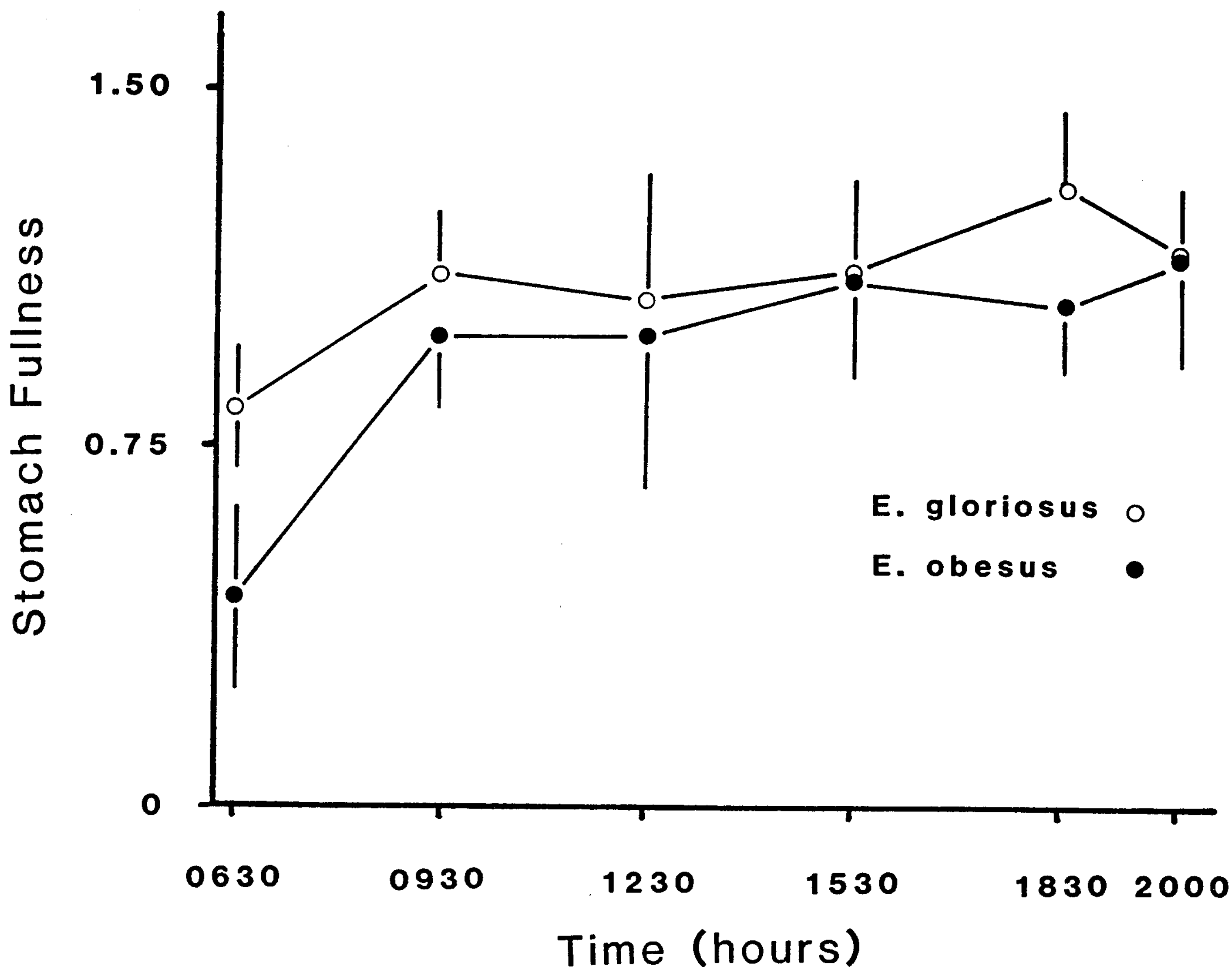
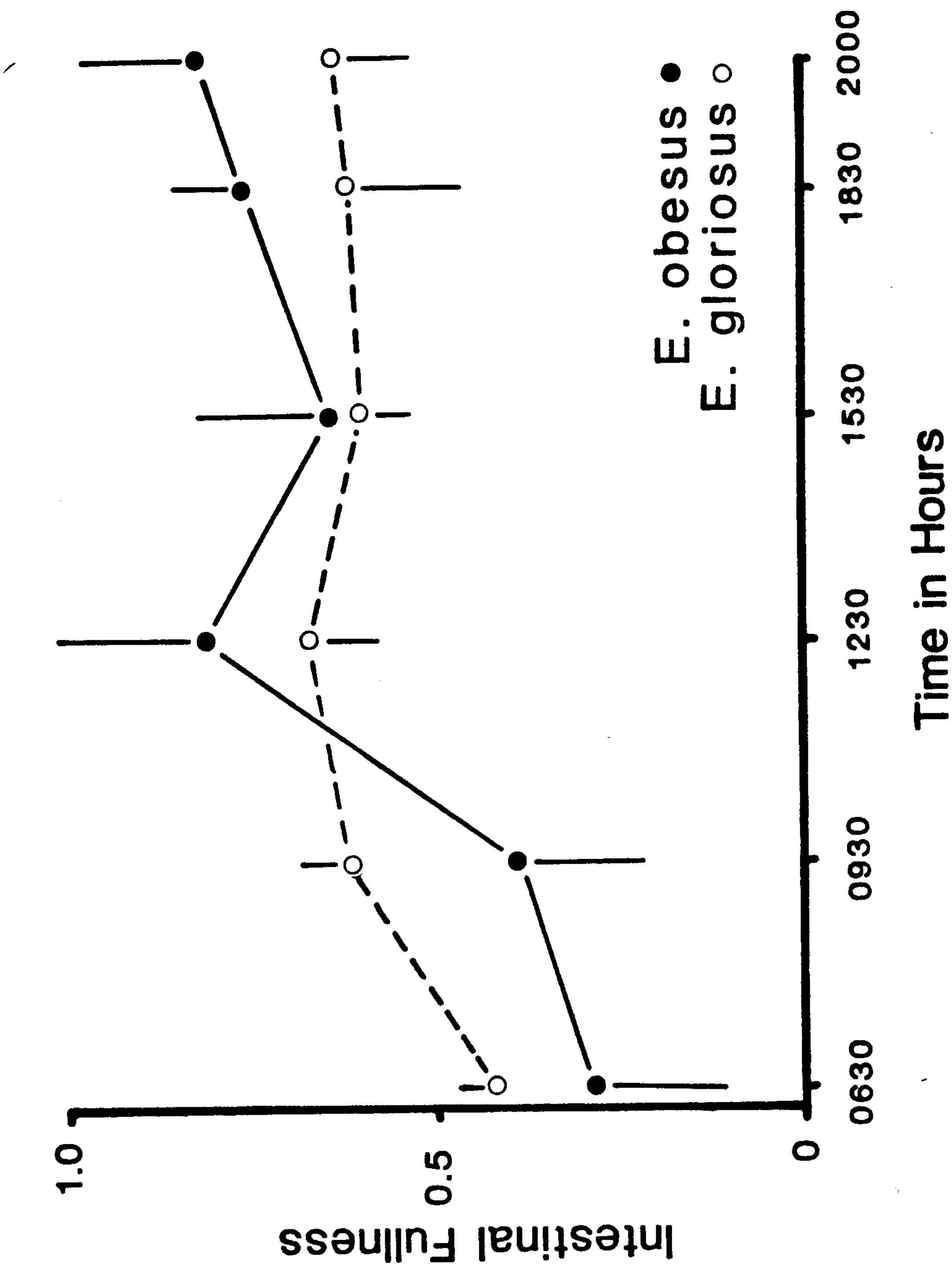
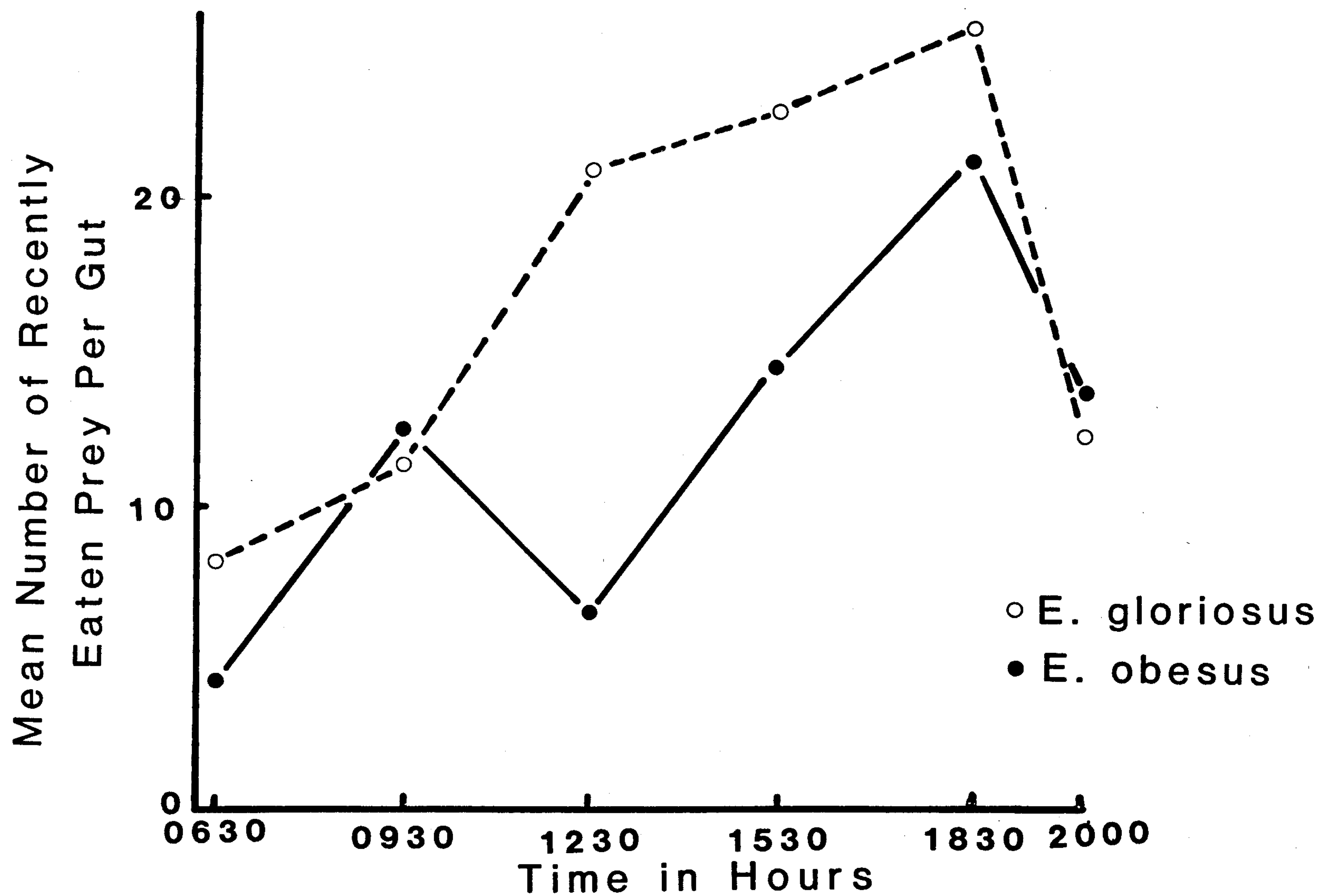

Stomach Fullness
1.50
0.75
0
0630
0930
1230
1530
1830
2000
Time (hours)
E. gloriosus
E. obesus

Figure 4.2 Arcsine of mean intestinal fullness (adjusted for standard length) versus time of day.



1.0
0.5
0
Intestinal Fullness
0630
0930
1230
1530
1830
2000
Time in Hours
E. obesus ●
E. gloriosus ○

Figure 4.3 Feeding rate as measured by the numbers of food items in digestion categories 1 and 2 per stomach.



Mean Number of Recently
Eaten Prey Per Gut
0
10
20
0630
0930
1230
1530
1830
2000
Time in Hours
E. gloriosus
E. obesus

Figure 4.4 DCA sample scores plotted against standard length, 2 July 1980.

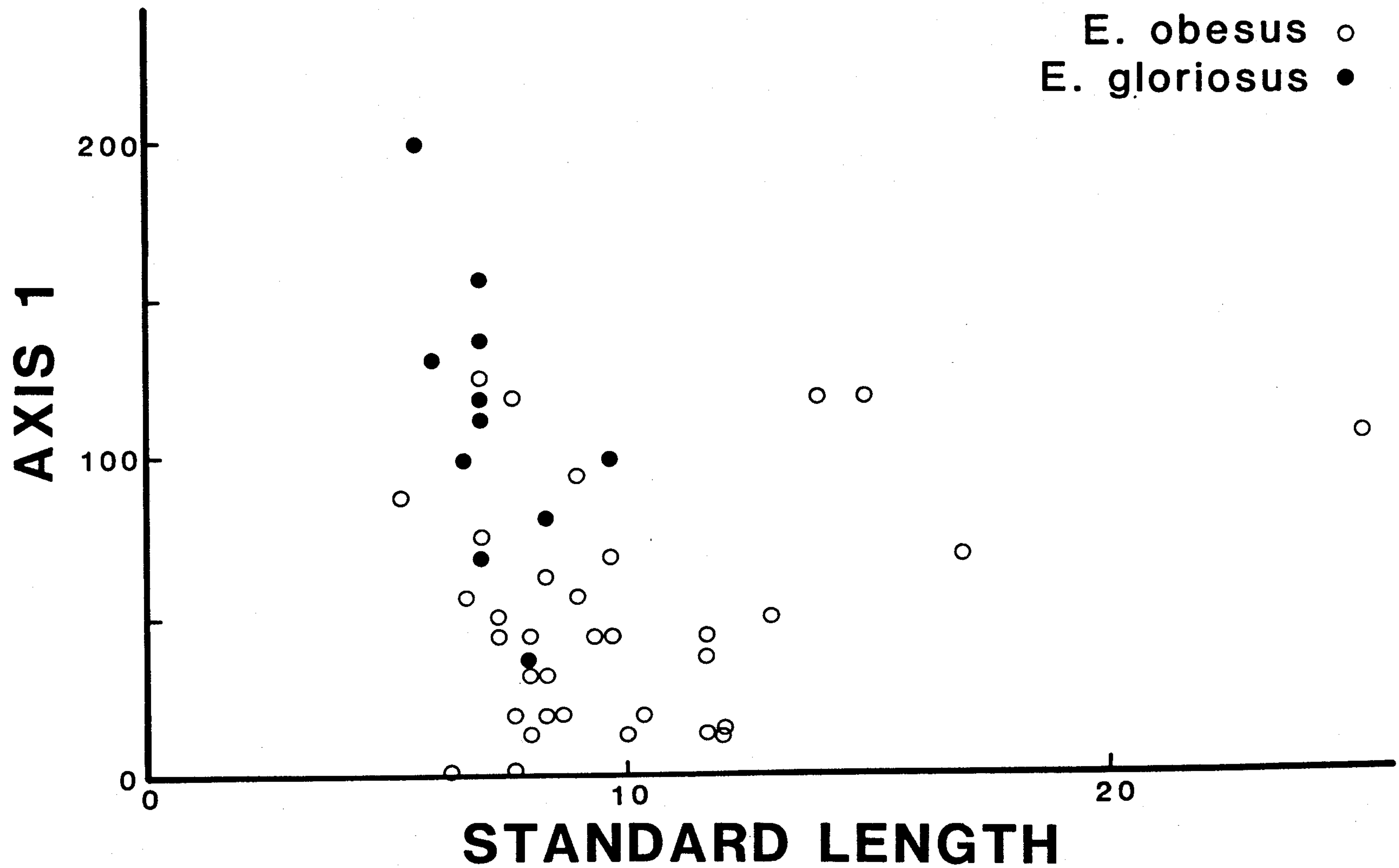

E. obesus
E. gloriosus
AXIS 1
200
100
0
0
10
20
STANDARD LENGTH

Figure 4.5. DCA sample scores plotted against standard length, 16 August 1979.

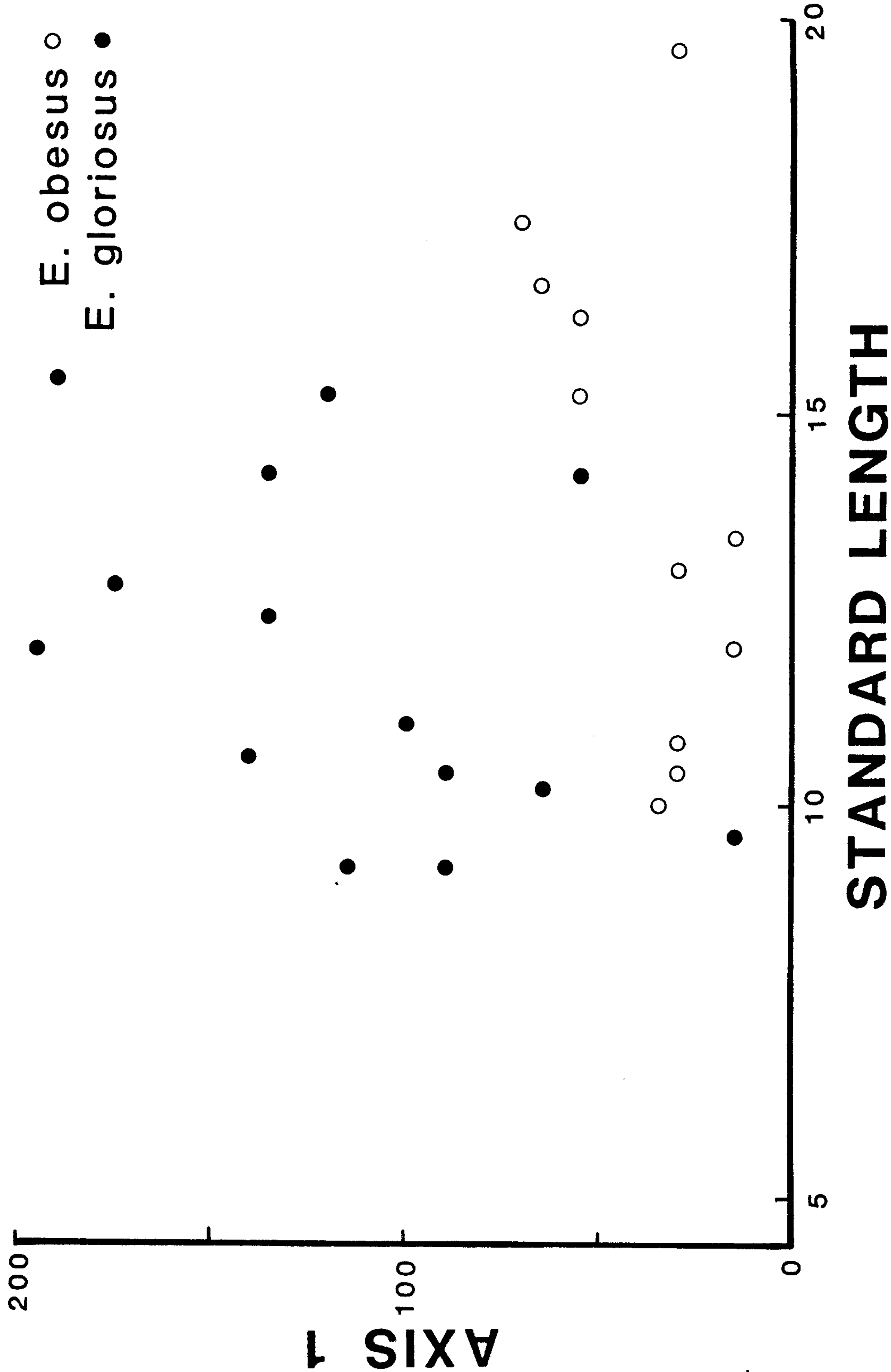

E. obesus ○
E. gloriosus ●
STANDARD LENGTH
AXIS 1
0
100
200
5
10
15
20

Figure 4.6 DCA sample scores plotted against standard length, 13 August 1980.

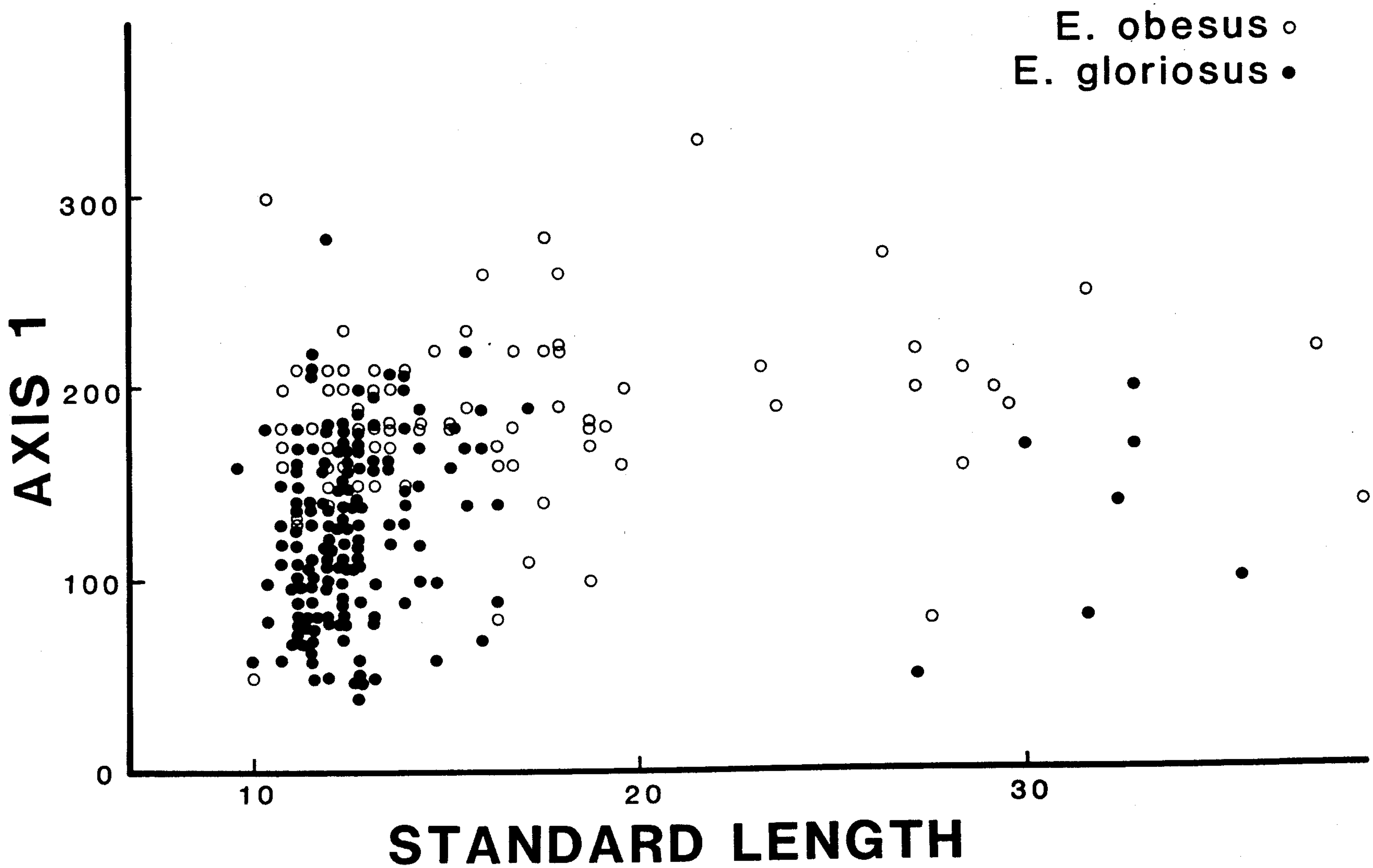

E. obesus
E. gloriosus
AXIS 1
300
200
100
0
10
20
30
STANDARD LENGTH

Figure 4.7 DCA sample scores plotted against standard length, 27 August 1980.

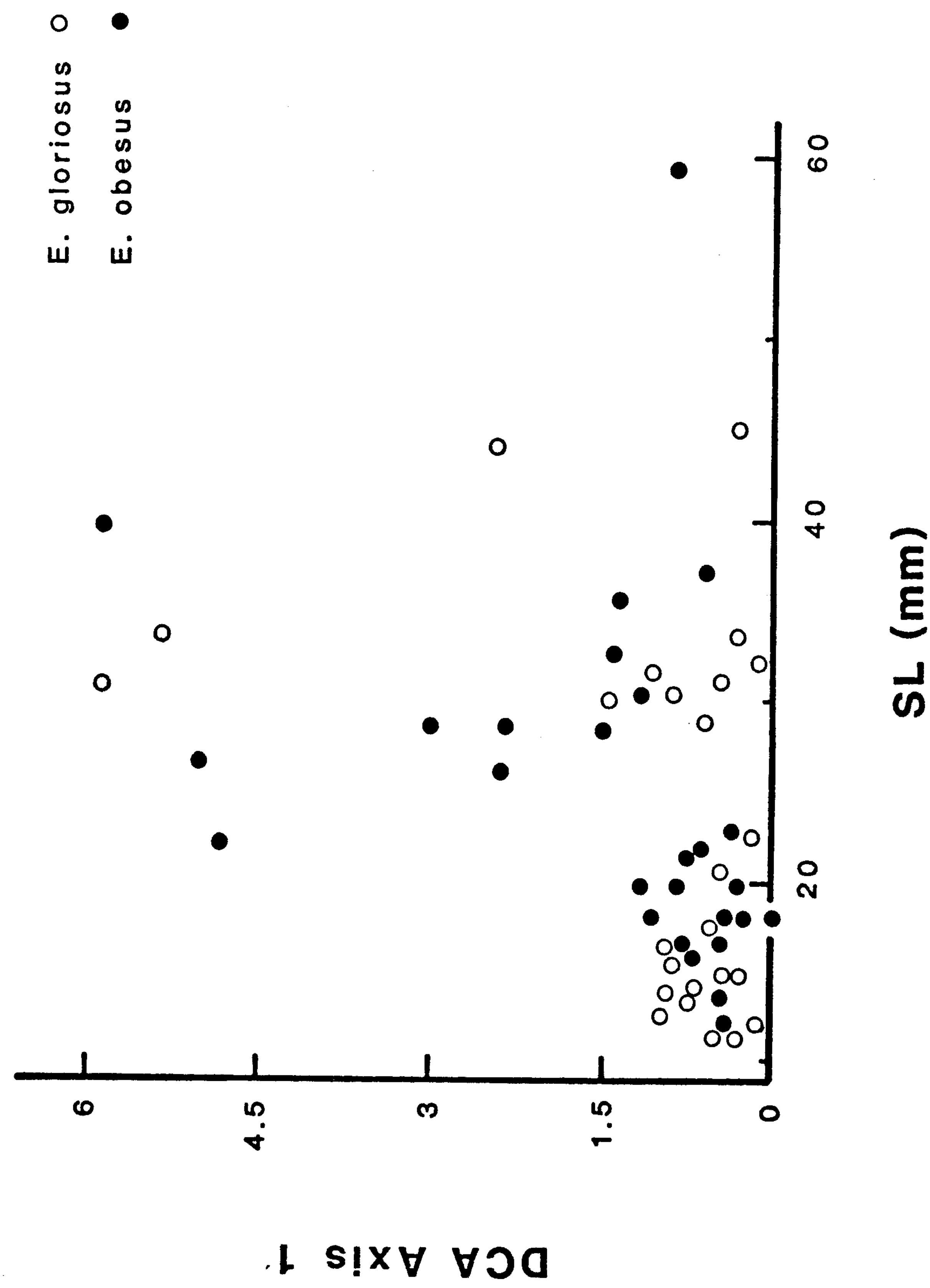
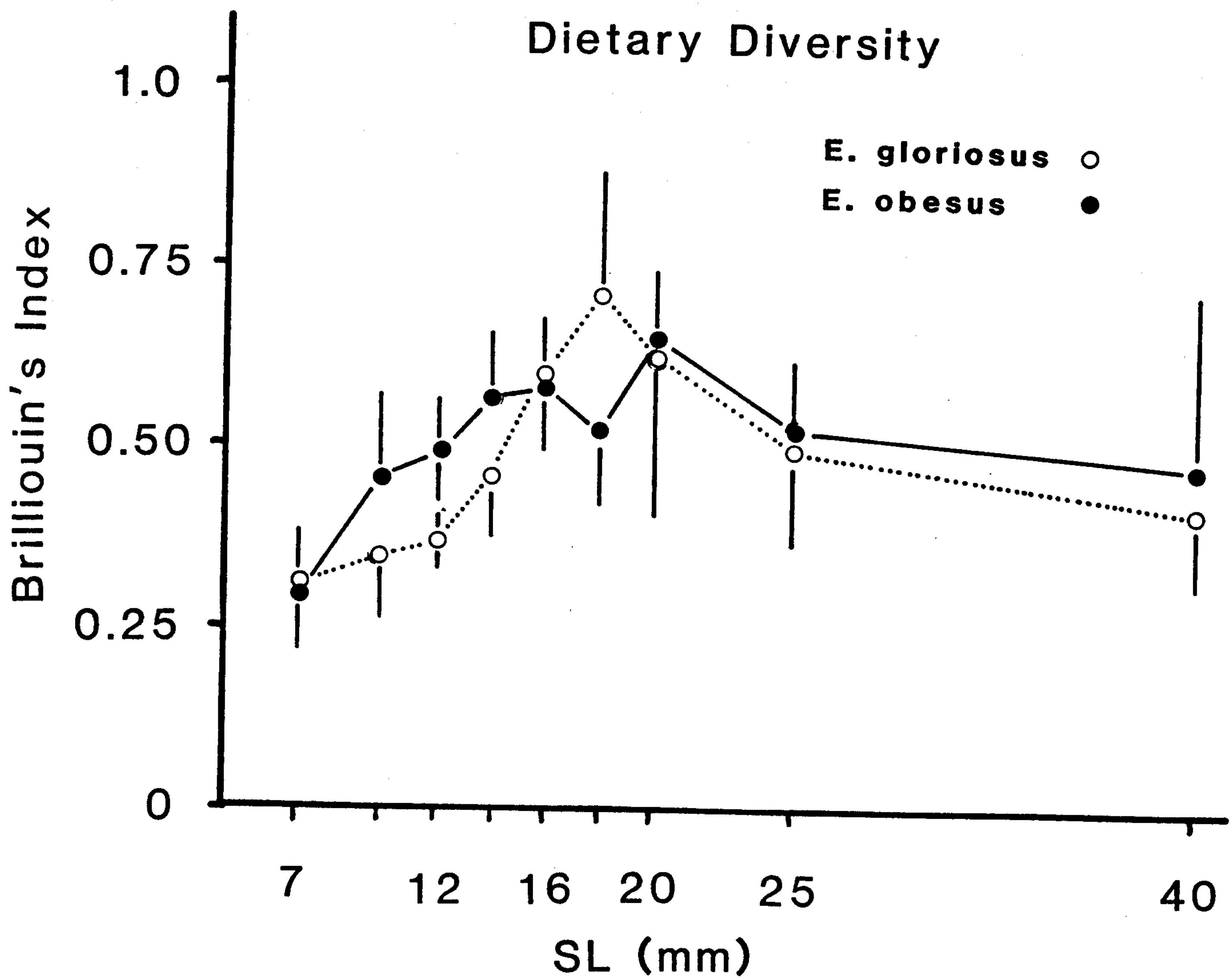

E. gloriosus
E. obesus
DCA Axis 1
SL (mm)
0
1.5
3
4.5
6
20
40
60

Figure 4.8 Mean dietary diversity (Brilliouin's Index) versus standard length.


Dietary Diversity
E. gloriosus
E. obesus
Brilliouin's Index
1.0
0.75
0.50
0.25
0
7
12
16
20
25
40
SL (mm)

CHAPTER V

NICHE ONTOGENY AND PROGRESSIVE DEVIATION

Introduction

Karl Ernst von Baer, the leading embryologist of the 19th century, proposed four laws of development in his classic 1828 text, "Entwicklunsgeschichte der Thiere." Von Baer's third law, the developmental divergence of related species, was called progressive deviation by Fritz Muller (1864), the German-Brazilian naturalist. Indeed, many related species show morphological (Muller, 1864, De Beer 1940, Blaxter 1974, Hunter 1980) or behavioral divergence (Brown and Colgan 1984, Carey 1985) during development. But do niches diverge concomitantly with morphology? Several authors have suggested that they do. Anurans, for example, often undergo extreme niche shifts, from an aquatic habitat to a terrestrial habitat, and, according to Wilbur (1980), the tadpoles are more alike in diet, morphology, and behavior than the adults. Similarly, Mushinsky et al. (1982) studied four species of water snake (*Nerodia*) that show both dietary shifts and dietary divergence as they grow. And according to Hunter (1981), many marine fishes begin life as diurnal planktivores having similar feeding behavior and diverge at metamorphosis. To answer this question, I compared niche ontogeny in two congeneric sunfishes, the banded sunfish (Enneacanthus gloriosus) and the bluespotted sunfish (E. obesus). These two species show progressive phenotypic deviation, but fail to show analogous divergence of their dietary habits.

Enneacanthus obesus and E. gloriosus are ideal for testing hypotheses related to niche ontogeny. They breed concurrently during spring and early summer, building nests among submerged aquatic plants (Breder 1936). Adults are morphologically alike, but larvae are nearly indistinguishable. Moreover, both species live in dense littoral vegetation, feed on the same kinds of small invertebrates, and grow to a maximum size of about 100 mm SL (Breder and Redmond 1929, Chable 1947, McLane 1955, Graham 1978, Cohen 1977).

To study niche ontogeny in these species I used detrended correspondence analysis (DCA) to infer underlying resource axes from dietary data. Dietary composition (i.e. the kinds of foods and their relative abundances) reflects many niche dimensions, including kind and size of prey, and prey and predator's behavior, habitat, and time of activity. The advantage of using dietary data to infer niches is that no prior decisions regarding niche dimensionality need to be made.

Materials and Methods

For morphological analysis, I collected 33 *E. gloriosus* and 24 *E. obesus* from Success Lake and Collier's Mill Pond, New Jersey. Fifteen morphometric characters were measured on live individuals sedated with Finquil (Sigma Chemical Company, St. Louis, Missouri). The morphometric characters, chosen because they were present on all sizes of larvae and juveniles, included standard length (or notochord length if the hypural elements were absent), total length, preanal length, head length, eye diameter, snout length, body depth, head width, maximum body width, predorsal length, maximum body depth, head depth, snout to maximum body depth length, median fin to hypural length, and peduncle depth. The head was severed from each fish, preserved in buffered formalin, and intestinal length was measured after stretching the intestine between two probes.

Three trophic characters, mouth width, mouth height, and number of jaw teeth, were omitted from the morphological analysis; I found no differences between the two species in mouth height or width (Table 5.1 and Graham 1978). Also, Sweeney (1972) found no differences in the shape and size of the premaxilla, maxilla, and dentary, and in the number of teeth in the two species. Intestine length was included in the analysis, because preliminary study of both species in Atco Lake, NJ had shown intestinal length to be longer in *E. obesus*.

The rationale for using characters that measure shape in a study of niche ontogeny stems from the relationships between shape, swimming dynamics, and habitat (Keast and Webb 1966). Enneacanthus obesus, as an adult, has a slightly deeper body (gibbose) than E. gloriosus. The gibbose body form imparts stability, by virtue of its large lateral area, which prevents rolling (Harris 1938). The price of increased stability, however, is a loss of speed. The gibbose body is more common among fishes inhabiting dense cover (Lagler et al. 1977).

Progressive phenotypic deviation during development was explored by examining the relationship between standard length and each species's scores on a canonical variable. The canonical variable was produced by the SAS CANDISC procedure (SAS Institute Inc. 1985), which performs a canonical discriminant analysis. The canonical scores of each species were regressed on standard length. To test the hypothesis that morphology diverges with increasing size, I used an analysis of covariance to test for heterogeneity of slopes.

For the dietary analysis, I collected fish from Success Lake, Ocean Co., New Jersey on 5 dates in 1979 and 1980. The first collection in each year was timed to the appearance of larval Enneacanthus, and a second collection followed a month later in 1979 and two weeks and three months later in 1980. On each date, I sampled continuously throughout the day, and in a variety of habitats. Fish were immediately placed on ice to prevent regurgitation, and were subsequently frozen at -60 C on returning to the laboratory.

After thawing the fish, I measured standard length of each fish, saved the body for electrophoretic analysis (see Chapter IV), removed the stomach (or the entire gut if the pyloric caecae were undeveloped), and mounted its contents in Kaizer's medium. Each fish's diet was quantified by counting individual prey. Prey were identified to the lowest possible taxon using Roback (1957), Ward and Whipple (1959), and Pennak (1978).

Dietary data, consisting of the counts of each kind of food within a gut, were analysed by detrended correspondence analysis (DCA) (see Chapter III). All fish of both species and both years were pooled for the analysis. I used DECORANA's downweighting option.

To test the hypothesis that diets diverge during development, I examined size-dependent overlap in the frequency distributions of the DCA scores. And to complement this approach, I used Horn's (1966) measure of overlap to compare mean dietary overlap between *E. obesus* and *E. gloriosus* for fish less than or equal to 15 mm SL and for fish greater than 15 mm SL. Horn's measure of overlap is a function of the proportions of each food category in the diets of each species.

Results

Enneacanthus obesus and E. gloriosus showed progressive morphological deviation during development. Canonical discriminant analysis produced one canonical axis that accounted for most of the morphological variation between the two species of Enneacanthus (Table 5.2). Variables with large positive coefficients were peduncle depth, preanal length, and total length. Those with large negative canonical coefficients, in contrast, were standard length and body depth. Enneacanthus obesus, with a mean of 1.681, had high canonical scores; E. gloriosus, with a mean of -1.223, had lower scores. The regression lines for the two species had heterogeneous slopes ($F = 8.75$, DF =1, 53, $p < 0.005$), and diverged with increasing size (Fig. 5.1).

There was no significant divergence in diet or in dietary overlap with increasing size. Mean dietary overlap (Table 5.3) among small fish of the two species was not significantly greater than mean dietary overlap among large fish of the two species ($t = 0.9733$, $P = 0.3825$). In addition, the DCA showed the diets of the two species converging with increased size.

The first DCA axis (Table 5.4) contrasted three species of cladocerans (Sida crystallina, Pleuroxus hastatus, and Ophryoxus gracilis, all with high scores) against two insects (Stenelmis and Scirtes) and a cladoceran (Anchistropus). Enneacanthus gloriosus and E. obesus smaller than 10 mm standard length had different distributions on this axis; E. gloriosus had low scores and E. obesus had high scores (Fig. 5.3). With increasing size, E. obesus's distribution shifted towards the left until, in fish larger than 20 mm, the overlap in distributions was nearly complete.

In contrast to the first DCA axis, the second axis contrasted a few species of larger prey (large seeds, corixid nymphs, dragonfly nymphs, etc.) against many species of smaller prey. There were no significant differences between E. obesus and E. gloriosus on this axis, but scores on this axis were highly correlated with standard length ($r = 0.479$, $p < 0.0005$).

Discussion

Although morphology diverges with increasing size in E. obesus and E. gloriosus, diet does not diverge. Indeed, as the DCA shows, it may even converge. This contrasts with observations on other species. Why don't E. obesus and E. gloriosus diverge in their use of resources?

Niche partitioning by larval Enneacanthus may be a means of avoiding larval competition. The two species are alike in morphology, life history, and food habits. Competition among larvae may be severe during years when resources are scarce, as when spawning doesn't coincide with the spring bloom. This hypothesis can be tested by field experimentation, and by comparing morphological divergence in sympatric and allopatric populations of the two species. If competition occurs, divergence should be greater between sympatric populations, and it should increase after yolk absorption.

Food habits, then, do not diverge in Enneacanthus. Is Enneacanthus an exception to von Baer's generalities? Few studies have rigorously examined dietary divergence in any other species. Although Mushinsky et al. (1982) show divergence in diet by water snakes, neither Wilbur (1980) nor Hunter (1981) support their claims of divergence with data. Thus, Enneacanthus may not be the exception. Ballard (1976) felt that von Baer's generalities were of little value: "evolutionary divergence has taken place at every stage in the life history, the earliest no less than the latest." Von Baer's third law, the progressive morphological deviation of related species, may not be applicable to the niches of related species.

Table 5.1 Analysis of covariance for the effect of species on mouth width and mouth height. Standard length is the covariate.

	Mouth Width		Mouth Height	
Source of Variation	DF	F	DF	F
Species	1	2.6 ns	1	0.0 ns
Standard Length	1	1274.7 ***	1	762.4 ***
Standard length x Species	1	0.5 ns	1	1.6 ns
Error	90		69	

*** $p < 0.001$

Table 5.2 Standardized canonical coefficients of the first canonical axis.

Character	Canonical Coefficients
Total length	9.8032
Standard length	-23.8027
Preanal length	16.8027
Head length	-0.8328
Eye diameter	-0.0197
Snout length	-1.2268
Body depth	-19.4466
Head depth	-1.5880
Maximum body depth	5.5962
Snout to maximum body depth	-4.2433
Head width	0.0770
Predorsal length	2.5574
Maximum body width	-4.9228
Median fin to hypural length	-3.5093
Peduncle depth	19.5936
Intestinal length	5.5904

Canonical correlation 0.8250 $p < 0.0002$

Table 5.3 Dietary overlap (Horn's Index) between *E. obesus* and *E. gloriosus* in Success Lake in 1979 and 1980. Sizes are less than or equal to 15 mm SL and greater than 15 mm. The means are not significantly different from one another (P > 0.10).

	Number of Stomachs					
	E. obesus		*E. gloriosus*		Overlap	
Date	5-15	15 +	5-15	15 +	5-15	15 +
1979						
2 July	36	-	12	-	0.620	-
16 August	8	5	12	2	0.541	0.618
1980						
4-7 July	3	20	1	4	0.449	0.553
13 July	37	40	142	40	0.662	0.570
27 August	2	46	37	28	0.243	0.568
Mean					0.503	0.577

Table 5.4 DCA prey scores, 1979 and 1980.

Prey	Axis 1	2	3	4
Arcella spp	124	3	158	166
Centropyxis spp	150	3	331	91
Spongilla sp	69	3	575	191
Bdelloidea sp	160	44	276	-99
Trichocerca spp	214	5	142	208
Keratella cochlearis	210	1	317	72
Lecane spp	4	4	89	232
Monostyla spp	16	3	81	248
Nematoda spp	186	4	327	40
Plumatella	153	0	334	24
Annelida spp	162	15	321	86
Sida crystallina	315	8	220	191
Latona parviremis	204	3	310	136
Diaphanosoma brachyurum	90	2	386	323
Simocephalus serrulata	188	3	326	48
Scapholebris mucronata	121	0	101	485
Ceriodaphnia reticulata	91	6	130	138
Ceriodaphnia spp	100	1	551	287
Bosmina longirostris	32	8	408	168
Eubosmina coregoni	121	2	459	273
Ophryoxus gracilis	285	3	398	139
Streblocerus serricaudatus	17	10	151	273
Ilyocryptus spinifer	157	2	230	44
Macrothrix laticornis	156	2	320	169
Eurycercus lamellatus	273	4	574	175
Monospilus dispar	209	0	38	122
Acroperus harpae	246	0	427	56
Kurzia latissima	39	132	48	291
Camptocercus rectirostris	92	8	288	1
Alona setulosa	3	2	57	129
Alona guttata	195	0	270	173
Alona affinis	239	6	349	250
Alona rectangula	90	4	207	226
Oxyurella tenuicaudis	74	0	323	68
Pleuroxus striatus	279	-1	196	337
Pleuroxus hamulatus	46	2	85	308
Pleuroxus hastatus	287	4	307	292
Pleuroxus denticulus	232	-4	290	365
Disparalona rostrata	212	-2	290	207
Alonella excisa	63	2	174	124
Anchistropus minor	-10	2	317	237

Table 5.4 Continued.

Prey	Axis 1	2	3	4
Chydorus bicornutus	100	2	341	176
Chydorus sphaericus	167	5	304	357
Polyphemus pediculus	82	10	317	146
Cyclopoidea spp	17	7	198	184
Nauplius spp	54	3	183	248
Harpacticoidea	85	6	270	179
Ostracoda spp	209	-4	594	0
Hydracarina spp	107	10	132	284
Oribatei	77	3	0	104
Dolomedes	64	5	10	193
Podura aquatica	52	22	58	52
Caenis sp	178	48	216	83
Dragonfly nymph	127	173	107	281
Damselfly nymph	119	6	294	105
Merragata spp	270	7	143	223
Microvelia sp	64	136	340	340
Notonecta spp	81	12	81	235
Pelocoris sp	21	180	164	363
Corixidae	0	220	333	184
Oxyethira sp	82	5	107	82
Oecetis sp	180	62	182	-26
Lepidoptera larva	48	37	247	430
Stenelmis spp	145	-5	26	415
Scirtes spp	-47	6	27	147
Cyphon spp	46	1	328	263
Pentaneura spp	183	9	133	212
Corynoneura taris	220	3	279	88
Psectrocladius elatus	282	11	266	134
Psectrocladius sp 3	144	5	335	205
Psectrocladius sp 4	18	7	353	130
Psectrocladius sp 6	118	4	332	384
Cricotopus spp	71	4	359	165
Orthocladius spp	104	9	296	84
Hydrobaenus spp	54	1	112	128
Pseudochironomus spp	148	4	228	333
Glyptotedipes spp	148	3	345	423
Chironomus spp	134	13	354	-41
Parachironomus spp	84	10	338	166
Stenochironomus spp	-52	6	221	195
Tendipes l. neomodestus	165	3	314	57
Kiefferulus spp	91	22	344	87
Polypedilum spp	200	1	66	265

Table 5.4 Continued.

Prey	Axis 1	2	3	4
Tanytarsus spp	174	33	299	139
Calopsectra spp	210	7	248	82
Alluadomyia spp	202	1	111	202
Caraphractus cinctus	84	129	49	231
Ferrissia parallela	77	16	39	-78
Fish	78	34	315	384
Pollen	203	-1	152	433
Unicellular Algae	274	5	143	195
Filamentus Algae	223	15	217	33
Seed	60	305	187	167

Figure 5.1 Regression of canonical scores on standard length in E. obesus and E. gloriosus.

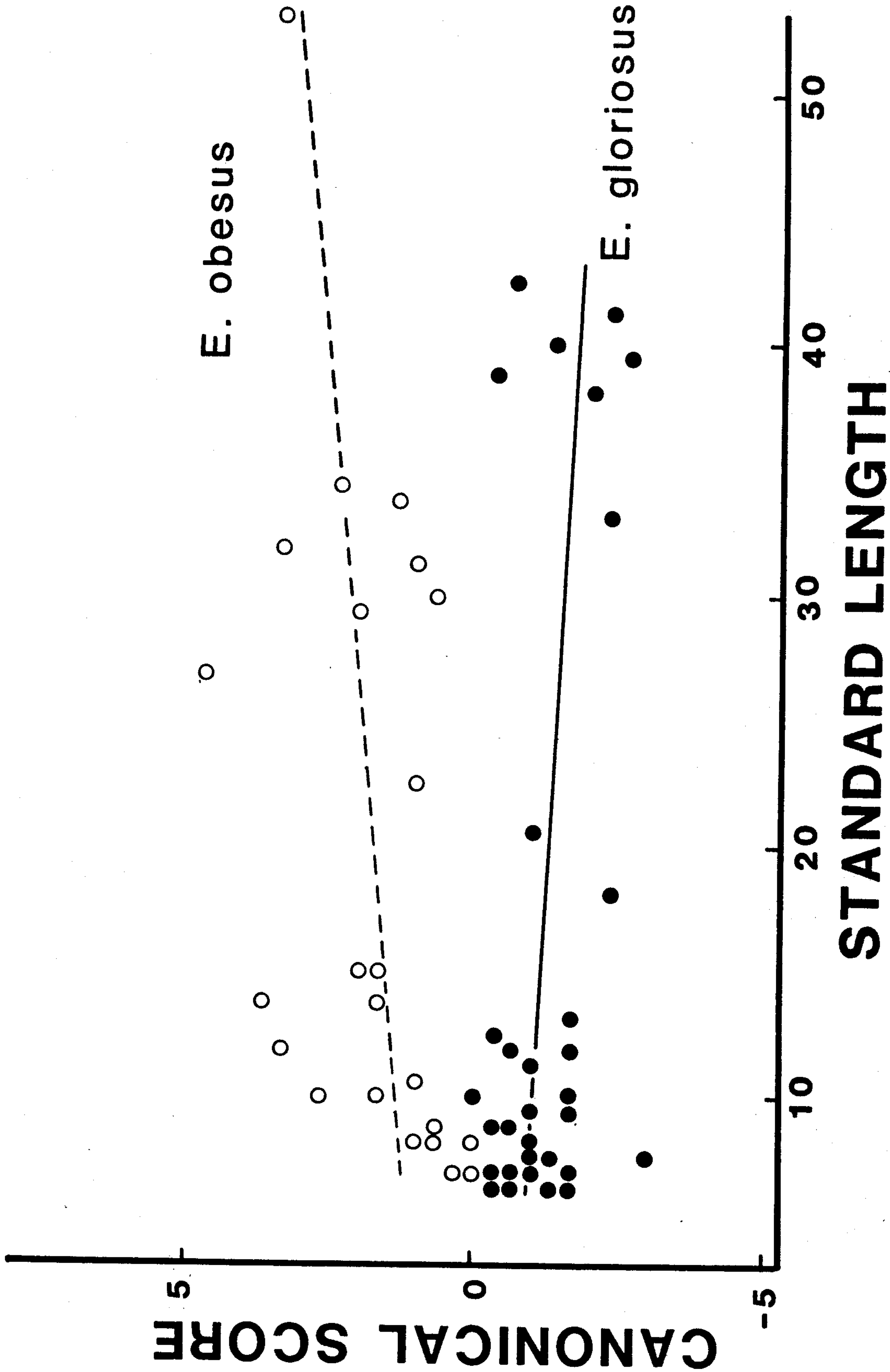
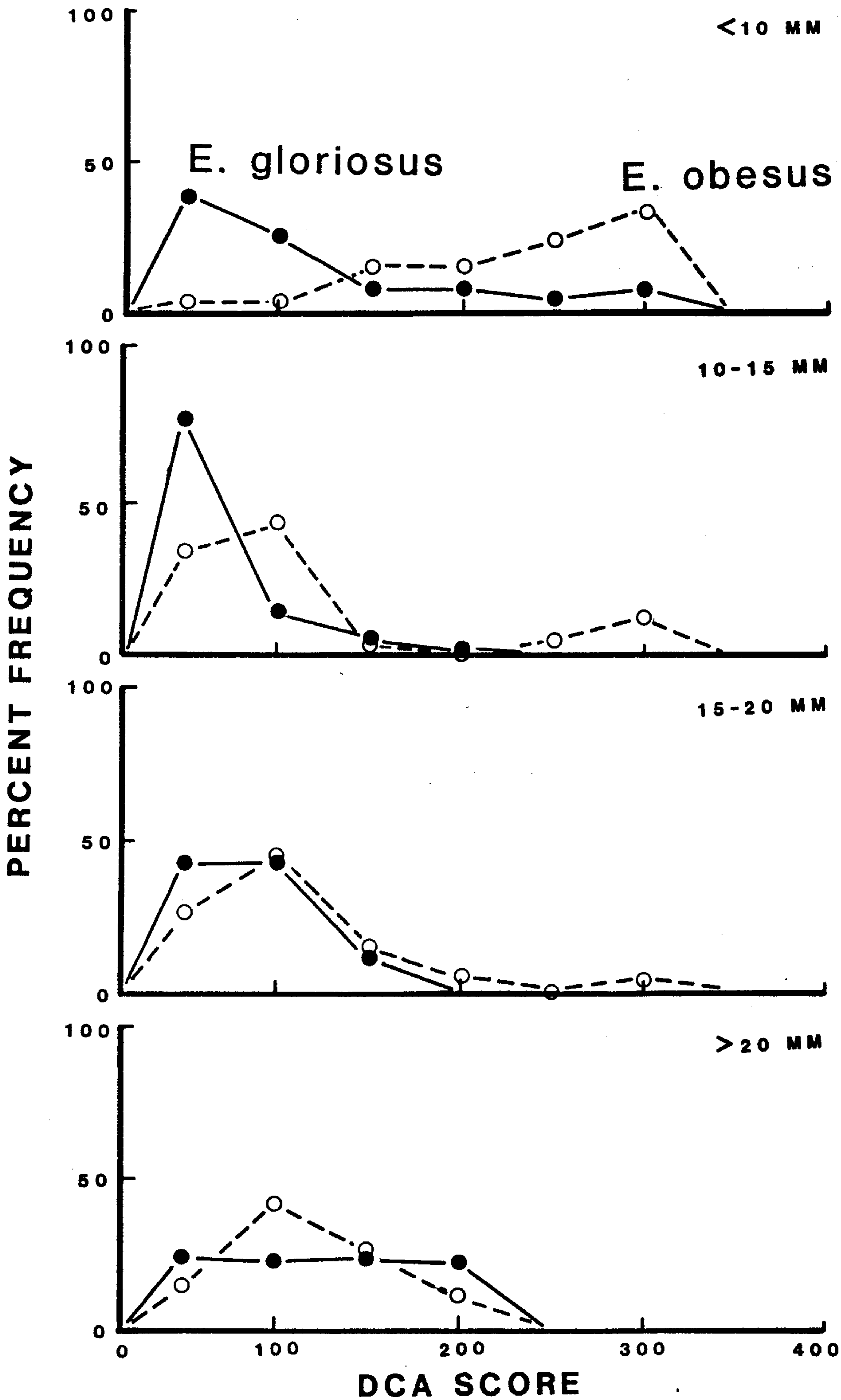

E. obesus
E. gloriosus
CANONICAL SCORE
5
0
-5
STANDARD LENGTH
10
20
30
40
50

Figure 5.2 Frequency polygons of DCA scores for 4 size categories of _E_. _obesus_ and _E_. _gloriosus_.


<10 MM
E. gloriosus
E. obesus
10-15 MM
15-20 MM
>20 MM
PERCENT FREQUENCY
DCA SCORE
0
50
100
0
100
200
300
400

IX. CONCLUSIONS

1. Morphological similarity between *E. obesus* and *E. gloriosus* is related to size. The two species show progressive morphological deviation with increasing size.

2. The food habits of *E. obesus* and *E. gloriosus* do not diverge concomitantly with morphology. The two species converge in diet with increasing size.

3. Detrended correspondence analysis discriminates between the diets of *E. gloriosus* and *E. obesus* better than either principal components analysis or factor analysis, and as well as discriminant analysis. In addition, it avoids the restrictive assumptions of discriminant analysis.

Appendix 7.1 Buffers and tissues optimally resolving isozymes of *E. obesus* and *E. gloriosus* by starch-gel electrophoresis.

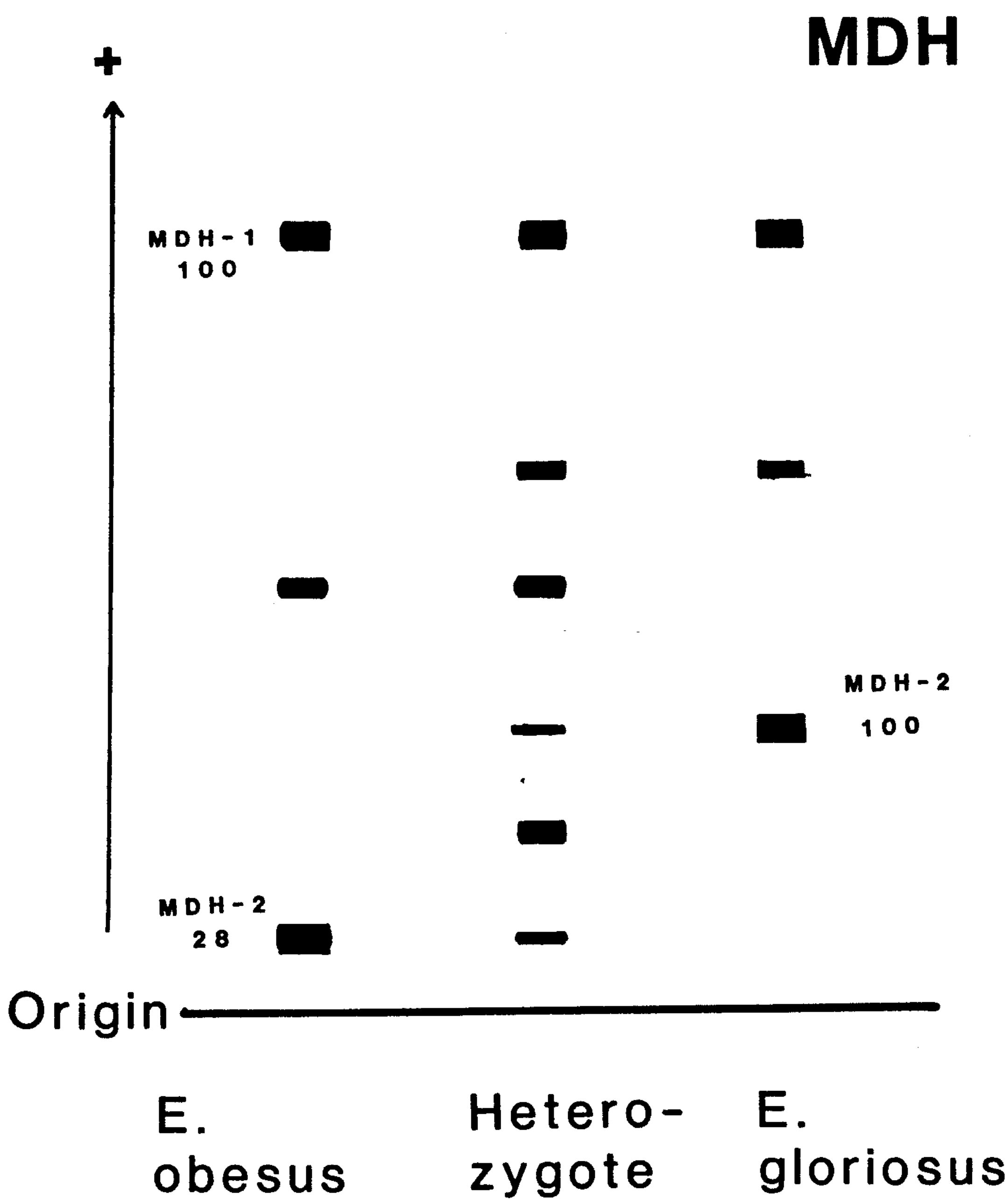
Enzyme	Abbreviation	Buffer *	Tissue **
Adenylate kinase	Ak	C	e, m
Alcohol dehydrogenase	Adh	C	l
Aspartate amino transferase	Aat	C	e, l, m, h, b
Esterase	Est	D	l, m, e
Fructose 1,6 diphosphorylase	Fdp	A, B, C	l, m
	G2pd	A	e, l, m
Glucose-6-phosphate dehydrogenase	G6pd	D	m
Glyceraldehyde-3-phosphate dehydrogenase	Gap	C	e, m, h, b
-glycerophosphate dehydrogenase	Gpd	A	l, m
Hexose-6-phosphate dehydrogenase	H6pd	B	e, l, m, b
Isocitrate dehydrogenase	Idh	C	e, l, m, h, b
Lactate dehydrogenase	Ldh	C	e, l, m h, b
Leucine amino peptidase	Lap	A	m
Malate dehydrogenase	Mdh	A, C	e, l, m, h, b
Malic Enzyme	Me	D	m
Peptidase	Pep	D	l, m
Phosphoglucomutase	Pgm	A	e, l, m
6-phosphogluconate dehydrogenase	Pgd	B	e, l
Phosphoglucose isomerase	Pgi	C	e, l, m, h
Pyruvate kinase	Pk	B	m
Tetrazolium oxidase	To	C	l

* Buffers are: A, tris-citrate pH 6.0; B, tris-citrate pH 6.8; C, aminopropylmorpholine pH 6.0; D, tris-versene-borate pH 8.0.

** Tissues are: eye (e), muscle (m), liver (l), heart (h), and brain (b).

Appendix 7.2 Electrophoretic phenotypes for Pgi-1, Pgi-2, and Mdh-2.


PGI
+
112
PGI-1
100
Origin
87
PGI-2
100
−
E. obesus
Het
E. gloriosus


MDH
+
MDH-1
100
MDH-2
100
MDH-2
28
Origin
E.
obesus
Hetero-
zygote
E.
gloriosus

Appendix 7.3 A list prey taxa and their habitats.

Taxa	Habitat*	References**
Phylum Protozoa		
Class Rhizopoda		
Order Testacida		
Arcellidae		
Arcella spp.	7, 8, 3	H
Difflugidae		
Difflugia spp.	7, 8, 3	H
Centropyxis spp.		
Phylum Porifera		
Class Demospongea		
Order Haplosclerina		
Spongillidae	9	P
Phylum Rotatoria		
Class Digonata		
Order Bdelloidea	8	P
unidentified species		
Class Monogonata		
Order Ploima		
Trichoceridae		
Trichocerca spp.		
Brachionidae		
Keratella cochlearis	3	H
Lecane spp.		
Monostyla spp.		
Phylum Nematoda		
unidentified species	7, 8	P
Phylum Bryozoa		
Class Phylactolaemata		
Plumatellidae		
Plumatella	9	P
Phylum Annelida		
Class Oligochaeta		
unidentified species	7	P

Appendix 7.3 Continued.

Taxa	Habitat	References
Phylum Arthropoda		
Class Crustacea		
Order Cladocera		
Sididae		
Sida crystallina	8	H, F
Latona parviremis	7	H
Diaphanosoma brachyurum	7	H
Daphnidae		
Simocephalus serrulatus	7, 8	H
Scapholeberis mucronata	1	H
Ceriodaphnia reticulata	3	H
Ceriodaphnia spp.	3	H
Bosminidae		
Bosmina longirostris	3	H, F
Eubosmina coregoni		
Macrothricidae		
Ophryoxus gracilis		
Streblocerus serricaudatus		
Acantholeberis curvirostris		
Ilyocryptus spinifer		
Macrothrix laticornis	7	H
Chydoridae		
Eurycercus lamellatus		
Monospilus dispar		
Acroperus harpae	8	F, WWW
Kurzia latissima		
Camptocercus rectirostris		
Alona setulosa		
Alona guttata		
Alona affinis	8	WWW
Alona rectangula		
Oxyurella tenuicaudis		
Pleuroxus striatus		
Pleuroxus hamulatus		
Pleuroxus hastatus		
Pleuroxus denticulus	8, 7	WWW
Disparalona rostrata		
Alonella excisa		
Anchistropus minor		
Chydorus bicornutus		
Chydorus sphaericus	8, 7, 3	WWW
Polyphemidae		
Polyphemus pediculus	3	H

Appendix 7.3 Continued.

Taxa	Habitat	References
Order Eucopepoda		
Suborder Cyclopoida		
unidentified species	7, 3	H
Suborder Harpacticoida		
unidentified species	7	H
Order Podocopa		
unidentified ostracods	7, 8	P
Class Arachnoidea		
Hydracarina and Halacaridae		
unidentified species	8, 7, 3	P
Oribatei		
unidentified species	8	H
Spiders		
Dolomedes spp.	1, 6	P
Class Insecta		
Order Collembola		
Poduridae		
Podura aquatica	1	P
Order Ephemeroptera		
Caenidae		
Caenis spp.	8, 7	
Order Odonata		
Suborder Anisoptera		
unidentified species		
Suborder Zygoptera		
unidentified species		
Order Hemiptera		
Hebridae		
Merragata spp.	1	P
Mesoveliidae		
Mesovelia spp.	1	P
Veliidae		
Microvelia spp.	1	P
Notonectidae		
Notonecta spp.	6	P
Naucoridae		
Pelocoris spp.	8	P
Corixidae		
unidentified species	6	P
Order Trichoptera		
Hydroptilidae		
Oxyethira spp.	8	R
Oecetis spp.	7	
Order Lepidoptera		
Pyralidae		
unidentified species	8	P

Appendix 7.3 Continued.

Taxa	Habitat	References
Order Coleoptera		
Elmidae		
Stenelmis spp.		
Helodidae		
Scirtes spp.		
Cyphon spp.		
Order Diptera		
Chironomidae		
Pentaneura spp.	7, 8	
Corynoneura taris		
Psectrocladius elatus		
Psectrocladius sp. 3		
Psectrocladius sp. 4		
Psectrocladius sp. 6		
Cricotopus slossonae		
Cricotopus spp.		
Orthocladius spp.		
Hydrobaenus spp.	7, 8	
Pseudochironomus spp.	7	
Glyptotendipes senilis		
Glyptotendipes spp.		
Chironomus spp.		
Parachironomus spp.		
Stenochironomus spp.	7	
Tendipes l. neomodestus		
Kiefferulus sp. 1		
Kiefferulus sp. 2		
Polypedilum illinoense		
Polypedlum sp. 1		
Polypedilum sp. 2		
Polypedilum sp. 3		
Tanytarsus jucundus		
Tanytarsus sp. 2		
Tanytarsus tribelos		
Tanytarsus t. obedians		
Calopsectra sp. 1		
Calopsectra sp. 2		
Heleidae		
Alluadomyia spp.	7, 8, 3	MC
Order Hymenoptera		
Caraphractus cinctus	6, 8	
terrestrial ant	1	

Appendix 7.3 Continued.

Taxa	Habitat	References
Phylum Mollusca		
Class Gastropoda		
Order Basommatophora		
Ancylidae		
Ferrissia parallela	8	D
Phylum Chordata		
Class Osteichthyes		
unidentified species		

* Key to habitats

1. Surface film - Organisms living on the upper face, or attached to the underface, of the surface film. Including terrestrial invertebrates trapped in the surface film.

2. Pupae - Either on their way to the surface or hanging from the surface film.

3. Planktonic - Weakly swimming or drifting in the water column.

4. Planktonic swimmers - Strong swimmers in the water column.

5. Benthic swimmers - Rest on bottom, but active swimmers when disturbed.

6. Divers

7. Benthic clingers, sprawlers, and burrowers

8. Clingers, climbers, sprawlers, and miners on vascular plant parts

9. Growing (encrusting) on inanimate submerged objects, such as twigs, branches, rocks, on pebbles.

Appendix 7.3 Continued.

** References

P - Pennak (1978)
H - Hutchinson (1967)
MC - Merritt and Cumins (1978)
D - R. Dillon (personal communication)
F - Fairchild (1981)
WWW - Whiteside, Williams, and White (1978)
R - Ross (1944)

Table 7.4 Mean number of prey (N) and percent frequency of occurrence (%F) of 0-year class E. gloriosus and E. obesus during July 1979 in Success Lake.

Food Item	E. gloriosus SL = 7.02 mm n = 12		E. obesus SL = 9.06 n = 37	
	N	% F	N	% F
Sida crystallina	1.083	16.667	6.919	75.676
Latona parviremis	.083	8.333		
Simocephalus serrulatus			.027	2.703
Ceriodaphnia	.250	8.333		
Bosmina longirostris	1.417	41.667	.730	13.514
Ophryoxus gracilis	.083	8.333	.216	18.919
Ilyocryptus spinifer	.083	8.333		
Eurycercus lamellatus	.417	33.333	.757	18.919
Acroperus harpae	.167	8.333	.541	29.730
Alona guttata			.027	2.703
Pleuroxus striatus			.162	8.108
Pleuroxus hastatus	.250	16.667	.351	27.027
Disparalona rostrata			.027	2.703
Chydorus sphaericus	.583	33.333	.135	8.108
unidentified cladoceran	.167	16.667	1.000	24.324
Cyclopoid Copepod (small)			.027	2.703
Cyclopoid Copepod (medium)	.500	33.333	.730	45.946
Cyclopoid Copepod (large)	.083	8.333	.351	27.622
Hydracarina and Halacaridae			.081	8.108

Appendix 7.4 Continued.

Food Item	*E. gloriosus*		*E. obesus*	
	N	% F	N	% F
Pentaneura			.081	8.108
Polypedilum illinoense			.054	5.405
Calopsectra sp. 1			.027	2.703
unidentified Chironomid larva	.167	16.667		
Alluadomyia	.083	8.333	.054	2.703
Unicellular Algae			.216	8.108
Filamentous Algae			.054	5.405

Appendix 7.5 Mean number of prey (N) and percent frequency of occurence (%F) of 0-year class *E*. *gloriosus* and *E*. *obesus* during August 1979 in Success Lake.

Food Item	*E*. *gloriosus* SL = 11.65 mm n = 14		*E*. *obesus* SL = 12.96 mm n = 11	
	N	% F	N	% F
Arcella	.071	7.143	.636	18.182
Trichocerca			.091	9.091
Keratella cochlearis	.357	28.571	.091	9.091
Monostyla			.091	9.091
unidentified Rotifer	.071	7.143		
Oligochaeta			.091	9.091
Sida crystallina	.071	7.143	.182	18.182
Diaphanosoma brachyurum	4.643	28.571		
Scapholeberis mucronata	.071	7.143	1.727	54.545
Ceriodaphnia	.071	7.143	.091	9.091
Bosmina longirostris	1.000	14.286		
Macrothrix laticornis	.071	7.143	.091	9.091
Alona guttata	.214	21.429		
Pleuroxus hastatus			.091	9.091
Alonella excisa	.143	7.143	.818	27.273
Chydorus sphaericus			.273	27.273
unidentified cladoceran	.357	28.571	.273	27.273
Cyclopoid Copepod (medium)	14.429	100.000	4.727	81.818
Cyclopoid nauplius	.286	14.286	1.091	27.273

Appendix 7.5 Continued.

	E. gloriosus		*E. obesus*	
	N	%F	N	%F
Hydracarina and Halacaidae	.143	14.286	1.727	63.636
Oribatei			1.273	45.455
Notonecta			.091	9.091
Oxyethira			.091	9.091
Stenelmis			.182	18.182
Pentaneura	.857	50.000	.818	54.545
Corynoneura taris			.091	9.091
Psectrocladius sp. 3	.071	7.143		
Pseudochironomus	.143	7.143	.091	9.091
Polypedilum sp. 1	.286	14.286	.455	27.273
Polypedilum sp. 2	.071	7.143	1.727	72.727
Calopsectra sp. 1	.143	14.286		
unidentified Chironomid larva	.286	21.429	.182	18.182
Alluadomyia	.143	7.143	.909	27.273
Caraphractus cinctus			.091	9.091
unidentified Aquatic Insect	.071	7.143	.273	27.273
Ferrissia parallela	.071	7.143		
Filamentous Algae			.545	9.091
Plant Part			.182	9.091
Pine Pollen	.143	7.143	.091	9.091

Appendix 7.6 Mean number of prey (N) and percent frequency of occurrence (%F) of 0-year class *E. gloriosus* and *E. obesus* during July 1980 in Success Lake.

	E. gloriosus SL = 7.68 mm n = 20 mm		*E. obesus* SL = 12.21 mm n = 3	
Food Item	N	% F	N	% F
Difflugia	.050	5.000		
Trichocerca	.100	10.000		
Keratella cochlearis	.050	5.000		
Oligochaeta	.050	5.000		
Sida crystallina	.900	30.000	5.000	100.000
Latona parviremis	.050	5.000		
Diaphanosoma brachyurum	1.100	30.000		
Ceriodaphnia	.450	20.000		
Bosmina longirostris	.250	25.000		
Ophryoxus gracilis	.150	10.000	1.000	66.667
Ilyocryptus spinifer	.100	10.000		
Eurycercus lamellatus			.667	33.333
Acroperus harpae	.050	5.000		
Alona affinis	.200	15.000		
Pleuroxus hastatus	.050	5.000	1.000	66.667
Anchistropus minor	.050	5.000		
Chydorus bicornutus	.100	10.000		
unidentified cladoceran			1.000	33.333

Appendix 7.6 Continued.

Food Item	*E. gloriosus* N	*E. gloriosus* % F	*E. obesus* N	*E. obesus* % F
Cyclopoid Copepod (small)	.900	20.000		
Cyclopoid Copepod (medium)	1.400	55.000	.667	33.333
Cyclopoid Copepod (large)	.150	5.000		
Caenis	.250	20.000		
Merragata			.333	33.333
Pentaneura	.100	10.000	1.333	66.667
Corynoneura taris	.050	5.000	.333	66.667
Psectrocladius elatus	.100	5.000	.333	33.333
Psectrocladius sp. 3	.150	15.000		
Calopsectra sp. 1	.200	20.000	.333	33.333
unidentified Chironomid larva			.333	33.333
unidentified Chironomid pupa	.050	5.000	.333	33.333
Unicellular Algae	.050	5.000	.333	33.333
Filamentous Algae	.200	15.000	1.333	33.333
Plant Part	.100	5.000		
Pine Pollen	.150	10.000		
Sand Grain	.150	10.000	.333	33.333
Detritus	.200	20.000	.333	33.333

Appendix 7.7 Mean number of prey (N) and percent frequency of occurrence (%F) of 0-year class E. gloriosus and E. obesus on 13 August 1980 at Success Lake.

Food Item	E. gloriosus SL = 12.44 mm n = 151		E. obesus SL = 13.26 mm n = 48	
	N	% F	N	% F
Arcella	.152	11.921	.208	16.667
Difflugia	.093	7.285		
Trichocerca	.093	6.623	.229	16.667
Keratella cochlearis	.477	14.570	1.979	25.000
Lecane	.007	.662	.063	4.167
Monostyla	.053	5.298	.083	8.333
unidentified Rotifer	.192	10.596	.125	12.500
Oligochaeta	.033	3.311	.063	4.167
Sida crystallina	.099	5.960	.083	8.333
Latona parviremis	.033	3.311	.021	2.083
Ceriodaphnia reticulata	.053	5.298	.021	2.083
Bosmina longirostris	.424	13.907	.083	8.333
Streblocerus serricaudatus	.066	3.311	.063	4.167
Ilyocryptus spinifer	.325	22.517	.292	18.750
Eurycercus lamellatus	.007	.662	.021	2.083
Acroperus harpae	.040	2.649	.083	6.25
Alona setulosa	.013	1.325		
Alona rectangula	.205	17.219	.083	8.333
Pleuroxus hamulatus	.013	.662		

Appendix 7.7 Continued.

Food Item	*E. gloriosus* N	*E. gloriosus* % F	*E. obesus* N	*E. obesus* % F
Pleuroxus hastatus	.020	1.325	.083	4.167
Disparalona rostrata	.040	2.649	.021	2.083
Alonella excisa	.252	17.881	1.375	39.583
Chydorus bicornutus	.139	8.609	.042	2.083
Chydorus sphaericus	.483	30.464	.396	18.750
unidentified cladoceran	.735	42.384	1.604	58.333
Cyclopoid Copepod (medium)	27.457	98.013	9.708	93.750
Cyclopoid nauplius	.517	20.530	.271	22.917
Harpacticoid Copepod	.046	3.311		
Hydracarina and Halacaidae	.629	33.775	1.979	70.833
Oribatei	.371	19.205	8.708	85.417
Dolomedes			.021	2.083
Podura aquatica	.020	1.325	.021	2.083
Caenis	.132	11.258	.042	4.167
Anisoptera	.007	.662		
Zygoptera			.083	8.333
Merragata	.007	.662	.021	2.083
Oxyethira	.132	9.272	.250	14.583
Oecetis	.007	.662		
unidentified Trichoptera	.007	.662		
unidentified Lepidoptera	.007	.662		
Scirtes	.007	.662	.021	2.083
Pentaneura	.411	27.815	.708	41.667
Orthocladius	.066	5.298	.042	4.167

Appendix 7.7 Continued.

Food Item	E. gloriosus N	E. gloriosus %F	E. obesus N	E. obesus %F
Parachironomus			.021	2.083
Polypedilum illinoense	.132	9.934	.438	33.333
Tanytarsus tribelos	.007	.662	.104	6.250
Calopsectra sp. 1	.146	11.921	.167	10.417
unidentified Chironomid larva	.987	48.344	4.625	70.833
unidentified Chironomid pupa	.007	.662	.042	4.167
Alluadomyia	.053	5.298	.125	12.500
Caraphractus cinctus	.007	.662	.208	16.667
unidentified Terrestrial Insect	.020	1.325	.063	2.083
unidentified Aquatic Insect	.066	4.636	.229	20.833
Ferrissia parallela	.199	8.609	.188	14.583
Unicellular Algae	.079	5.960	.083	8.333
Filamentous Algae	.192	5.960	.292	8.333
Plant Part	.013	1.325	.042	2.083
Pine Pollen	.086	1.325	.021	2.083
Detritus	.013	1.325	.021	2.083

Appendix 7.8 Mean number of prey (N) and percent frequency of occurrence (%F) of 1+-year class E. gloriosus and E. obesus on 13 August 1980 at Success Lake.

Food Item	E. gloriosus SL = 29.88 mm n = 8		E. obesus SL = 23.27 mm n = 29	
	N	% F	N	% F
Arcella			.034	3.448
Monostyla			.034	3.448
Oligochaeta	.125	12.500		
Sida crystallina			.034	3.448
Latona parviremis	.125	12.500	.034	3.448
Streblocerus serricaudatus	.125	12.500		
Ilyocryptus spinifer			.172	13.793
Alona setulosa	.250	12.500		
Alona rectangula			.034	3.448
Pleuroxus hamulatus			.034	3.448
Pleuroxus hastatus			.034	3.448
Alonella excisa			.690	10.345
Chydorus sphaericus	.125	12.500	.310	27.586
unidentified cladoceran			.414	31.034
Cyclopoid Copepod (medium)	2.000	75.000	2.276	58.621
Cyclopoid nauplius	.125	12.500	0.103	6.897
Harpacticoid Copepod			.034	3.448
Hydracarina and Halacaridae	.125	12.500	.621	24.138
Oribatei	.875	25.000	5.690	75.862

Appendix 7.8 Continued.

Food Item	*E. gloriosus*		*E. obesus*	
	N	%F	N	%F
Dolomedes			.103	10.344
Podura aquatica	.250	25.000	.069	6.897
Caenis	1.000	62.500	.793	37.931
Anisoptera			.103	6.897
Merragata			.034	3.448
Notonecta	.125	12.500	.034	3.448
Corixid adult	.125	12.500		
Oxyethira			.483	27.586
Oecetis	.375	25.000	.034	3.448
Pentaneura	.625	50.000	.414	24.138
Orthocladius			.069	3.448
Polypedilum illinoense			.241	20.690
Tanytarsus tribelos			.138	10.345
Calopsectra sp. 1	.125	12.500	.172	13.793
unidentified Chironomid larva	.875	50.000	1.793	65.517
unidentified Chironomid pupa			.034	3.448
Alluadomyia			.207	20.690
Caraphractus cinctus	.250	25.000	.069	6.897
unidentified Terrestrial Insect	.125	12.500	.172	13.793
unidentified Aquatic Insect			.276	24.138
Ferrissia parallela	.125	12.500	1.552	44.828
Fish	.125	12.500		

Appendix 7.8 Continued.

Food Item	E. gloriosus N	E. gloriosus %F	E. obesus N	E. obesus %F
Filamentous Algae	.125	12.500	.241	6.897
Plant Part			.069	6.897
Pine Pollen			.034	3.448
Seed	.250	12.500	.034	3.448
Sand Grain	.125	12.500		
Detritus	.125	12.500	.034	3.448

Appendix 7.9 Mean number of prey (N) and percent frequency of occurrence (%F) of 0-year class *E. gloriosus* and *E. obesus* during August 1980 in Success Lake.

	E. gloriosus SL = 13.83 mm n = 53		*E. obesus* SL = 15.30 mm n = 11	
Food Item	N	% F	N	% F
Arcella	.075	7.547	.091	9.091
Difflugia	.132	7.547		
Centropyxis			.091	9.091
Porifera gemmule	.019	1.887		
Bdelloid Rotifer	.264	11.321	1.727	27.273
Trichocerca	.019	1.887	.091	9.091
Keratella cochlearis	.377	16.981	.818	18.182
Monostyla	.038	3.774		
Nematoda	.057	1.887		
Plumatella	.057	5.660		
Plumatella floatoblast	.019	1.887		
Oligochaeta	.528	41.509	.636	63.636
Sida crystallina	.642	35.849	.192	9.091
Latona parviremis	.170	15.094	.182	9.091
Diaphanosoma brachyurum	.226	20.755	.182	18.182
Simocephalus serrulatus	.132	13.208	.182	18.182
Scapholeberis mucronata	.019	1.887		
Bosmina longirostris	5.075	47.170	1.182	36.364
Ilyocryptus spinifer	1.113	49.057	1.727	45.455

Appendix 7.9 Continued.

Food Item	*E. gloriosus* N	*E. gloriosus* % F	*E. obesus* N	*E. obesus* % F
Macrothrix laticornis	.132	9.434	.091	9.091
Eurycercus lamellatus	.038	3.774		
Acroperus harpae	.189	18.869	3.818	27.273
Alona guttata	.660	39.623	1.364	45.455
Oxyurella tenuicaudis			.091	9.091
Disparalona rostrata	.340	20.755	.545	27.273
Alonella excisa	.038	3.774	3.000	36.364
Chydorus bicornutus	.019	1.887		
Chydorus sphaericus	1.509	58.491	2.273	63.636
unidentified cladoceran	.208	18.868	.364	18.182
Cyclopoid Copepod (small)	4.226	37.736	1.000	36.364
Cyclopoid Copepod (medium)	22.906	94.339	5.182	100.000
Cyclopoid Copepod (large)	.321	20.755	.364	18.182
Cyclopoid nauplius	.415	33.962	.091	9.091
Ostracoda			.091	9.091
Hydracarina and Halacaidae	.208	16.981	1.091	63.636
Oribatei	.038	1.887	5.812	63.636
Caenis	.075	5.660	.455	9.091
Anisoptera	.019	1.887		

Appendix 7.9 Continued.

Food Item	*E. gloriosus* N	*E. gloriosus* % F	*E. obesus* N	*E. obesus* % F
Zygoptera	.038	3.774	.091	9.091
Corixid nymph	.019	1.887		
Oxyethira	.170	15.094	.091	9.091
Oecetis				
unidentified Trichoptera			.182	18.182
unidentified Lepidoptera	.057	5.660		
Pentaneura	.567	32.075	.455	36.364
Corynoneura taris			.455	27.273
Psectrocladius sp. 3	.019	1.887		
Psectrocladius sp. 4	.038	3.774		
Cricotopus slossonae	.509	32.075	.727	36.364
Orthocladius	.170	9.434	.364	9.091
Stenochironomus	.019	1.887		
Tendipes l. neomodestus	.038	3.774	.091	9.091
Kiefferulus sp. 1	.019	1.887		
Polypedilum illinoense	.075	7.547	.273	27.273
Polypedilum sp. 2			.091	9.091
Tanytarsus tribelos	.019	1.887		

Appendix 7.9 Continued.

Food Item	*E. gloriosus* N	*E. gloriosus* % F	*E. obesus* N	*E. obesus* % F
Tanytarsus t. obedians	.038	3.774		
Calopsectra sp. 1	.642	35.849	.727	36.364
Calopsectra sp. 2	.038	3.774	.091	9.091
unidentified Chironomid pupa	.057	5.660	.091	9.091
Alluadomyia	.075	7.547	.182	18.182
Ferrissia	.019	1.887	.091	9.091
Unicellular Algae	.113	7.547	.182	18.182
Filamentous Algae	1.849	45.283	3.727	72.727
Plant Part	.057	5.660		
Pine Pollen	.132	7.547	.182	18.182
Sand Grain	2.792	28.302	.364	36.364

Appendix 7.10 Mean number of prey (N) and percent frequency of occurrence (%F) of 1+-year class _E_. _gloriosus_ and _E_. _obesus_ during August 1980 in Success Lake.

	_E_. _gloriosus_ SL = 32.45 mm n = 12		_E_. _obesus_ SL = 24.46 n = 37	
Food Item	N	% F	N	% F
Arcella	.250	16.667	.081	8.108
Difflugia	.250	8.333	.054	5.405
Porifera gemmule			.027	2.703
Bdelloid Rotifer			1.324	8.108
Trichocerca			.027	2.703
Keratella cochlearis			.027	2.703
Monostyla			.027	2.703
Nematoda			.108	5.405
Plumatella	.083	8.333	.243	2.703
Oligochaeta	.250	25.000	.540	43.243
Sida crystallina	.083	8.333	.378	18.919
Latona parviremis	.083	8.333	.162	13.514
Diaphanosoma brachyurum	.083	8.333		
Simocephalus serrulatus	.083	8.333	.054	5.405
Scapholeberis mucronata			.027	2.703
Bosmina longirostris	.583	16.667	.378	16.216
Ilyocryptus spinifer	.417	16.667	1.081	32.432
Macrothrix laticornis			.108	2.703
Monospilus dispar			.027	2.703

Appendix 7.10 Continued.

Food Item	*E. gloriosus* N	*E. gloriosus* % F	*E. obesus* N	*E. obesus* % F
Acroperus harpae	.083	8.333	.297	10.811
Kurzia latissima			.027	2.703
Alona guttata			.054	5.405
Pleuroxus hastatus			.054	2.703
Disparalona rostrata			.135	10.811
Alonella excisa			.108	2.703
Chydorus bicornutus			.081	2.703
Chydorus sphaericus	.083	8.333	.595	27.027
Polyphemus pediculus			.081	5.405
unidentified cladoceran	.083	8.333	.270	16.216
Cyclopoid Copepod (small)	.167	16.667	.595	29.730
Cyclopoid Copepod (medium)	.667	25.00	1.973	59.459
Cyclopoid Copepod (large)	.250	8.333	.730	32.432
Cyclopoid nauplius			.054	5.405
Harpacticoid Copepod			.027	2.703
Hydracarina and Halacaidae			1.000	29.730
Oribatei			1.324	45.946
Caenis	.167	16.667	.297	18.919
Anisoptera			.027	2.703

Appendix 7.10 Continued.

Prey Item	*E. gloriosus* N	*E. gloriosus* % F	*E. obesus* N	*E. obesus* % F
Zygoptera	.083	8.333	.216	16.216
Hebrus			.216	10.811
Mesovelia			.054	2.703
Microvelia			.054	5.405
Pelocoris			.108	5.405
Corixid adult	.333	33.333	.162	10.811
Corixid nymph			.027	2.703
unidentified Hemiptera			.081	8.108
Oxyethira			.135	13.514
Oecetis sp.			.027	2.703
unidentified Trichoptera	.083	8.333	.027	2.703
unidentified Lepidoptera			.054	5.405
unidentified Coleoptera			.027	2.703
Pentaneura	.167	8.333	.541	24.324
Corynoneura taris	.083	8.333	.270	10.811
Psectrocladius sp. 3			.054	5.405
Cricotopus slossonae	.083	8.333	.243	16.217
Orthocladius	.583	8.333		
Hydrobaenus			.027	2.703

Appendix 7.10 Continued.

Prey Item	*E. gloriosus* N	*E. gloriosus* % F	*E. obesus* N	*E. obesus* % F
Glyptotendipes senilis	.083	8.333		
Glyptotendipes spp.			.027	2.703
Chironomus			.054	5.405
Tendipes l. neomodestus	.083	8.333		
Kiefferulus sp. 2	.167	8.333		
Polypedilum illinoense			.514	21.622
Polypedilum sp. 2			.027	2.703
Polypedilum sp. 3			.054	5.405
Tanytarsus tribelos	.083	8.333	.081	2.703
Tanytarsus t. obedians	.083	8.333		
Calopsectra sp. 1	1.333	33.333	1.405	29.730
Calopsectra sp. 2			.054	5.405
unidentified Chironomid larva	.417	33.333	.432	24.324
unidentified Chironomid pupa	.250	16.667	.135	10.811
unidentified Chironomid adult			1.297	18.919
Alluadomyia			.486	32.432
Caraphractus cinctus			.216	16.216
ant			.027	2.703
unidentified Aquatic Insect	.083	8.333	.054	5.405
Ferrissia parallela	.167	8.333	.189	13.514
Unicellular Algae			.081	2.703
Filamentous Algae	3.917	41.667	12.324	56.757

Appendix 7.10 <u>Continued</u>.

Prey Item	*E. gloriosus* N	*E. gloriosus* % F	*E. obesus* N	*E. obesus* % F
Plant Part			.027	2.703
Pine Pollen	.167	8.333	.162	13.514
Seed	.833	41.667	.135	10.811
Sand Grain	2.167	41.667	6.432	45.946
Detritus	.167	16.667		

Appendix 7.11 Mean number of prey (N) and percent frequency of occurrence (%F) of 0-year and 1+-year class *E. gloriosus* during October 1980.

Food Item	0-year class SL = 16.00 mm n = 19		1+-year class SL = 20.05 mm n = 14	
	N	% F	N	% F
Difflugia	.053	5.263	.214	21.429
Centropyxis			1.357	7.143
Porifera spicules			.143	14.286
Bdelloid Rotifer	.053	5.263		
unidentified Rotifer	.211	21.053		
Nematoda	.158	84.210	.500	35.714
Plumatella	.158	15.789	.214	7.143
Oligochaeta	.789	78.947	.429	42.857
Sida crystallina	.053	5.263	.071	7.143
Latona parviremis	.105	5.263		
Simocephalus serrulatus	.368	21.053	.143	14.286
Scapholeberis mucronata	.053	5.263		
Bosmina longirostris	3.158	57.895	3.714	42.857
Eubosmina coregoni	.368	10.526		
Ilyocryptus spinifer	.895	57.895	.357	21.429
Macrothrix laticornis	.211	21.053		
Acroperus harpae	.053	5.263	.143	14.286
Camptocercus rectirostris	.105	10.526		
Alona guttata	.263	15.789	.429	21.429
Alona affinis	.053	5.263	.071	7.143

Appendix 7.11 Continued.

Food Item	0-year class N	0-year class % F	1+ -year class N	1+ -year class % F
Alona rectangula	.158	15.789	.143	7.143
Pleuroxus striatus	.105	10.526		
Pleuroxus hastatus	.211	10.526		
Pleuroxus denticulus	.053	5.263		
Alonella excisa	2.474	78.947	2.071	57.143
Chydorus bicornutus	1.211	42.105	1.143	42.857
Chydorus sphaericus	1.474	57.895	.714	42.857
unidentified cladoceran	.105	10.526	.143	14.286
Cyclopoid Copepod (small)	16.316	84.211	5.929	35.714
Cyclopoid Copepod (medium)	5.105	100.000	2.357	64.286
Cyclopoid Copepod (large)	.421	16.667	.500	50.000
Cyclopoid nauplius	.526	15.789	.071	7.143
Harpacticoid Copepod	.053	5.263		
Hydracarina and Halacaridae	.579	42.105	.714	57.143
Oribatei	.579	31.579	.500	28.571
Caenis	.789	36.842	.857	57.143
Zygoptera			.214	14.286
Corixid adult			.143	14.286
Corixid nymph			.071	7.143
Oxyethira	.053	5.263	.286	28.571
unidentified Trichoptera	.053	5.263	.286	14.286
unidentified Lepidoptera	.053	5.263	.071	7.143
Cyphon	.053	5.263		
Pentaneura	.263	21.053	.071	7.143

Appendix 7.11 Continued.

Food Item	0-year class N	0-year class % F	1+ -year class N	1+ -year class % F
Corynoneura taris			.143	14.286
Psectrocladius sp. 3	.105	10.526		
Psectrocladius sp. 6	.105	10.526		
Cricotopus slossonae	2.316	52.632	2.286	64.286
Cricotopus sp.	.053	5.263		
Hydrobaenus	.105	10.526		
Glyptotendipes	.053	5.263	.571	21.429
Chironomus	.684	10.526	.071	7.143
Parachironomus	.053	5.263	.214	21.429
Polypedilum illinoense	.158	15.789	.143	14.286
Tanytarsus jucundus	.053	5.263	.071	7.143
Tanytarsus sp. 2	.158	10.526	.071	7.143
Tanytarsus tribelos	.105	5.263		
Tanytarsus t. obedians			.143	14.286
Calopsectra sp. 1	.842	47.368	.571	42.857
unidentified Chironomid larva			.643	35.714
unidentified Chironomid pupa	.105	10.526	.071	7.143
Alluadomyia	.053	5.263		
Ferrissia parallela	.368	31.579	.214	14.286

Appendix 7.11 Continued.

Food Item	0-year class		1+ -year class	
	N	% F	N	% F
Filamentous Algae	.526	68.421	.214	14.286
Plant Part	.211	15.789	.429	42.857
Pine Pollen	.211	15.789		
Sand Grain	.368	15.789	.857	7.143
Detritus	.368	15.789	.071	7.143

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