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Ecomorphological diet predictions: an assessment using inland silverside (*Menidia beryllina*) and longear sunfish (*Lepomis megalotis*) from Lake Texoma

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Abstract

The functions of an organism's morphological structures indicate the organism's potential resource use (fundamental niche). While this information often is also used to predict differences in actual resource use (realized niche) among individuals or species, such predictions may not be accurate because the maximum abilities may not be useful to the organism under specific conditions or in specific environments. We investigated the importance of six previously studied morphologically based performance abilities/constraints in structuring the diet of *Menidia beryllina* (inland silverside) and *Lepomis megalotis* (longear sunfish) in Lake Texoma, a reservoir in the Red River basin (Oklahoma-Texas, USA). Of the six morphological characteristics measured (number of gill rakers, length of gill rakers, space between gill rakers, eye lens diameter, mouth size, mouth protrusibility), only one characteristic for *M. beryllina* (mouth size) and three for *L. megalotis* (space between rakers, mouth size, and raker length) correlated with the gut contents as predicted by previous functional morphology studies. This indicates that caution should be exercised when making untested predictions about the ecology of an organism based on its functional morphology.

Introduction

Ecomorphological research (Keast & Webb, 1966; Sage & Selander, 1975; Findley, 1976; Ricklefs & Cox, 1977; Smartt, 1978; Gatz, 1981; Miller, 1984; Mittlebach et al., 1992; Shelton et al., 1995; Turingan et al., 1995) has demonstrated that the functions of an organism's morphological structures set maximum limits for the organism's potential resource use (i.e., fundamental niche-Hutchinson 1957). For example, the largest sized prey a predator can handle and ingest is often limited by the predator's mouth size. These morphology-ecology relationships are often used to predict differences in resource use among individuals or species. However, these predictions assume that differences in potential resource use (fundamental niche) always leads to differences in actual resource use (realized niche-Hutchinson 1957). Despite its importance, this assumption has often been overlooked and morphology has been assumed to be an accurate measure of ecological behavior (Findley, 1976; Ricklefs & Cox, 1977; MacNeill & Brandt, 1990; Wel & Desheng, 1990; Aksnes & Giske, 1993; Sibbing et al., 1994; Wainwright, 1996). The purpose of this study was to investigate the role potential resource use plays in structuring actual resource use by fish at the intraspecific level.

There are several reasons why differences in potential resource use between individuals may not lead to differences in actual resource use. First, a morphological structure may only be useful during specific periods of the organism's life (i.e., specific stages of ontogeny [Osse, 1985], specific seasons [Wiens & Rotenberry, 1980], or under specific conditions of competition [Werner & Hall, 1976, 1979] or resource abundance [Wainwright, 1987, 1988]). Therefore, selection encountered under these specific conditions can maintain the morphological difference between individuals, but this difference may have no effect on resource use of the individuals over the majority of their lives. Second, the morphological structure may have more than one potential function (Barel, 1983). Only one function needs to be utilized for the structure to be adaptive. Other potential functions may not be used. Thirdly, the morphological structure may not be used due to the absence of a specific behavior or motor pattern that is required for the morphology to serve its function (Wainwright & Lauder, 1992). Fourth, a morphological structure may persist only as a genetic artifact if it is linked to a useful gene or has only recently lost its usefulness to the organism such that natural selection has not yet eliminated it from the population.

Although functional morphology often does correlate with an animal's potential resource use (Keast & Webb, 1966; Sage & Selander, 1975; Findley, 1976; Ricklefs & Cox, 1977; Smartt, 1978; Gatz, 1981; Miller, 1984; Mittlebach et al., 1992; Shelton et al., 1995; Turingan et al., 1995), we argue that these correlations should not be assumed accurate without testing to confirm the relevance of the morphological ability/constraint to the organism under the conditions in its specific environment (Wainwright, 1987, 1991; Sibbing, 1988; Kotrschal, 1989; Douglas & Matthews, 1992).

The purpose of this study was to determine if intraspecific differences in morphologically established performance constraints/abilities lead to differential resource use by organisms in their environment. To accomplish this, we tested to see if differences in six morphological characteristics (number of gill rakers, length of gill rakers, space between gill rakers, eye lens diameter, mouth size, and mouth protrusibility) were reflected by corresponding differences in food use by two littoral fishes (*Menidia beryllina* [Cope] [inland silverside] and *Lepomis megalotis* [Rafinesque] [longear sunfish]) in Lake Texoma, a reservoir in Oklahoma and Texas, USA. The six investigated morphological characteristics have well documented functional significance to food selection (Table 1), and are therefore generally thought to predict diet. However, because these fishes do not have a long evolutionary history in this ecosystem (the system has only been impounded since 1944 and *M. beryllina* have only been observed in the system since 1953 [Riggs & Bonn, 1959]), we hypothesized that for both species, individual differences in morphology would not be related to differences in diet. To test this, we first determined the potential capabilities of each individual by measuring morphological characteristics and comparing them to diet predictions from the functional morphology literature. We then compared these potential capabilities to the actual diet (determined by gut contents analysis).

Description of site studied

Lake Texoma is a large (36 000 ha) impoundment in Oklahoma and Texas. It was impounded in 1944 when the Denison Dam was constructed at the junction of the Red and Washita Rivers. The Red and Washita arms of the reservoir have a maximum depth of about 18 m; the maximum depth of the main basin by the dam is 22–26 m (Matthews et al., 1985). Since the time of impoundment, the reservoir has experienced large annual water fluctuations (Cone et al., 1986) which have deterred macrophyte growth (Gelwick & Matthews, 1990). The lake has unusually high salinity (750–1200 micro-mhos [Gelwick & Matthews, 1990]). Average secchi depth is 1.0–1.8 m, but is considerably less during periods of heavy runoff (Matthews et al., 1985).

Materials and methods

Menidia beryllina and *L. megalotis* were selected for this study due to their high littoral zone abundance in Lake Texoma (Gelwick & Matthews, 1990) and their distinctly different morphologies. From September 24 to November 18, 1993 we collected fish approximately weekly from the Rock Creek Cove of Lake Texoma using a 4.5 m seine. Additional fish samples from 1980–1988 were obtained from W. J. Matthews' Lake Texoma fish collection housed at the University of Oklahoma Biological Station. This collection contains fish collected from many locations on Lake Texoma using seines of various sizes.

We attempted to use approximately equal numbers of fish from each year, each season (spring, summer, and fall), and each sample (3–5 fish per species if available). We also tried to use the widest size range possible. All fish were fixed in 10% formalin for approximately 7 days and then stored in 50% isopropyl alcohol.

To determine the morphology of each individual, we used Helios calipers to measure the total length, mouth width (maximum lateral distance across the inside of the closed mouth), and mouth protrusibility (snout length with mouth open minus snout length with mouth closed) for each individual fish. Next we measured the lens diameter of the left eye (linear distance between the anterior-most and posterior-most part of

Table 1. The predicted relationship between morphology of fish and trophic ability based on the functional morphology literature.

Ecomorphology prediction from the literature	Citations
Prey Size	
Fish with smaller spaces between rakers eat smaller prey	Suyehiro 1943[2]; Alexander 1967a[4]; Kliewer 1970[1]; Beumer 1978[2]; Wankowski 1979[1]; Schmidt & O'Brien 1982[1]; Gross & Anderson 1984[1]; Kumar & John 1986[2]; Mummert & Drenner 1986[1]; Gibson 1988[1]; van den Berg et al. 1992[3]; Hoogenboezem et al. 1993[1] – but note cautions by Wright et al. 1983[1], van den Berg et al. 1993[2].
Fish with larger eyes (lenses) eat smaller prey	Blaxter & Jones 1967[1]; Hester 1968[1]; Hairston et al. 1982[1]; Breck & Gitter 1983[1]; Miller et al. 1993[3].
Fish with larger mouths eat larger prey	Northcote 1954[3]; Lawrence 1957[1]; Hartman 1958[1]; Thomas 1962[2], Alexander 1967a[4]; Larson 1976[1]; Werner 1977[2]; Beumer 1978[2]; Gatz 1979[2]; Wankowski 1979[1]; Matthews et al. 1982[2]; Dewey 1988[3]; Prejs et al. 1990[1]; Hambright 1991[1]; Mookerji & Ramakrishna Rao 1994[1]; Shelton et al. 1995[1] – but see Hart & Hamrin 1988[1].
Prey Type	
Fish with more rakers are more planktivorous	Hagen & Gilbertson 1971[1]; Lindsey 1981[2]; Crowder 1984[1]; Gross & Anderson 1984[1]; Bornbusch 1988[2]; Hessen et al. 1988[2]; Malmquist 1992[1]; Humphries 1993[2] – but see Kliewer 1970[1].
Fish with longer rakers are more planktivorous and fish with shorter rakers are more benthivorous	Kliewer 1970[1]; Bentz 1976[2]; Chao & Musick 1977[2]; Beumer 1978[2]; Lindsey 1981[2]; Crowder 1984[1]; Gross & Anderson 1984[1]; Dewey 1988[3]; Magnan 1988[1]; Malmquist 1992[1]; Mullaney & Gale 1996[1].
Fish with smaller spaces between rakers are more planktivorous and fish with larger spaces between rakers are more benthivorous	Magnuson & Heitz 1971[4]; Bentz 1976[2]; Gross & Anderson 1984[1]; Ibrahim & Huntingford 1988[1]; Robinson et al. 1993[1] – but note Suyehiro 1943[2]; Kliewer 1970[1]; Robinson et al. 1993[1].
Fish with larger eyes (lenses) are more planktivorous	Chao & Musick 1977[2].
Fish with more mouth protrusability are more benthivorous	Suyehiro 1943[2]; Alexander 1967a[4], 1967b[2]; Chao & Musick 1977[2]; Motta 1984[4]; Osse 1985[4]; Elshoud-Oldenhave et al. 1989[2].

[1] Intraspecific study.
[2] Interspecific study.
[3] Both intraspecific and interspecific relationships studies.
[4] Study not specific to either intra- or interspecific relationships.

the lens) using an optical micrometer. Lens diameter was the eye size measurement chosen because it is a very good estimate of visual acuity (Hester, 1968; Collin & Pettigrew, 1989; Shand, 1994). After removing the first gill arch on the left side, we counted the number of gill rakers (including rudimentary rakers) on the upper and lower limb of the gill arch. We then measured the length of each raker as the linear distance between the tip of the raker and the center of its point of attachment to the gill arch, and measured the space between the base of each pair of adjacent rakers. All gill raker morphology was measured using an optical micrometer.

To determine the range of prey types and sizes eaten by each individual, we first removed the entire gut from the fish. For *M. beryllina*, which lacks a distinct stomach, all prey items up to the first bend in the intestine were categorized as surface, pelagic, or benthic dwelling and counted. For *L. megalotis*, all prey items in the stomach were similarly enumerated. Prey items which could occur in more than one category (i.e. *Chaoborus*) were measured (see below) but not enumerated into a category. Because such items were rarely encountered, this probably did not significantly bias the gut contents analysis. Additionally, we measured the maximum width (excluding all legs, spines, wings, etc.) of the anterior-most 100 intact prey items (or all items if the gut contained <100 items) using an optical micrometer. Prey which had been macerated or partially digested were not measured but were enumerated by identifying head capsules or other digestion-resistant structures (Bowen, 1983).

All measurements were made to the nearest 0.1 mm. Optical micrometer measurements for *M. beryllina* and *L. megalotis* were made at 25 × and 10 × magnification respectively with an Olympus SZ3060 dissecting microscope.

Table 2. Variables analyzed by Pearson's product moment coefficient correlation analysis to determine if *Menidia beryllina* and *Lepomis megalotis* from Lake Texoma used differences in morphology to intraspecifically partition their food niches.

Measured prey variable	Morphology of fish
Prey Size (mean prey width)	Mean space between gill rakers
	Eye lens diameter
	Mouth width
% of Prey in gut that were pelagic	Number of gill rakers
	Mean gill raker length
	Mean space between gill rakers
	Eye lens diameter
% of Prey in gut that were benthic	Mean gill raker length
	Mean space between gill rakers
	Mouth protrusibility

All pairs of variables in Table 2 were tested for significant correlations. The tests were performed on the data from the two fish species separately. Prior to this analysis, an ANOVA followed by a Tukey Test was performed to determine if any of the measured prey variables showed significant seasonal differences. When no seasonal differences in prey variables were found, data from all seasons were pooled and a Pearson product moment correlation analysis and subsequent t-test (testing the null hypothesis of $r = 0$) were used to test for linear relationships between the variables. When seasonal differences in prey variables were detected, we used a stepwise multiple regression analysis and subsequent F-test to determine if the two variables were still significantly correlated when the variation due to season had been controlled.

Results

We analyzed a total of 106 *M. beryllina* and 116 *L. megalotis*. Five *M. beryllina* and 14 *L. megalotis* had no discernible items in the gut and were subsequently dropped from the analysis, yielding a sample size of 101 *M. beryllina* and 102 *L. megalotis*. These samples consisted of approximately equal numbers of individuals collected during spring (33 *M. beryllina*, 33 *L. megalotis*), summer (32 *M. beryllina*, 32 *L. megalotis*), and fall (36 *M. beryllina*, 37 *L. megalotis*). There were no significant seasonal differences in the type (surface, pelagic, or benthic dwelling) of prey eaten by fish of either species (Figure 1). Similarly, no seasonal differences were found for the prey size consumed by *L. megalotis* (Figure 1). *Menidia beryllina* did however consume significantly smaller prey in the fall than during the spring or summer (Figure 1).

A summary of the morphological characters and measured gut contents of both species are in Tables 3 and 4 respectively. Despite the wide range of fish sizes analyzed, the range of mean gill raker spaces for *M. beryllina* was fairly small (0.1 mm). All other measured morphological characteristics for both species had a relatively large range (Table 3). While most *M. beryllina* predominately ate pelagic prey (zooplankton) and most *L. megalotis* ate predominately benthos (chironomids), the range in the percent of prey types (surface, pelagic, or benthic dwelling) eaten by each species was relatively high (Table 4). Similarly, the range of prey sizes eaten by each species was large (Table 4).

None of the measured morphological characteristics that functionally enhance an individual's ability to eat pelagic prey (i.e. greater number of gill rakers, longer raker length, smaller raker spaces, or larger eye size [Table 1]) were significantly ($p < 0.05$) correlated with the percent of pelagic prey in the gut for either species (Figure 2). For *Menidia beryllina*, there was additionally no measured morphological characteristic that enhances an individual's ability to eat benthic prey (i.e. shorter gill raker length, larger raker spaces, or greater mouth protrusibility [Table 1]) that significantly correlated with the percent of benthic prey in the gut (Figure 3). However, for *Lepomis megalotis*, there was a significant negative correlation found between mean gill raker length and the percent of benthic prey in the gut ($R^2 = 0.044$, $p = 0.03$) (Figure 3). *Lepomis mega-*

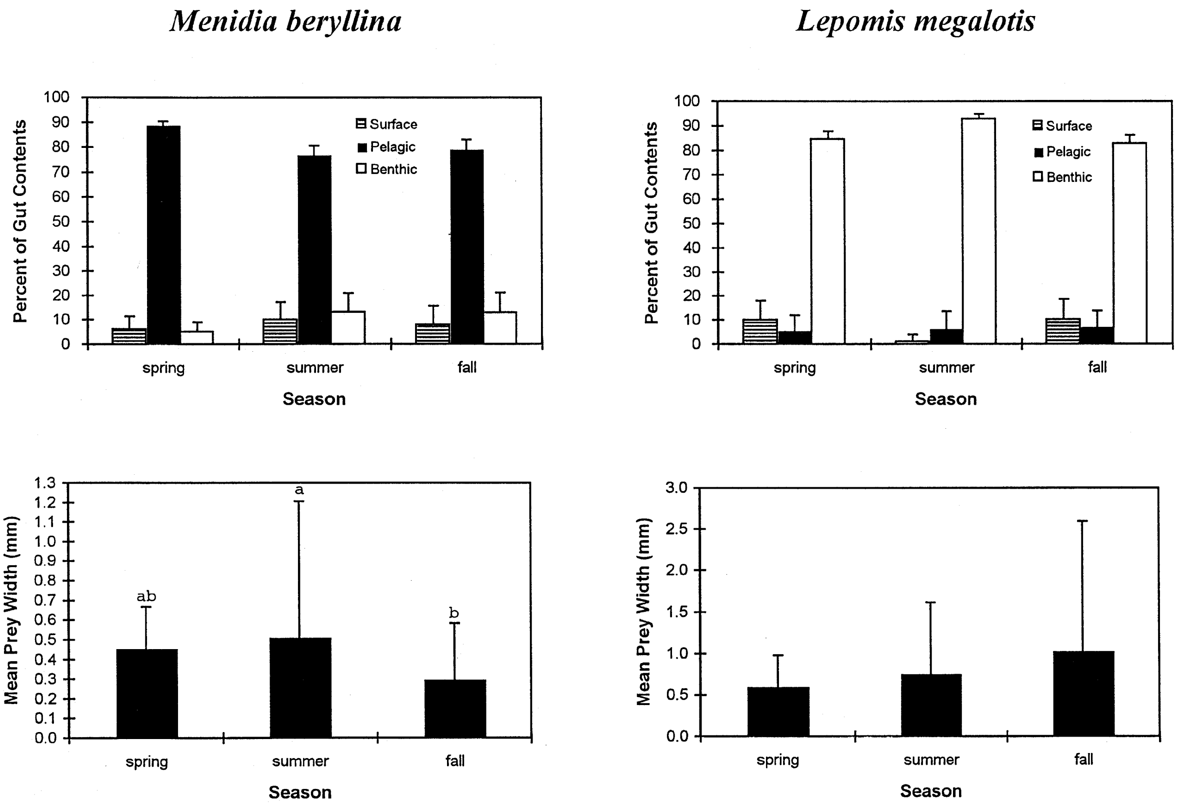

Figure 1. Seasonal differences in the percent surface prey, percent pelagic prey, percent benthic prey, and mean prey width found in the guts of *Menidia beryllina* and *Lepomis megalotis* from Lake Texoma. Different letters indicate significant ($p<0.05$) differences across seasons. Bars represent ± S.E.

Table 3. Summary of measured morphological characteristics for *Menidia beryllina* and *Lepomis megalotis* collected from Lake Texoma. Measurements are in millimeters unless indicated otherwise.

	Menidia beryllina				*Lepomis megalotis*			
Morphology	Minimum	Maximum	Mean	S.D.	Minimum	Maximum	Mean	S.D.
Number of gill rakers	17.0	22.0	20.1	1.1	10.0	14.0	12.2	0.8
Mean gill raker length	0.4	1.4	0.9	0.2	0.2	1.0	0.5	0.2
Mean space between gill rakers	0.1	0.2	0.2	0.0	0.1	1.0	0.5	0.2
Eye lens diameter	0.9	2.3	1.6	0.3	1.0	5.6	2.9	0.8
Mouth width	0.9	4.1	2.4	0.7	1.7	14.0	7.1	3.1
Mouth protrusion	<0.1	2.4	1.1	0.5	<0.1	6.2	1.2	0.8
Total length	31.1	110.3	68.7	18.3	44.3	142.1	95.6	29.4

lotis also showed a significant relationship between mean raker space and the percent of benthic prey in the gut ($R^2 = 0.070$, $p = 0.007$) (Figure 3), but in the opposite direction of what is expected based on the functional morphology literature (space between rakers is expected to correlate positively with the percent of benthic prey in the [Magnuson & Heitz, 1971; Bentz, 1976; Gross & Anderson, 1984; Ibrahim & Huntingford, 1988; Robinson et al., 1993]). Mouth protrusion was not significantly correlated with the percent of benthic prey in the gut for *L. megalotis* (Figure 3).

Both species had significant positive correlations between mouth width and mean prey width ($F = 9.096$, $p = 0.0002$ for *M. beryllina*; $R^2 = 0.173$, $p = 0.0001$ for

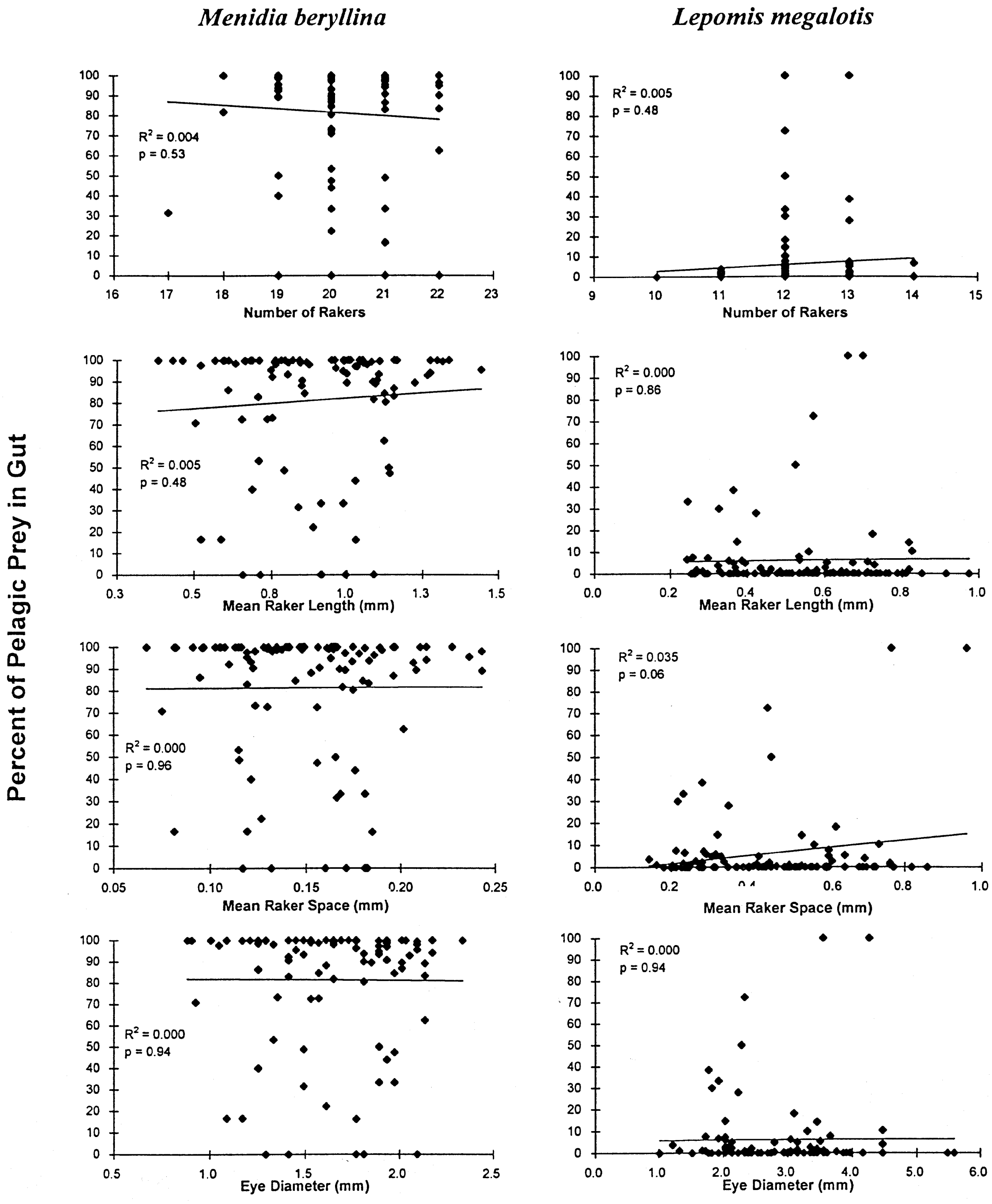

Figure 2. Results of Pearson product moment correlation analysis comparing morphology of *Menidia beryllina* and *Lepomis megalotis* from Lake Texoma with the percent of pelagic prey found in their guts.

Table 4. Summary of measured gut contents characteristics for *Menidia beryllina* and *Lepomis megalotis* collected from Lake Texoma.

Gut Contents Variable	*Menidia beryllina*				*Lepomis megalotis*			
	Minimum	Maximum	Mean	S.D.	Minimum	Maximum	Mean	S.D.
% Surface prey	0.0%	97.6%	8.1%	19.5%	0.0%	100.0%	7.2%	21.7%
% Pelagic prey	0.0%	100.0%	81.4%	30.0%	0.0%	100.0%	6.1%	17.1%
% Benthic prey	0.0%	100.0%	10.5%	23.9%	0.0%	100.0%	86.7%	26.3%
Mean prey width (mm)	0.1	2.6	0.4	0.3	0.2	8.2	0.8	1.1

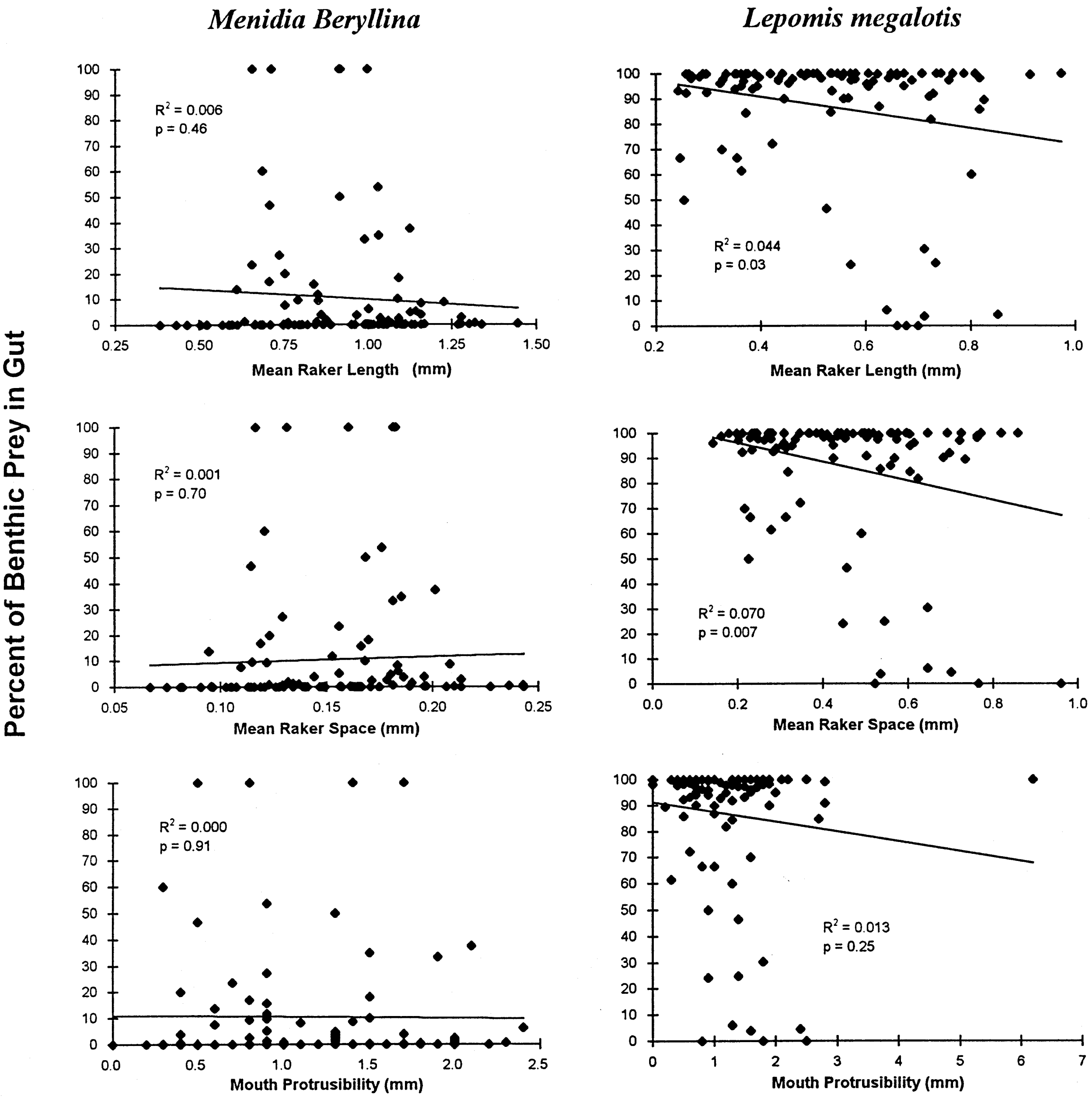

Figure 3. Results of Pearson product moment correlation analysis comparing morphology of *Menidia beryllina* and *Lepomis megalotis* from Lake Texoma with the percent of benthic prey found in their guts.

L. megalotis) (Figure 4). Additionally, mean gill raker space and mean prey width were significantly positively correlated for *L. megalotis* ($R^2 = 0.184$, $p = 0.0001$) (Figure 4). *Lepomis megalotis* also showed a significant relationship between eye lens diameter and mean prey width ($R^2 = 0.156$, $p = 0.0001$) (Figure 4), but in the opposite direction of what is expected based on the functional morphology literature (larger eye size allows better visual acuity and is expected to correlate negatively with prey size [Hester, 1968; Chao & Musick, 1977; Hairston et al., 1982]). *Menidia beryllina* had no significant correlation between raker space and prey width nor between eye lens diameter and prey width (Figure 4).

Discussion

For all measured morphological characteristics except raker spacing, there was a wide range of sizes between individuals (Table 4). It is well documented that these measured morphological characteristics have different functionality for feeding when they have different sizes (Table 1). Therefore, according to the paradigm that functional morphology predicts ecology, this should result in individuals with different morphology eating different prey. However, of the six characteristics measured on each species only one for *M. beryllina* (mouth width) and three for *L. megalotis* (mean raker space, mouth width, and mean raker length) correlated with differences in diet in a way consistent with its size-based functionality.

This lack of correlation between potential and actual resource use could be caused by one of two situations. Either fish could not find prey types that their functional morphology was best adapted to exploit or they encountered these prey types but chose to selectively feed on other prey types (presumably because of optimal foraging considerations [Pyke et al., 1977]). Because prey abundance data were not available for the fish from Matthews' fish collection (1980–1988 samples), it is not possible to distinguish with certainty between these two possibilities. There is, however, evidence to suggest that the lack of correlation was not due to a lack of appropriate prey types/sizes. First, most samples contained some individuals that had predominantly eaten pelagic prey and some individuals that had predominately eaten benthic prey, indicating that both prey types were available to all individuals. Therefore the lack of correlations between morphology and percent of pelagic or benthic prey in the gut are not likely caused by a lack of available prey. Secondly, the predominate prey types were zooplankton for *M. beryllina* and chironomids for *L. megalotis*. Both of these prey types are present as small juveniles before they reach the larger sizes which were found in the guts of both fish species. Because new cohorts of these species are produced throughout most of the seasons analyzed, it is unlikely that small zooplankton and chironomids were unavailable. It is more likely that eating larger prey provided individuals with small prey adapted morphology a better net energy gain than using the extremes of their morphological ability to exploit the less utilized, smaller prey (Pyke et al., 1977).

Regardless of the cause for the lack of correlation between functional morphology and actual resource use, the data clearly show that for most morphological characteristics, greater potential resource use (wider fundamental niche) was not reflected by differential resource use (changes in fundamental niche). There were, however, some morphological variations between individuals that did correlate with differences in diet. Mouth size was strongly correlated with prey size for both species and mean raker space and mean raker length correlated strongly with prey size and percent of benthic prey in gut respectively for *L. megalotis*. It is possible that niche partitioning related to these morphological differences (or to intraspecific differences in morphological characters not measured in this study) sufficiently reduced competition and caused further niche partitioning based on other morphological differences to be unnecessary.

Conclusions

In addition to this study, several other authors have found evidence to suggest that ecomorphology diet predictions were not accurate for the environments they were studying (Gatz, 1979; Wiens & Rottenberry, 1980; Kotrschal, 1989; Pohla & Goldschmid, 1989; Lageland & Nost, 1995; Wanzenbock, 1995). Clearly, this indicates that, at times, ecomorphology predictions are not accurate. Caution should therefore be used when making untested predictions about the trophic ecology of an organism based on its functional morphology (Wainwright, 1987, 1991; Kotrschal, 1989; Douglas & Matthews, 1992). This is especially important in systems that have only recently been formed (such as the Lake Texoma Reservoir) or which have recently experienced disturbances or exotic species introductions. Ecomorphology predictions may be use-

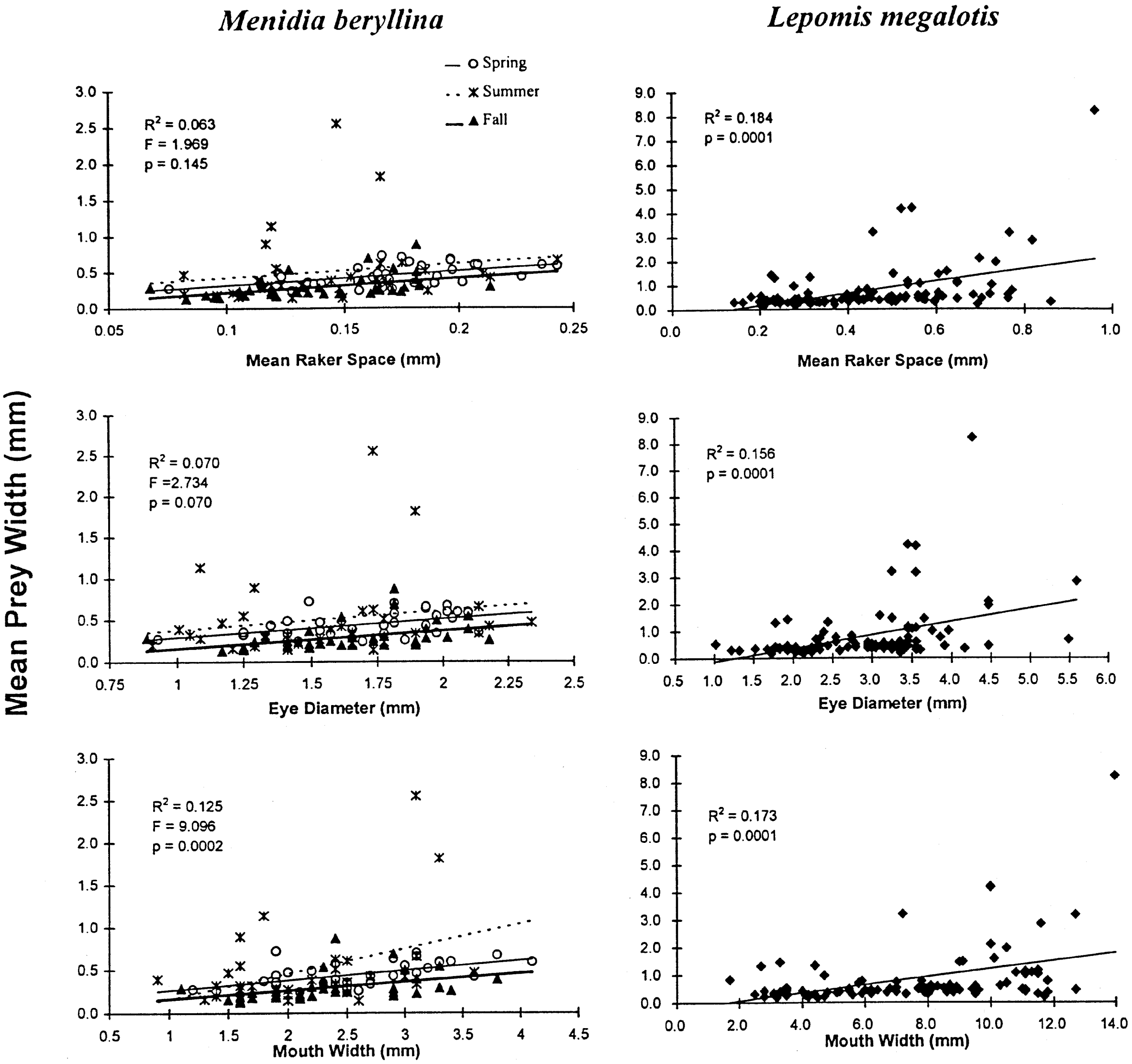

Figure 4. Results of stepwise multiple regression (*Menidia beryllina* – controlling for seasonal differences in prey width) and Pearson product moment correlation (*Lepomis megalotis*) analyses comparing fish morphology with mean prey width of their gut contents. For *M. beryllina* graphs, R^2-values are from a regression model with both season and fish morphology as predictor variables of prey width. With only season as a predictor of prey width $R^2 = 0.044$. An F-test was used to test for significant increases in R^2-values when the fish morphology variable was added as a predictor variable to the season-prey width model.

ful for determining the potential resource use of an organism (but see Drenner et al., 1987), however, many factors influence which parts of this fundamental niche become important to the organism under the specific conditions of its environment (Sibbing, 1988). Unless these factors are considered, ecomorphology predictions could lead to erroneous conclusions about the ecology of an organism in some situations.

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