

# Morphological Change in the Tessellated Darter (*Etheostoma olmstedii*) Following the Introduction of the Banded Darter (*E. zonale*) to the Susquehanna River Drainage

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**The strong connection between ecology and morphology in fishes predicts that ecologically relevant morphological features will change in concert with changes in habitat use and feeding ecology even over relatively short timescales following species introduction. Here, this hypothesis is tested by examining the trophic morphology of specimens of the native Tessellated Darter, *Etheostoma olmstedii*, collected at Catatonk Creek, Candor, Tioga Co., NY, USA, between 1961 and 2002. The collections of *E. olmstedii* bracket a 1980 range expansion by the non-native Banded Darter, *E. zonale*. Examination of the *E. olmstedii* specimens revealed that the length of the buccal cavity relative to body size increased following the invasion of Catatonk Creek by *E. zonale*. An increase in buccal cavity length (BCL) is expected to result in higher suction feeding performance measured as volumetric flow rate of water through the mouth. Such an increase in BCL may enable *E. olmstedii* to exert greater suction forces on prey and as a result, post-invasion *E. olmstedii* may be able to capture more elusive prey or to take prey from habitats with smaller substrates than pre-invasion *E. olmstedii*. The functional and potential ecological consequences of the increase in BCL suggest that the morphological change may be linked to a shift by *E. olmstedii* to more marginal habitats following the invasion of *E. zonale*.**

THE introduction of non-native fishes is a major threat to the preservation of the North American freshwater fish fauna (Rahel, 2000, 2002). Since the late 1600s, at least 70 exotic fishes have been introduced to freshwater habitats in North America (Dextrase and Coscarrelli, 2000), and an additional 200 native fishes have been transferred to freshwater environments outside of their historic range (Rahel, 2000). The detrimental effects of introduced fishes are varied. Introduced species have been linked to large-scale environmental changes, such as declines in water quality and vegetation removal (Taylor et al., 1984; Welcomme, 1984), the degradation of native genetic stocks through hybridization, the introduction of parasites and pathogens, as well as to ecological shifts by native species (Taylor et al., 1984; Goodchild, 2000). The latter effects are the result of competition with or predation by introduced species and typically manifest as changes in habitat usage and prey choice (Welcomme, 1984; Taylor et al., 1984; Ross, 1991; Goodchild, 2000). Ecological shifts of this type are one of the most immediate as well as one of the most common effects of species introductions (Ross, 1991) and have been observed in a wide variety of fish taxa following the introduction of a predator or competitor species (Fausch and White, 1981; Crowder, 1984; Magnan and FitzGerald, 1984; Hearn and Kynard, 1986; Gray, 1998; Gray and Stauffer, 2001; Gray et al., 2005).

In fishes, variation in the shape and size of the head and jaws is often correlated with functional variation that is in turn linked to differences in prey type and habitat use (Gatz, 1979; Wainwright, 1987; Motta, 1988). Thus, changes in functionally relevant morphological features are likely to be linked to changes in selection pressures resulting from

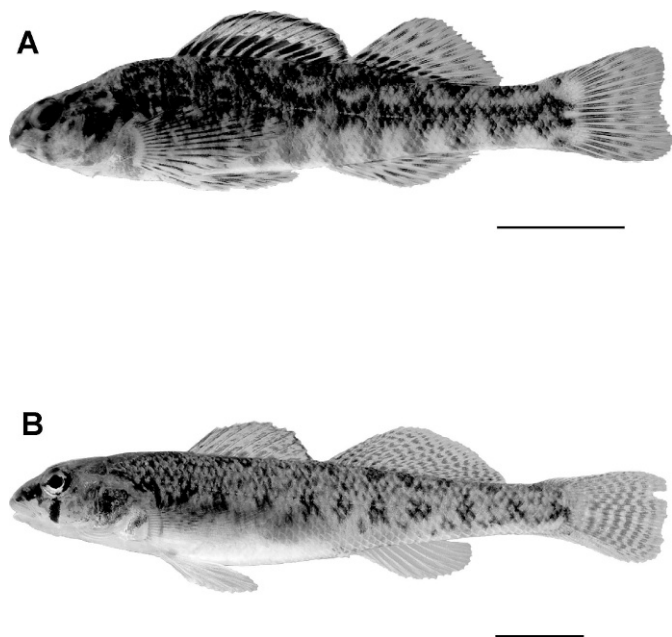
habitat and prey shifts that occur following the introduction of a competitor species. However, few studies to date have tested for change in trophic morphology following species introduction. For instance, Crowder (1984) found that the mean number of gill rakers in the Bloater, *Coregonus hoyi*, decreased by 2.1 gill rakers in 15 years following the introduction of the Alewife, *Alosa pseudoharengus*, to Lake Michigan. The results of numerous studies in which trophic morphology was compared between populations of the same species in allopatry and in sympatry with a competitor species (e.g., Robinson and Wilson, 1994) provide additional evidence to support the hypothesis that the trophic morphology of a native species will change following the introduction of a competitor species. Here, an extensive time-series of collections of a native species of darter *Etheostoma olmstedii* (Percidae: Etheostomatinae) that bracket a natural range expansion by an introduced congener is used to test the hypothesis that changes in trophic morphology will occur in a native species following the introduction of a putative competitor.

Historically, the range of the Banded Darter, *Etheostoma zonale* (Fig. 1A), extended from Minnesota and western New York in the north to Louisiana and Mississippi in the south and included tributaries of both the Allegheny and Mississippi rivers (Fig. 2A). In 1971, *E. zonale* was collected for the first time in the Susquehanna River drainage at Little Pine Creek, Lycoming Co., PA, following what was likely a human-mediated introduction in the late 1950s or 1960s (Kneib, 1972). By 1975, *E. zonale* was collected approximately 400 km downstream from the site of its first capture (Denoncourt et al., 1975; Fig. 2B), and by October 1980, it had reached central New York; two individuals of both sexes

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Submitted: 18 October 2006. Accepted: 14 January 2008. Associate Editor: J. F. Webb.

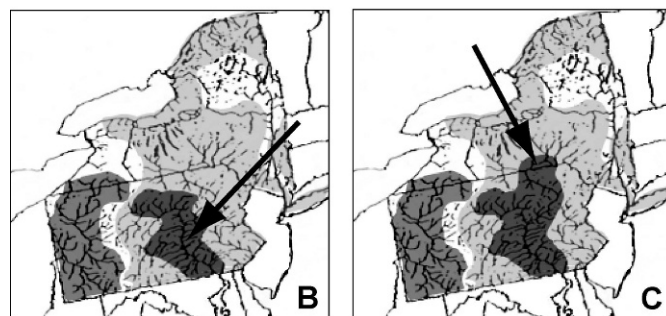
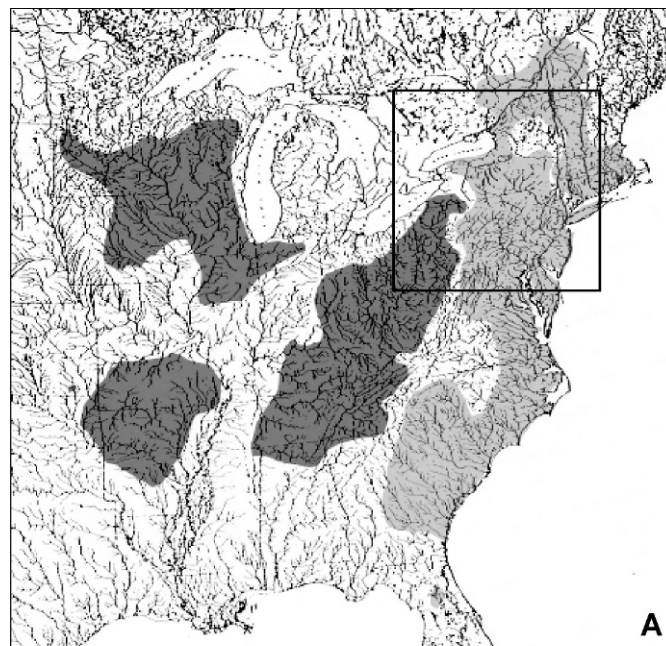
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**Fig. 1.** External morphology of (A) the Banded Darter, *Etheostoma zonale*, and (B) the Tessellated Darter, *E. olmstedii*. Scale bars = 1 cm.

were collected at Catatonk Creek, Candor, Tioga Co., NY (Greenberg, 1982; Fig. 2C). Today, *E. zonale* is one of the most abundant darter species at many localities in the Susquehanna River system (Raesly et al., 1990).

At the time of its introduction, two other darter species, the Shield Darter, *Percina peltata*, and the Tessellated Darter, *E. olmstedii* (Fig. 1B), inhabited the Susquehanna River system. Although the natural ranges of the three species do not overlap (Lee et al., 1980; Page, 1983), *E. zonale* successfully established itself in the drainage. The successful establishment of the Banded Darter was most likely facilitated by its ecological differences from *P. peltata* and its aggressive exclusion of *E. olmstedii* from riffle habitats. *Percina peltata* possesses a functional swimbladder (Page, 1983) and spends the majority of its time above the bottom. As a result, *P. peltata* rarely interacts with the two bottom-dwelling *Etheostoma* species (Gray and Stauffer, 2001). In allopatry, both *E. zonale* and *E. olmstedii* occupy riffles over rocky substrate (Smith, 1985; Jenkins and Burkhead, 1994; Etnier and Starnes, 1993). However, *E. olmstedii* is a habitat generalist and occupies both rocky and sandy substrates in areas lacking flow as well as those with low to moderate flow (Kuehne and Barbour, 1983; Page, 1983; Gray et al., 2005). *Etheostoma zonale* is relatively more specialized and typically occupies rocky substrates ranging in size from gravel to large rocks and boulders in flowing water of various speeds (Kuehne and Barbour, 1983; Page, 1983). When *E. olmstedii* and *E. zonale* occur in sympatry, as they do in the Pennsylvania portion of the Susquehanna, the species interact relatively frequently. Despite its smaller adult body size, *E. zonale* is nearly always the aggressor in these interactions (Gray and Stauffer, 2001). *Etheostoma olmstedii* responds to this aggression by shifting its habitat; it occurs almost exclusively in shallow areas of very low flow and small (i.e., sand or mud) substrate when it co-occurs with *E. zonale* (Gray, 1998; Gray and Stauffer, 2001; Gray et al., 2005). Thus, *E. zonale* out-competes *E. olmstedii* for habitat when the species occur in the same community (Gray, 1998; Gray and Stauffer, 2001; Gray et al., 2005).



**Fig. 2.** Recent changes in the geographic distribution of *E. olmstedii* (light gray) and *E. zonale* (dark gray) based on Lee et al. (1980), Greenberg (1982), and Page (1983). (A) Both species' historic ranges, (B) the species' ranges in 1985, approximately 15 years after the introduction of *E. zonale* to Little Pine Creek, PA (indicated by arrow), a tributary of the Susquehanna River, and (C) the species' present ranges. In (C), an arrow indicates the location of the study site: Catatonk Creek, Candor, Tioga Co., NY.

## MATERIALS AND METHODS

**Morphological data collection.**—Forty-seven adult *E. olmstedii* and 37 adult *E. zonale* specimens collected at Catatonk Creek between 1961 and 2002 and 1984 and 2002, respectively, were cleared and double stained (bone and cartilage) following the protocol of Taylor and Van Dyke (1985; Table 1). The standard length (SL) of each specimen was measured and used as an estimate of body size. Given the tendency of many fish species to exhibit allometric growth patterns, specimens were selected such that mean SL was similar among years within each species to ensure that any observed among-year morphological variation was not the result of differences in specimen size.

Ecologically relevant characters are among the most likely characters to change in response to changes in habitat type or prey availability or the introduction of a putative competitor. Thus, seven additional characters on the head and oral jaws that are known to function in prey capture and vary with habitat type in other groups of fishes were measured on each specimen. These characters, measured

**Table 1.** Number of Specimens Examined by Year. Beginning in 1984, specimens of both species were collected in the same seine hauls.

Year	Number of <i>E. olmstedii</i>	Number of <i>E. zonale</i>
1961	5	
1979	5	
1981	4	
1984	8	8
1988	10	10
1998	10	10
2002	5	7
total	47	35

using a dissecting microscope with an ocular micrometer, are the combined length of the hypohyal and ceratohyal bones (HL), the length of the dentigerous arm of the premaxilla (PL), the length of the buccal cavity (BCL) from the dentary to the hyoid symphysis, gape width (GW), the distance between the left and right coronoid processes of the dentary of the closed mouth, length of the lower jaw out-lever, the distance from the anterior-most tip of the dentary to the center of the quadrate-articular jaw joint, length of the lower jaw closing in-lever, the distance from the insertion of the adductor mandibulae on the coronoid process of the articular to the center of the quadrate-articular jaw joint, and length of the lower jaw opening in-lever, the distance from the center of the quadrate-articular joint to the insertion of the interoperculo-mandibular ligament on the retroarticular process of the articular (Fig. 3). Lower jaw in-lever and out-lever measurements were used to calculate opening and closing lever ratios (OLR and CLR, respectively) by dividing the length of the appropriate in-lever by the length of the out-lever.

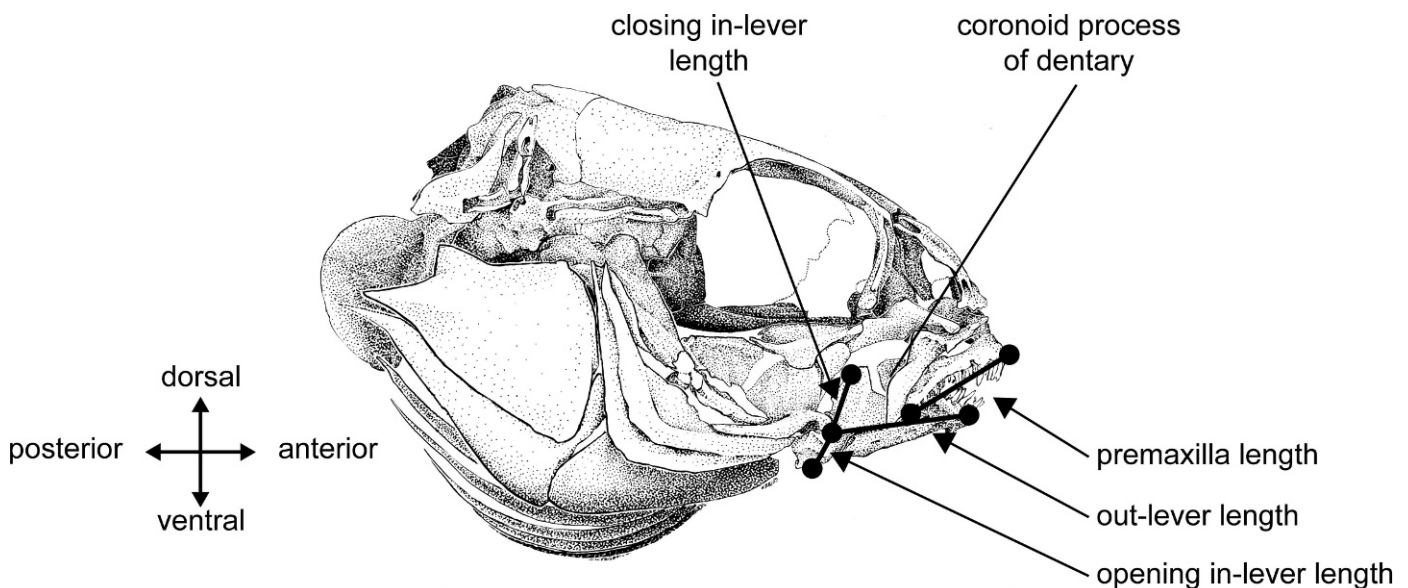
Premaxilla length (PL), BCL, and GW are all measures of the size of the mouth; PL is a measure of the size of the mouth opening, whereas BCL and GW are measurements of the length and width of the buccal cavity, respectively.

Mouth size is strongly correlated with prey size in both sunfishes and black basses (Centrarchidae: Wainwright, 1996) and sea basses (Serranidae: Wainwright and Richard, 1995) and is likely to show a similar correlation with prey size in darters (Percidae).

Buccal cavity length (BCL) and GW have additional functional relevance because the majority of teleosts generate suction forces to capture prey (Norton and Brainerd, 1993). According to a model developed for centrarchids (Carroll et al., 2004), the surface area of the buccal cavity (effectively: BCL  $\times$  GW), in combination with the force generated by the epaxial musculature and the moment of area of the buccal surface, can be used to predict the maximum capacity for suction pressure in the mouth, a parameter that is mechanically linked to water velocity and often used as a metric of suction feeding performance (Higham et al., 2006). Differences in suction feeding performance have been correlated with differences in prey choice in centrarchids. Species that generate greater suction forces typically feed on more elusive prey than those that generate lower suction forces (Collar et al., 2005).

During a typical strike by a suction feeding fish, the fish approaches its prey and expands its buccal cavity by simultaneously raising its head, opening its mouth, and lowering its hyoid apparatus (Richard and Wainwright, 1995). The rapid expansion of the buccal cavity creates a negative pressure gradient within the mouth and more rapid expansion of the buccal cavity produces a stronger pressure gradient (Svånback et al., 2002). As a result of the pressure gradient, water and any prey entrained in the water rush into the fish's mouth. The length of the hyoid bone therefore reflects the expansion capacity of the buccal cavity and the potential volume of water that flows into the mouth during prey capture (de Visser and Barel, 1996).

Variation in lower jaw opening and closing lever ratios also has well-known functional consequences and ecological correlates in other groups of fishes (Westneat, 1994; Wainwright and Richard, 1995). Both ratios quantify the trade-off between speed of jaw movement and the force exerted at the jaw tip. A lower CLR and OLR indicates that



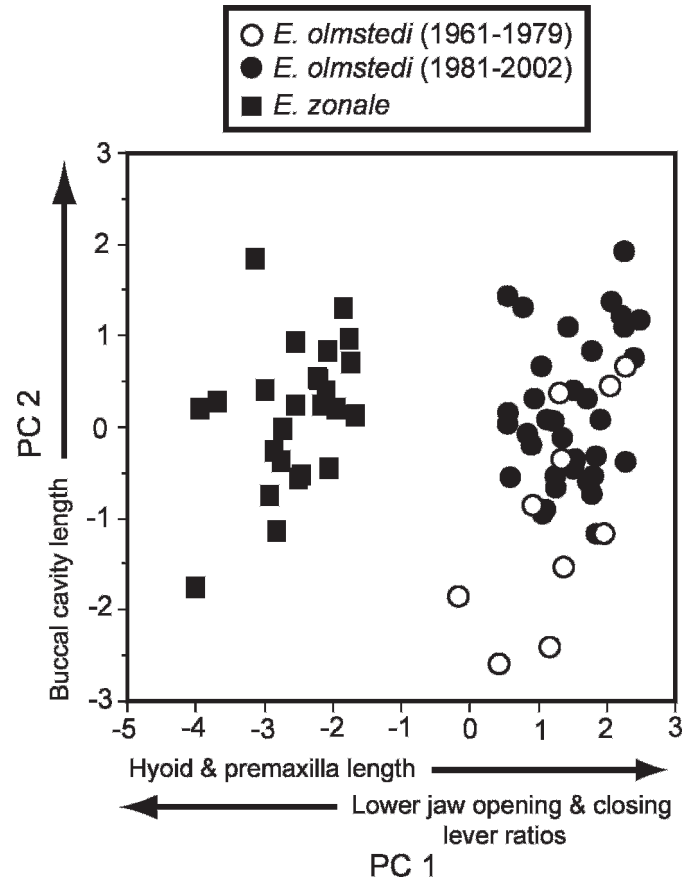
**Fig. 3.** Lateral view of the skull of a Banded Darter collected at Catatonk Creek in 1998. Thickened lines indicate actual distances measured for premaxilla length, out-lever length, closing in-lever length, and opening in-lever length. The coronoid process of the dentary, a landmark used to measure gape width, is also indicated. Scale bar = 1 cm.

the velocity of mouth during closing and opening respectively increases while the bite force experienced at the tip of the jaw decreases. Species that consume elusive prey typically have lower lever ratios than species that feed on slow moving, hard-bodied prey, all else being equal (Westneat, 1994).

**Statistical analyses.**—Measurements of BCL, GW, HL, and PL were log transformed in order to make the variance similar among treatments and to linearize the relationship between each character and log SL. Log BCL, GW, HL, and PL were positively correlated with log SL, and, thus, the characters were body size-corrected prior to statistical analysis. Size-corrected values of BCL, GW, HL, and PL are the residuals of a regression of each character against log SL; measurements from all specimens of both species were included in the regression analysis to facilitate interspecific morphological comparison. A principal component (PC) analysis on the correlations among size corrected measurements of BCL, GW, HL, and PL as well as OLR and CLR was used to identify the most important axes of variation in head and jaw shape. Principal component analysis identifies the  $n$  mutually perpendicular axes that describe, in decreasing order, the greatest amount of variation among a given number of samples with  $n$  characters.

Morphological measurements were not autocorrelated among years for either species (i.e., the morphology of individuals collected at time  $t$  was not significantly correlated with the morphology of those collected at time  $t + 1$  nor was the morphology of individuals collected at time  $t + 2$  correlated with the morphology of individuals collected at  $t + 1$ , etc., in a linear regression analysis; Sokal and Rohlf, 1995). Given that the data were effectively independent among time points, *E. olmstedii* specimens were divided into two time classes based on the year of collection: “pre-invasion” specimens collected prior to 1980 and “post-invasion” specimens collected after 1980. Residuals of all characters and PCs were normally distributed within each time class and variance was similar among time classes (Levene’s test,  $P > 0.05$ ; Levene, 1960). A mixed model ANOVA was used to determine whether *E. olmstedii* changed in trophic morphology following the introduction of *E. zonale*. ‘Time class’ (pre- or post-invasion) was included as a fixed factor, and ‘year’ nested within ‘time class’ (year [time class]) was included as a random factor. The model was tested in JMP v. 8.1 (SAS Institute, Inc.) using a standard least squares approach with the EMS error estimation option. The error associated with (year [time class]) for each of the characters and the informative PC axes (i.e., axes with eigenvalues near 1) was used to test for a significant ‘time class’ effect. A sequential Bonferroni approach (Rice, 1989) was used on the six characters and the PCs to modify significance levels to account for multiple tests. A discriminant function analysis that included size-corrected BCL, GW, HL, PL, and OLR and CLR was also used to determine the probability with which pre- and post-invasion *E. olmstedii* could be assigned to the correct time class based on trophic morphology.

Changes in the pattern of morphospace occupation between time classes of *E. olmstedii* and between species were examined by calculating the Euclidean distance between pre- and post-invasion *E. olmstedii*, pre-invasion *E. olmstedii* and the mean position of *E. zonale* from all years *E. zonale*, and post-invasion *E. olmstedii* and the mean position



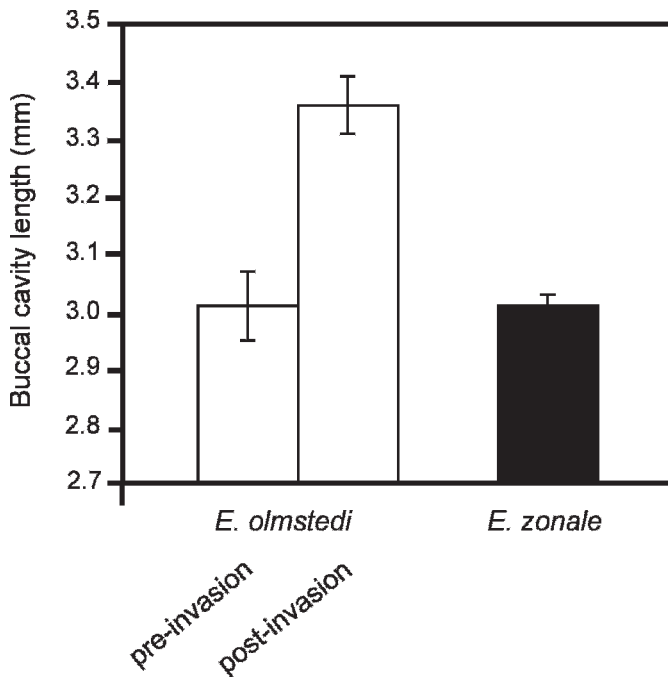
**Fig. 4.** Scatterplot of the PC scores on the first two principal component (PC) axes of all *E. olmstedii* and *E. zonale*. Individuals with higher PC 1 scores have longer hyoid and premaxilla bones and lower closing and opening lever ratios than individuals with lower scores. Individuals with higher PC 2 scores have a longer buccal cavity than individuals with lower scores.

of *E. zonale* from all years on the six PC axes. The total Euclidean distance between species (or time classes) is equal to the square root of the sum of the squared differences between species (or time classes) along each PC axis. The variance around the distance between pre-invasion *E. olmstedii* and *E. zonale* was similar to that between post-invasion *E. olmstedii* and *E. zonale* ( $F_{36,9} = 1.495$ ,  $P > 0.05$ ). Thus, a  $t$ -test was used to ask whether the Euclidean distance between pre-invasion *E. olmstedii* and *E. zonale* differed from the distance between post-invasion *E. olmstedii* and *E. zonale*.

Finally, patterns of morphological change in *E. zonale* between 1984 and 2002 were examined. A linear regression was used to identify the characters and PC axes that exhibited a significant increasing or decreasing trend of change through time. A sequential Bonferroni approach was used on the six characters and the six PC axes to modify  $P$ -values to account for multiple tests.

## RESULTS

In combination, PC axes one and two describe 82.6% of the variation among the specimens of pre- and post-invasion *E. olmstedii* and *E. zonale* (PC 1 = 68.8%, PC 2 = 13.8%; Fig. 4). Of the six characters, HL and PL and CLR and OLR are strongly correlated with PC 1, whereas only BCL is strongly correlated with PC 2. In the space defined by the two axes, *E. olmstedii* and *E. zonale* differ in morphology (Fig. 4); the two species occupy non-overlapping regions of morphospace.

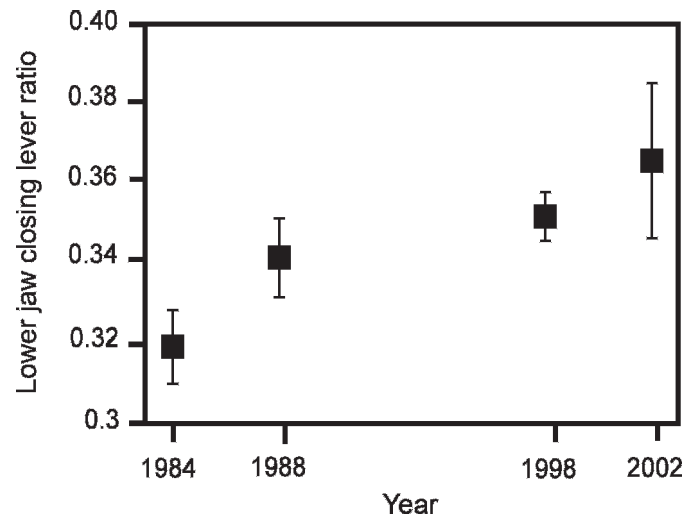


**Fig. 5.** Buccal cavity length (BCL;  $\pm 1$  SE) of typical adult pre- and post-invasion *E. olmstedii* and *E. zonale*. Mean and SE for each species and time class were calculated using the mean SL of adult *E. olmstedii* (52.5 mm) and *E. zonale* (51.3 mm) and the appropriate least squares regression equation of log SL vs. log BCL. BCL was similar between pre-invasion *E. olmstedii* and *E. zonale* but differed significantly between pre- and post-invasion *E. olmstedii*.

*Etheostoma olmstedii* always has higher scores than *E. zonale* on PC axis 1. However, *E. olmstedii* from both time classes have scores that are qualitatively similar to *E. zonale* on PC axis 2.

The distribution of pre- and post-invasion *E. olmstedii* in morphospace suggests that the two time classes are morphologically distinct. Four pre-invasion *E. olmstedii*, but no post-invasion *E. olmstedii*, have scores less than  $-1.15$  on PC 2 (Fig. 4). In fact, pre-invasion *E. olmstedii* have significantly lower scores on PC 2 than do post-invasion *E. olmstedii* ('time class' effect,  $F_{1,6.56} = 8.67$ ,  $P = 0.022$ ). Despite a significant increase in PC 2 scores between pre- and post-invasion *E. olmstedii*, the Euclidean distance between post-invasion *E. olmstedii* and *E. zonale* in the morphospace of all principal component was the same as the distance between pre-invasion *E. olmstedii* and *E. zonale* ( $t$ -test,  $df = 45$ ,  $t = 0.217$ ,  $P = 0.831$ ). Both distances, however, were approximately 2.5 times greater than the distance between pre- and post-invasion *E. olmstedii*.

Using differences in the six head and jaw characters, it is possible to assign *E. olmstedii* specimens to the correct time class with greater than 82% accuracy (discriminant function analysis, 17.3% misclassification rate). In addition to differences in the head and jaw characters encompassed by PC 2, pre-invasion *E. olmstedii* also had significantly shorter buccal cavities than post-invasion *E. olmstedii* ('time class' effect,  $F_{1,6.877} = 8.0$ ,  $P = 0.026$ ). Specifically, the BCL of the average adult *E. olmstedii* in Catatank Creek (SL = 52.5 mm) increased by more than 11.1% (adult of average size: pre-invasion =  $3.01 \pm 0.06$  mm, post-invasion =  $3.36 \pm 0.05$  mm; Fig. 5) following the invasion of *E. zonale*. However, this difference was not significant after Bonferroni correction for multiple tests.



**Fig. 6** Mean ( $\pm 1$  SE) lower jaw CLR of *E. zonale* specimens collected from Catatank Creek between 1984 and 2002. The closing lever ratio of the lower jaw of *E. zonale* exhibited a marginally significant increase in size between 1984 and 2002 after correcting for multiple tests (linear regression,  $r^2 = 0.196$ ,  $P = 0.0088$ ).

The BCL of *E. zonale* did not change significantly following its invasion of Catatank Creek (linear regression,  $r^2 = 0.0920$ ,  $P = 0.132$ ). Thus, pre-invasion *E. olmstedii*, but not post-invasion *E. olmstedii*, had buccal cavities that were similar in length to those of *E. zonale* (Fig. 5). In contrast, however, the lower jaw CLR of *E. zonale* showed a marginally significant increase from  $0.322 \pm 0.0099$  to  $0.372 \pm 0.021$  between 1984 and 2002 after correction for multiple tests (linear regression,  $r^2 = 0.196$ ,  $P = 0.0088$ ). The increase in CLR decreased the similarity of *E. zonale* to *E. olmstedii* (*E. olmstedii* pre- and post-invasion mean CLR =  $0.216 \pm 0.0262$ ; Fig. 6).

## DISCUSSION

The trophic morphology of *E. olmstedii* in Catatank Creek changed following a natural range expansion by an introduced congener *E. zonale*. The buccal cavity of post-invasion *E. olmstedii* was significantly longer relative to body size than that of pre-invasion *E. olmstedii*. The increase in BCL likely has important functional consequences that in turn have ramifications for habitat use and prey capture. The functional relevance of the observed morphological change suggests that the change may be linked to a previously documented habitat shift by *E. olmstedii* when it occurs with *E. zonale*.

The buccal cavity length of an average adult *E. olmstedii* in Catatank Creek (52.5 mm SL) increased by approximately 0.33 mm in the 22 years following the invasion by *E. zonale*. It is important to note, however, that the small number of specimens measured in some years adds uncertainty to the estimate of the magnitude of the change. Measurement of a larger number of individuals per year would yield more precise estimates of the morphology of both species and improve confidence in any subsequent calculations made with this data such as the magnitude of morphological change.

It has been shown that, all else being equal, the area of the expanded buccal cavity (approximated by  $BCL \times GW$ ) is negatively correlated with suction pressure capacity and is therefore positively correlated with volumetric flow rate of

water into the mouth (Carroll et al., 2004). High volumetric flow rates are often associated with predation on more elusive prey (Higham et al., 2006). Thus, assuming that the osteological and myological features involved in suction feeding function similarly between pre- and post-invasion *E. olmstedii*, the longer buccal cavity likely enables post-invasion *E. olmstedii* to generate greater volumetric flow rates than pre-invasion *E. olmstedii*.

The functional consequences of the increase in BCL may in turn have ecological ramifications for *E. olmstedii*. Among fishes, there is a general relationship between suction feeding performance and prey type (Collar et al., 2005). High volume flow is typically associated with species that capture more elusive prey. For example, black basses (Centrarchidae: *Micropterus* sp.) generate higher volumetric flow rates than closely related sunfishes (*Lepomis* sp.; Higham et al., 2006) and also have diets that include a higher percentage of elusive prey items (e.g., fish and crayfish; Collar et al., 2005). Thus, the increase in BCL in post-invasion *E. olmstedii* may enhance the species' ability to capture elusive prey.

Such a change in prey capture ability may be beneficial to *E. olmstedii* in light of the previously described habitat shift it undergoes in the presence of *E. zonale* (Gray, 1998; Gray and Stauffer, 2001; Gray et al., 2005). When the two species co-exist, *E. olmstedii* most often occurs in marginal habitats with small substrates such as sand and low flow because it is aggressively excluded from rocky riffles by *E. zonale* (Gray and Stauffer, 2001; Gray et al., 2005). The ability to generate higher volumetric flow rates during suction feeding may be beneficial to *E. olmstedii* in marginal habitats. Specifically, greater suction forces may facilitate the removal of prey from small diameter substrates such as sand and cobble that are often loose and easily disturbed. Among other darters, species that feed in sand typically have a longer buccal cavity than species that feed on large diameter substrate (R. L. Carlson, unpubl. data).

The trophic morphology of *E. zonale* also changed following its invasion of Catatonk Creek; the lower jaw CLR showed a marginally significant increase in size between 1984 and 2002. Like BCL, an increase in lower jaw CLR has functional consequences that may in turn be related to a change in habitat or prey type. Given that no other morphological changes occurred, *E. zonale* collected in 2002 are predicted to be able to close their lower jaw with greater force per unit input force than individuals collected in 1984. Among wrasses and parrotfishes (Labridae), species that consume a greater proportion of hard-bodied prey have a higher lower jaw CLR (Westneat, 1994; Wainwright et al., 2004).

The increase in lower jaw CLR in Catatonk Creek *E. zonale* lacks a clear link to interactions with *E. olmstedii* for several reasons. First, previous research indicates that *E. zonale* does not alter its patterns of habitat use in the presence of *E. olmstedii* (Gray and Stauffer, 2001; Gray et al., 2005). Second, *E. zonale* that colonized Catatonk Creek came from a population that co-occurs with *E. olmstedii* (Greenberg, 1982). Thus, interactions with *E. olmstedii* may not have provided any new selection pressures to the invasive species. Finally, *E. zonale* differed in CLR from the *E. olmstedii* present in Catatonk Creek at the time of the invasion, suggesting that two species already differed in prey type. Thus, the change cannot be readily attributed to competition for shared prey resources. In fact, it is possible to attribute the

change in the CLR of *E. zonale* in Catatonk Creek to one or more other factors unrelated to the presence of *E. olmstedii*. Habitat and prey availability may differ slightly between the stream or river that is home to the parent population of *E. zonale* and Catatonk Creek. Thus, the morphological change observed in the Catatonk Creek population of *E. zonale* may be the result of adaptation to novel abiotic features of Catatonk Creek and to corresponding differences in prey availability. Additional research is needed, however, including careful comparison of the habitat occupied by the parent population of *E. zonale* to that of Catatonk Creek, in order to conclusively determine whether such adaptation provides a viable explanation for the observed morphological change in *E. zonale*.

Rapid morphological, behavioral, or physiological change by native species has been linked to the introduction of novel prey, predators, or competitors, in a diverse array of plant and animal taxa (Carroll et al., 2005; Strauss et al., 2006). In a few cases, evidence directly links changes in the native species to interactions with the introduced species. For example, Phillips and Shine (2004) found that the head size (a character directly related to prey size) in two snake species decreased significantly following the introduction of a toxic and potentially lethal prey item, the Cane Toad, *Bufo marinus*. The authors suggest that there was strong selection for smaller head size in the two snakes because larger toads are more toxic and therefore more likely to be lethal to the snakes. In this study, the functional relevance of the morphological characters makes it possible to link the morphological change to an ecological shift by *E. olmstedii* in the presence of invading *E. zonale*. Although additional data must be gathered in order to establish a more direct causal link between the invasive species and the observed morphological change in the native species, the results of this study are suggestive and inspire further investigation of the system.

#### MATERIAL EXAMINED

*Etheostoma olmstedii*: CUMV 38268 (CS), CUMV 56345 (CS), CUMV 66539 (CS), CUMV 70676 (CS), CUMV 71514 (CS), CUMV 81854 (CS), CUMV 86812 (CS).

*Etheostoma zonale*: CUMV 70677 (CS), CUMV 71517 (CS), CUMV 81855 (CS), CUMV 86811 (CS).

#### ACKNOWLEDGMENTS

J. Friel and C. Dardia at the Cornell University Museum of Vertebrates kindly supplied specimens for analysis. P. Wainwright, A. Wright, and D. Collar offered useful comments and helpful suggestions on earlier drafts of this manuscript. I. Hart prepared the illustration of the skull, and R. Harrington provided the photographs. An NSF Graduate Research Fellowship and a Center for Population Biology (UC Davis) research grant provided funding for this work.

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