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Brain morphology and turbidity preference in *Notropis* and related genera (Cyprinidae, Teleostei)

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Synopsis

The size of seven neural structures was compared in 51 species of *Notropis, Pteronotropis, Cyprinella, Luxilus, Lythrurus,* and *Hybopsis,* and related to the turbidity of the species' habitat. This last parameter was assessed for each species by personal communication with 42 ichthyologists. To control for size differences among species, all analyses were performed on the residuals from a regression of each character on standard length. Principal components analysis (PCA) of the residuals produced four significant PC-axes that together explained 65% of the total variation represented in the original variables. The size of brain structures concerned with vision, olfaction, and gustation was correlated with habitat turbidity. Two-way Analyses of Covariance (ANCOVAs) revealed significant differences between species in the size of all structures. Sexual dimorphism was found in the size of the olfactory bulb and the cerebellum, and significant two-way interactions (species vs. sex) were detected for the telencephalon, optic lobes, cerebellum, vagal lobe, and the eye. Cluster analysis indicated that neither similar turbidity preference nor shared phylogeny is alone sufficient to explain the observed differences in brain morphology.

Introduction

Parallel changes in the size of specific brain parts and ecological adaptations have been demonstrated in many vertebrate taxa, ranging from fish (e.g. Kishida 1979, Kotrschal & Junger 1988) to bats (Baron & Jolicoeur 1980) and primates (see Jolicoeur et al. 1983). Fish are particularly useful for comparative studies because the primary targets of sensory modalities are distinct brain divisions which can be measured easily in the intact brain (e.g. the facial and vagal lobe for taste, the optic lobe for vision, and the olfactory bulb for smell). Minnows of the genus *Notropis* and related genera are especially useful for such studies because this group comprises a large number of closely related species that occupy a variety of diverse habitats.

When investigating the relationship between brain morphology and ecological parameters one presumes that the size of a specific neural structure is related to its functional potential. Such a relationship is evident, for example, in zebra finches where differences in song performance are paralleled by changes in the size and neuronal characteristics of brain nuclei controlling song (Nottebohm & Arnold 1976, Arnold 1980, Nottebohm 1980). To identify correlations between the size of specific brain parts and ecological parameters the primary structures for the senses should be most useful, as they generally have fewer functions than those as-

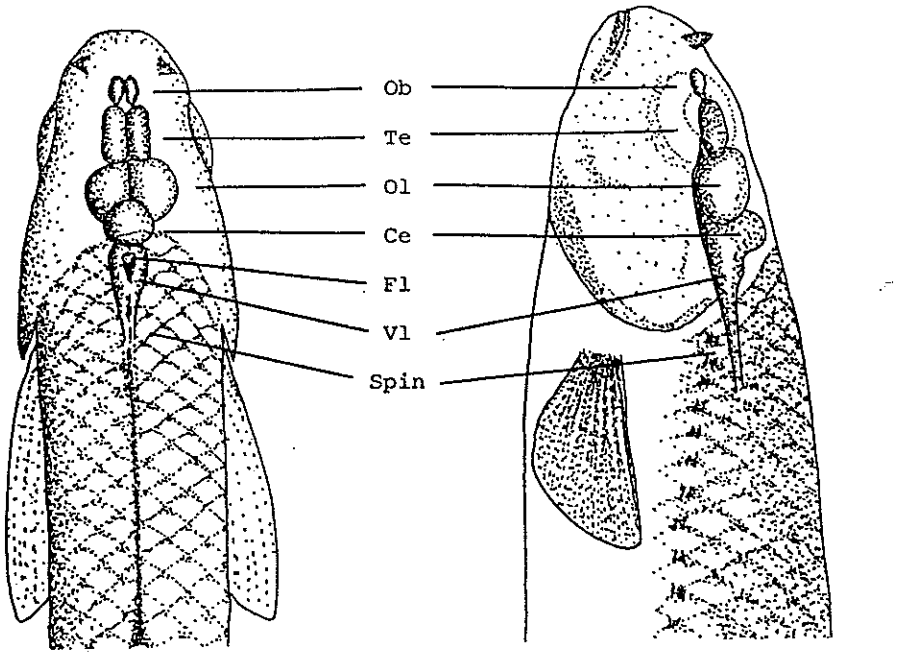

Fig. 1. Dorsal (left) and lateral (right) view of the brain of *Notropis stramineus*. Abbreviations are olfactory bulb (Ob), telencephalon (Te), optic lobes (Ol), cerebellum (Ce), facial lobe (Fl), vagal lobe (Vl), and spinal chord (Spin).

sociated with complex behaviors, such as learning or courtship. We have hypothesized that, in clear water, vision is superior to all other sensory modalities for evaluating the environment and that with increasing turbidity species rely more on other senses, such as taste, hearing, smell or touch. Therefore, we predict that species adapted to turbid environments have relatively smaller structures associated with vision, and relatively larger brain parts associated with taste, hearing, olfaction or taste.

Teleost olfaction, which is routed to the olfactory bulb (Fig. 1), is used primarily for social communication, and in most species is of little or no use in foraging (Finger 1988). The telencephalon appears to be important in the integration of olfactory as well as visual and gustatory stimuli (Friedlander 1983, Davis & Kassel 1983), as well as for many more complex tasks such as learning, and agonistic or social behaviors (Demski 1983). Eyes and optic lobes are intimately related to vision, the latter being the primary target of retinal fibers. The cerebellum plays a central role in proprioception, motor coordination, and eye movement (Demski 1983). Taste in fish is used both in locating food and in evaluating it once found. Stimuli are relayed primarily to structures in the medulla oblongata, specifically sensory nuclei of the nervus glossopharyngeus (IX), n. facialis (VII), and n. vagus (X). The last two form prominent lobes in minnows. The main neural structure involved in locating food is the facial lobe, innervating taste buds on the general body surface and the front portion of the mouth cavity. Information about the quality of a food item is derived from the glossopharyngeal lobe, which innervates taste buds in the back of the mouth and the first gill slit, and the vagal lobe, which supplies taste buds in the remaining gill slits, as well as the palatal and sublingual organs (Kanwal & Caprio 1987, Gomahr et al. 1988).

This study investigates whether the relative size of the eye, olfactory bulb, telencephalon, optic tectum, cerebellum, facial lobe, and vagal lobe in 51 species of minnows is related to the level of turbidity in the preferred habitat of each species. Next, the size of these brain structures is compared between sexes and among species. Finally, species are clustered according to brain morphology to

determine whether such an arrangement more closely approximates an ecological or phylogenetic classification.

Materials and methods

Although the genus *Notropis* was once thought to contain just under one half of all nearctic cyprinids (Coburn 1982), it recently has been revised extensively by Mayden (1985, 1990) whose nomenclature is followed herein.

The validity of this study depends on accurately classifying the species according to their habitat. The determination of the physical parameters of the preferred habitat is a difficult task, as these parameters vary in accordance with the season and the weather. This necessitates a large number of fish collections and measurements of water clarity throughout the range of the species which must span all seasons and include several years. At best, such data are available for only a few of the 51 species included in this study (cf. Felley & Hill 1983) and it would be unrealistic to empirically determine the habitat turbidity of the remainder. As a more economic approach, we asked 42 ichthyologists who have extensive field experience with this group of fish, to identify the turbidity levels in which 90% of individuals of each species might be expected to occur. The categories were very clear (1), clear (2), average (3), turbid (4), and very turbid (5). The responses for a particular species were averaged to obtain an estimate of the mean turbidity (MT) of that species.

Only adult specimens, a total of 476 (4–24 per species), were examined to avoid the potential effects of ontogenetic changes (e.g. developmental constraints, allometry, and changes in the functional importance of sensory modalities during development). Total and standard length (tip of the snout to base of caudal fin) were measured to the nearest 0.5 mm, and weight to the nearest 0.001 g. Sex was determined by examining the gonads. Under a dissecting microscope, the skull was opened dorsally and the brain exposed from olfactory bulbs to the rostral end of the spinal cord. The length and width of olfactory bulb, telencephalon, optic tectum, cerebellum, facial lobe, and vagal lobe were measured to the nearest 0.05 mm, using 10 × magnification and an ocular grid. The diameter of the eye was measured along the nasal-temporal axis to the nearest 0.05 mm. In the case of paired structures, measurements were made on the right side except in a few cases where this side was damaged. Although procedures for the preservation of specimens, such as fixation in formalin or storage in ethanol, result in tissue shrinkage, shrinkage was assumed to be uniform across brain areas. As the general shape of the brain was very similar in all species, the size of each structure was estimated as the product of length and width.

Comparative neuroanatomical studies have commonly suffered from the difficulty of comparing portions of the brain in specimens of different size (Geiger 1956a, b, Stephan 1960, Kotrschal & Junger 1988). Considerable controversy has been raised in the literature concerning the effects of body size and methods for an adequate removal (see Sneath & Sokal 1973). As all species included in this study are similar in size (ranging in length from 4–9 cm) and shape, such problems are reduced. However, as a precaution, all subsequent analyses were performed on the residuals of a linear regression on standard length, either directly or by the use of Analyses of Covariance (ANCOVAs). Standard length, rather than body weight, was chosen to represent body size, because it is less influenced by physiological and nutritional factors.

A principal components analysis (PCA) was performed on the log-transformed residuals (Procedure FACTOR, SPSSX Inc. 1988) to determine the main factors subsuming the variation in brain morphology. These residuals represent 'size-free' neuroanatomical variation. Pearson's correlation coefficients (Procedure CORRELATION, SPSSX Inc. 1988) were calculated between the scores on the significant PC-axes with Eigenvalues ≥ 1.00, and the mean turbidity. For each species, means for the first three PC-axes were plotted (Proc G3D, SAS Institute Inc. 1985) to display the dispersion of different sensory modalities among species with different turbidity preferences. Two-way ANCOVAs with species and sex as treatment effects, and standard length as covariate (Procedure MANO-

VA, SPSSX Inc. 1988), were performed on the size of each structure measured, permitting the evaluation of differences in brain morphology among species, between sexes, or as a result of an interaction between species and sex. Sufficient sample sizes of each sex were obtained for 28 species (cf. Table 2). To achieve homogeneity of variances all variables (unless otherwise stated) were subjected to the Box-Cox transformation (Sokal & Rohlf 1981). A sine transformation was applied to telencephalon, and cosine transformations were applied to the optic lobe and eye. Finally, cluster analysis (Procedure CLUSTER, SPSSX Inc. 1988) was performed on the species averages of the transformed data. Similarities were based upon the squared Euclidian distance derived from the standardized variables, and clusters were assembled by the unweighted pair-group method using arithmetic averages (UPGMA).

Material examined

For each species the museum acronym and number is listed first, followed by the number of specimens in parenthesis, and the location and the year of collection. Institutional acronyms are: University of Kansas (KU); Fort Hayes State University (FHSU); William J. Matthews (WJM); Jeffrey R. Bek and Eric M. Surat (BS); A.J. Gatz (AJG); own collection (RH).

Genus *Pteronotropis: P. euryzonus* KU 21905 (5), unknown location AL, 1987.

Genus *Cyprinella: C. analostana* KU 15367 (5), Alamance Creek NC, 1967; AJG, (4), Maho Creek DE, year unknown. *C. callistia* KU 20483 (5), Crooked Cr. AL, 1982. *C. camura* KU 15821 (5), Spring River KS, 1974; FHSU 150 (5), Shoal Creek KS, 1966. *C. galactura* KU 7866 (5), James River MO, 1963; WJM 1285 (5), Piney Creek AR, 1982. *C. lepida* WJM 1661 (5), Nueces River TX, 1984. *C. lutrensis* RH (10), Brazos River TX, 1987. *C. ornata* KU 4446 (5), Rio Papigochic Mex, 1958. *C. proserpina* WJM 362 (5), Devils River TX, 1978. *C. spiloptera* KU 8628 (5), Wapsipinicon River IA, 1964. *C. venusta* RH (5), Main Llano River TX, 1987; RH (5), Pennington Creek OK, 1987. *C. whipplei* KU 18088 (5), Big River MO, 1975; WJM 835 (3), Kiamichi River OK, 1981; WJM 836 (2), Kiamichi River OK, 1981.

Genus *Luxilus: L. albeolus* WJM 258 (10), Dixie Caverns Channel VA, 1978. *L. cardinalis* KU 21284 (5), Spring Creek OK, 1980. *L. cerasinus* BS 76 (10), Roanoke River VA, 1979. *L. chrysocephalus* RH (10), Blue Creek OK, 1987. *L. cornutus* KU 3758 (5), Mill Creek kS, 1957; FHSU 1852 (5), Byram River CN, 1966. *L. pilsbryi* KU 8023 (5), Mill Creek AR, 1964; WJM 1281 (5), Mill Creek AR, 1982. *L. zonatus* KU 19091 (5), Roubideaux Creek MO, 1981.

Genus *Lythrurus: Ly. ardens* KU 11614 (5), Pitman Creek KY, 1966; AJG (6), Maho Creek DE, year unknown. *Ly. fumeus* WJM 562 (10), Old River Slough AR, 1980. *Ly. roseipinnis* KU 16857 (7), Bayou Bacon MS, 1976. *Ly. umbratilis* KU 15562 (5), Diamond Creek KS, 1984; FHSU 126 (5), Shoal Creek KS, 1966.

Genus *Notropis: N. amabilis* KU 2144 (5), Guadalupe River TX, 1951. *N. atherinoides* WJM 2300 (10), North Canadian River OK, 1987. *N. baileyi* KU 14537 (5), Mill Creek AL, 1969. *N. bairdi* KU 3400 (10), Wichita River TX, 1955. *N. boops* RH (10), Pennington Creek OK, 1987. *N. buchanani* KU 18449 (2), Spring River KS, 1980. *N. chihuahua* WJM 1339 (5), Terlingua Creek TX, 1983. *N. chiliticus* WJM (4), Dan River VA, 1979. *N. girardi* KU 2330 (5), Canadian River OK, 1952. *N. greenei* KU 6632 (5), Illinois River AR, 1960. *N. heterodon* KU 14255 (5), Mississippi River MN, 1968. *N. hudsonius* FHSU 1849 (10), Shetucket River CN, 1969. *N. nubilis* KU 20818 (5), Flat Creek MO, 1983; WJM 1284 (5), Piney Creek AR, 1982. *N. ozarcanus* KU 12656 (5), White River MO, 1967. *N. petersoni* KU 17161 (5), Alexander Springs FL, 1976. *N. potteri* WJM 474 (5). Lake Texoma OK, 1980; WJM 485 (3), Lake Texoma OK, 1980. *N. procne* BS 14 (1), Bottom Creek VA, 1978; BS 59 (5), Bottom Creek Pool VA, 1978. *N. rubellus* KU 18441 (5), Shoal Creek KS, 1980; FHSU 132 (5), Spring River KS, 1966. *N. snelsoni* WJM (7), Cucumber Creek OK, ?. *N. stramineus* WJM 2268 (10), Crutcho Creek OK, 1987. *N. telescopus* KU 5621 (5), Current River MO, 1960; WJM 1285 (5), Piney Creek AK, 1982. *N. texanus* WJM 562 (10),

Old River Slough AR, 1980. *N. topeka* FHSU 293 (10), Mill Creek KS, 1968. *N. volucellus* KU 10584 (5), Lower Cullen Lake MN, 1965; WJM 562 (5), Old River Slough AR, 1980. *N. xaenocephalus* KU 20268 (5), Hillabee Creek AL, 1982.

Genus *Hybopsis: H. dorsalis* KU 4839 (5), North Platte River NA, 1959; WJM (5), Big Creek MO, 1974. *H. longirostris* KU 8799 (5), Upatoi Creek GA, 1964. *H. sabinae* WJM 1281 (10), Mill Creek AR, 1982.

undescr. sp. WJM 2345 (5), Blue River OK, 1988.

Results

The MTs and coefficients of variation for each species are listed along with the phylogenetic classification in Table 1. According to this survey, species of the genera *Notropis, Pteronotropis, Cyprinella, Luxilus,* and *Lythrurus* generally occupy habitats ranging from very clear to moderately turbid.

Species means for all measured morphological variables are listed in Tables 2 and 3. PCA of the regression residuals produced four PC-axes, each with an Eigenvalue ≥ 1, cumulatively accounting for 64.8% of the total variation among individuals. Different sensory structures showed high loadings (Table 4) on different PC-axes. Visual structures and the cerebellum loaded most highly on PC1, the olfactory bulb on PC2, the facial lobe on PC3, and the vagal lobe on PC4. PCA separates the species according to the relative importance of vision, smell, taste on general body surface, and taste in the back of the mouth, respectively.

A significant correlation existed between MT and each of the first three PC-axes, indicating that brain morphology is intimately related to the turbidity level where the species is found. The correlation between the turbidity of the preferred habitat and PC1 was negative ($r = -0.372$, $N = 48$, $0.001 \leq p < 0.01$), demonstrating that the size of structures with high loadings on this axis, specifically the primary optic structures and the cerebellum, are larger in clear water species. A positive association between PC2 ($r = 0.439$, $N = 48$, $0.001 \leq p < 0.01$) and PC3 ($r = 0.285$, $N = 48$, $0.01 \leq p < 0.05$) and the preferred turbidity suggests the olfactory bulb and the facial lobe are larger in turbid water species. No significant correlation was found between PC4 and mean turbidity ($r = 0.033$; $N = 48$, $p > 0.05$). Species means of the scores on the first three PCA-axes are plotted in three dimensions in Figure 2.

The results of two-way ANCOVAs of the size of the olfactory bulb, telencephalon, optic lobe, cerebellum, facial lobe, vagal lobe, and eye indicate that the size of these structures differed significantly ($p < 0.001$) among species (Table 5). The olfactory bulb was larger in males ($0.01 \leq p < 0.05$) and the cerebellum was larger in females ($0.001 \leq p < 0.01$). Significant interactions ($p < 0.001$) were found in the size of the telencephalon, optic lobes, cerebellum, and eye, as well as the vagal lobe ($0.01 \leq p < 0.05$).

The dendrogram produced by the UPGMA cluster analysis indicated that differences in brain size cannot be explained sufficiently by either MT or phylogenetic relatedness alone. The existence of several clusters (Fig. 3) provides evidence for similarities in brain morphology based on common descent. The brain of *C. lepida* proved very similar to its close relative *C. lutrensis* (A), and most species of *Luxilus* (B) and *Lythrurus* (C) clustered together, regardless of MT. On the other hand, brains from several less closely related species with similar MTs clustered together, such as in the case of *N. boops, L. chrysocephalus* and *C. venusta* (D). In addition, species of *Cyprinella* are spread across the entire dendrogram. *L. zonatus* and *L. pilsbryi,* as well as *L. cornutus* and *L. chrysocephalus,* clustered far apart, even though they are closely related phylogenetically and are found in similar habitat turbidity.

Discussion

The correlations between brain structure and habitat turbidity reported here are in accord with other studies that relate brain morphology and ecological parameters in fish (e.g. Miller & Evans 1965, Davis & Miller 1967, Rao 1967, Kishida 1979, Kotrschal

Table 1. Results of a survey of 42 ichthyologists to estimate habitat turbidity of 100 species of *Notropis* and related genera. Averages (mean turbidity, MT) range from 1 to 5, with 1 representing very clear water and 5 very turbid water. N indicates the number of responses for a particular species, and CV variation in opinions expressed.

Phylogenetic classification	N	MT	CV
Genus *Pteronotropis:*			
P. hypselopterus	2	2.00	–
P. signipinnis	3	2.17	0.35
P. welaka	5	2.40	0.52
P. hubbsi	6	2.42	0.38
Genus *Cyprinella:*			
C. lutrensis	27	3.52	0.16
C. formosa	2	2.25	–
C. lepida	2	1.75	–
C. proserpina	4	1.63	0.30
C. spiloptera	17	2.79	0.24
C. camura	13	2.46	0.26
C. whipplei	21	2.52	0.28
C. analostana	9	2.72	0.19
C. chloristia	3	3.33	0.09
C. venusta	19	2.82	0.25
C. galactura	15	2.00	0.30
C. pyrrhomelas	4	1.50	0.27
C. xaenura	1	3.00	–
C. caerulea	3	1.33	0.22
C. trichroistia	4	2.13	0.30
C. gibbsi	1	2.00	–
C. callistia	5	2.40	0.27
C. nivea	6	2.75	0.22
C. leedsi	2	3.25	–
C. callitaenia	1	3.00	–
Genus *Luxilus:*			
L. zonatus	8	1.63	0.22
L. pilsbryi and			
L. cardinalis	16	1.69	0.26
L. cornutus	19	2.47	0.27
L. chrysocephal.	22	2.41	0.23
L. albeolus	9	2.33	0.24
L. coccogenis	8	2.13	0.27
L. cerasinus	7	2.21	0.18
Genus *Lythrurus:*			
L. fumeus	14	2.71	0.30
L. lirus	3	2.17	0.35
L. ardens	14	2.43	0.17
L. umbratilis	24	2.85	0.22
L. roseipinnis	3	2.83	0.20
L. bellus	4	3.25	0.15
L. atrapiculus	2	3.00	–
Genus *Notropis:*			
subgenus *Alburnops:*			
N. edwardreneyi	2	3.75	–
N. blennius	14	3.61	0.15
N. simus	3	2.50	0.20
N. girardi	12	3.67	0.16
N. potteri	10	3.60	0.23
N. buccula	2	3.25	–
N. bairdi	11	3.77	0.22
volucellus species group:			
N. heterolepis	9	1.78	0.25
N. ozarcanus	5	1.60	0.26
N. spectrunculus	8	1.81	0.33
N. emiliae	23	2.96	0.23
N. maculatus	12	2.92	0.23
N. buchanani	15	3.67	0.22
N. volucellus	24	2.73	0.20
N. stramineus	23	3.13	0.23
N. atrocaudalis	8	2.75	0.38
N. mekistocholas	3	2.17	0.35
N. procne	8	2.94	0.14
N. braytoni	2	2.50	–
N. chihuahua	4	2.75	0.32
subgenus *Hydrophlox:*			
N. rubellus	27	2.22	0.33
N. rubricroceus	5	1.60	0.26
N. chiliticus	8	2.44	0.23
N. baileyi	6	2.08	0.28
N. chlorocephalus	5	1.90	0.29
N. lutipinnis	8	2.00	0.33
N. leuciodus	10	2.10	0.29
N. nubilus	10	1.65	0.25
N. chrosomus	4	1.63	0.39
texanus species group:			
N. petersoni	7	2.93	0.18
N. heterodon	5	1.50	0.33
N. anogenus	2	1.75	–
N. topeka	2	2.50	–
N. ortenburgeri	7	2.36	0.34
N. altipinnis	7	2.71	0.18
N. cummingsae	8	2.19	0.24
N. texanus	10	2.75	0.29
N. chalybaeus	17	2.77	0.26
N. boops	24	1.94	0.38
N. xaenocephalus	3	1.67	0.17
subgenus *Notropsis:*			
N. candidus			
N. shumardi	10	3.50	0.19
N. oxyrhynchus	3	3.67	0.16
N. jemezanus	5	3.10	0.29
N. atherinoides	24	3.29	0.17
N. perpallidus	8	2.44	0.20
N. amabilis	5	1.90	0.66
N. amoenus	5	2.90	0.23
N. stilbius	6	2.17	0.12
N. photogenis	11	2.46	0.28
N. telescopus	13	1.89	0.27
N. ariommus	5	2.30	0.33
N. scepticus	4	2.63	0.28
N. semperasper	3	2.17	0.13
unclear position within *Notropis:*			
N. scabriceps	3	2.50	0.00
N. asperifrons	1	1.00	–
N. hypsilepis	2	3.25	–
N. hudsonius	13	2.73	0.26
Genus *Hybopsis:*			
H. amnis	10	3.10	0.23
H. alborus	6	2.83	0.18
H. dorsalis	11	3.05	0.09
H. sabinae	7	3.07	0.33
H. longirostris	6	3.33	0.18
H. bifrenatus	3	3.00	0.33
unclear phylogenetic position:			
N. greenei	11	1.73	0.20
N. harperi	1	2.00	–
N. rupestris	1	2.50	–
N. snelsoni	2	3.25	–

Table 2. Summary statistics for all examined species. The statistics for each species are sample size (N), ratio of males to females (M : F), weight (W) in grams, total length (TL), standard length (SL), brain length (BL), olfactory bulb length (OBL), olfactory bulb width (OBW), telencephalon length (TEL), telencephalon width (TEW), and optic lobe length (OLL) in mm.

Species	N	M:F	W	TL	SL	BL	OBL	OBW	TEL	TEW	OLL
L. albeolus	10	5:2*	2.02	71.55	57.87	7.73	0.97	0.67	1.93	0.89	2.47
N. amabillis	16	13:3	1.54	58.19	46.91	6.43	0.91	0.56	1.69	0.94	2.40
C. analostana	9	5:4	1.77	60.22	48.58	6.53	0.94	0.59	1.72	0.84	2.04
Ly. ardens	11	2:9	2.35	70.00	56.60	7.55	0.98	0.69	1.93	0.87	2.53
N. atherinoides	20	15:5	1.72	61.35	49.51	6.75	1.15	0.74	1.80	0.91	2.00
N. baileyi	5	1:4	1.48	55.00	44.30	6.96	0.85	0.63	1.74	0.57	2.17
N. bairdi	20	13:7	1.69	55.90	45.04	6.66	1.01	0.71	1.83	0.86	1.82
N. boops	21	13:8	1.94	62.00	50.04	6.71	1.08	0.71	1.86	0.98	2.43
N. buchanani	2	0:2	0.52	41.00	32.82	5.10	0.60	0.50	1.40	0.50	1.55
C. callistia	5	3:2	2.49	71.20	57.58	8.06	1.05	0.80	2.08	0.77	2.64
C. camura	10	3:7	3.76	72.20	58.40	7.63	1.08	0.83	1.70	0.88	2.35
L. cerasinus	10	3:7	4.25	77.15	64.46	8.41	1.07	0.77	2.08	0.98	2.63
N. chihuahua	5	2:3	0.90	49.00	38.38	6.49	0.75	0.51	1.80	0.78	1.93
N. chiliticus	4	3:1	1.61	57.63	46.45	6.73	0.76	0.56	1.81	0.65	2.14
L. chrysoceph.	10	5:5	7.94	87.50	70.94	8.67	1.44	1.03	2.23	1.23	2.99
L. cornutus	10	6:4	8.38	91.90	74.55	8.99	1.22	0.84	2.20	0.98	2.83
N. dorsalis	10	0:0*	1.80	61.10	49.30	6.74	1.04	0.75	1.81	0.82	1.90
N. euryzonus	5	1:4	0.65	43.20	34.63	5.28	0.54	0.41	1.11	0.63	1.87
Ly. fumeus	10	1:9	0.601	49.10	39.46	5.50	0.68	0.53	1.43	0.76	1.88
C. galactura	10	3:7	5.52	86.60	70.21	8.06	1.14	0.79	1.91	0.94	2.74
N. girardi	9	8:1	1.23	50.77	40.84	5.74	0.80	0.61	1.52	0.71	1.71
N. greenei	5	0:5	1.46	62.20	50.20	6.76	0.89	0.54	1.82	0.58	2.02
N. heterodon	5	1:4	1.07	55.00	44.30	5.76	0.65	0.39	1.53	0.76	1.96
N. hudsonius	10	0:10	3.41	74.20	60.04	8.03	1.29	0.90	2.02	0.88	2.35
C. lepida	5	2:3	1.60	54.20	43.64	7.01	0.82	0.66	1.81	0.93	2.39
H. longirostris	5	3:2	1.04	51.60	41.51	6.36	0.80	0.63	1.74	0.67	1.84
C. lutrensis	24	14:10	3.34	66.42	53.66	7.16	0.93	0.69	1.94	1.02	2.37
N. nubilus	10	3:7	2.72	71.00	57.42	7.34	1.06	0.68	1.87	0.79	2.35
N. ornatus	5	2:3	1.90	54.80	44.14	6.44	0.78	0.62	1.42	0.82	2.08
N. ozarkanus	5	2:3	1.40	61.00	49.22	6.14	0.89	0.60	1.96	0.82	1.94
N. petersoni	5	2:3	0.75	47.80	38.40	6.13	0.71	0.54	1.70	0.56	1.86
L. pilsbryi	15	4:11	5.05	86.87	70.42	9.07	1.19	0.72	2.18	0.88	3.11
N. potteri	8	7:1	1.01	48.31	38.82	6.16	0.78	0.62	1.66	0.71	1.91
N. procne	8	4:4	1.36	60.13	48.50	6.39	0.84	0.57	1.79	0.59	1.80
C. proserpina	5	2:3	0.80	46.30	37.17	5.76	0.75	0.49	1.52	0.83	1.79
Ly. roseipinnis	7	5:2	1.05	55.43	44.65	6.46	0.79	0.60	1.67	0.75	1.99
N. rubellus	10	6:4	1.67	58.80	47.42	7.11	1.07	0.69	1.74	0.71	2.19
H. sabinae	10	8:2	1.61	57.45	46.31	6.76	0.74	0.59	1.98	0.77	2.03
N. snelsoni	7	4:3	0.31	38.79	31.01	5.51	0.46	0.36	1.64	0.53	1.70
C. spiloptera	5	2:3	1.54	60.60	48.89	6.33	0.82	0.56	1.63	0.83	2.03
N. stramineus	10	1:9	1.76	58.30	47.01	6.89	1.10	0.65	1.88	0.76	2.03
N. telescopus	10	4:6	2.11	69.90	56.52	8.18	0.90	0.62	2.33	0.65	2.67
N. texanus	10	5:5	1.06	53.95	43.44	6.69	0.71	0.53	1.91	0.85	2.14
N. topeka	10	1:9	1.48	53.50	43.07	6.22	0.94	0.58	1.47	0.71	1.92
Ly. umbratilis	10	4:6	1.55	58.40	47.09	6.42	0.91	0.62	1.56	0.66	2.10
undescr. sp.	5	3:2	1.94	57.10	46.02	6.66	0.82	0.61	1.62	0.86	2.11
C. venusta	24	20:4	2.92	68.17	55.09	7.25	1.05	0.79	1.95	1.05	2.65
N. volucellus	10	1:9	1.15	55.75	44.92	6.28	0.80	0.52	1.72	0.76	1.82
C. whipplei	10	2:8	3.59	69.50	56.19	7.17	1.03	0.68	1.68	0.77	2.33
N. xaenoceph.	5	5:0	1.65	60.40	48.73	6.72	0.66	0.57	1.88	0.70	3.06
L. zonatus	5	0:5	5.45	88.80	72.01	8.96	1.23	0.85	2.03	0.89	2.96

* The sex of the remaining specimens could not be determined, because the gonads had been removed previously.

Table 3. Summary statistics for all examined species. The statistics for each species are optic lobe width (OLW), cerebellum length (CBL) and width (CBW), facial lobe length (FLL) and width (FLW), vagal lobe length (VLL) and width (VLW), and eye diameter (ED). All measurements are in millimeters.

Species	OLW	CBL	CBW	FLL	FLW	VLL	VLW	ED
L. albeolus	2.02	1.38	1.56	0.58	0.58	1.39	0.60	4.63
N. amabilis	1.87	1.62	2.08	0.31	0.33	1.38	0.49	4.29
C. analostana	1.66	1.28	1.27	0.46	0.44	1.38	0.44	3.37
Ly. ardens	1.91	1.57	1.71	0.40	0.41	1.32	0.53	4.07
N. atherinoides	1.54	1.59	1.92	0.46	0.43	1.46	0.44	3.47
N. baileyi	1.55	1.24	1.38	0.70	0.51	1.33	0.50	3.24
N. bairdi	1.52	1.54	1.94	0.65	0.66	1.74	0.49	3.07
N. boops	1.98	1.62	2.09	0.45	0.47	1.46	0.54	4.48
N. buchanani	1.18	0.95	1.10	0.35	0.28	0.95	0.40	3.05
C. callistia	2.12	1.90	2.00	0.45	0.56	1.58	0.59	3.92
C. camura	1.98	1.65	1.62	0.49	0.50	1.59	0.54	3.80
L. cerasinus	2.17	1.61	1.70	0.61	0.67	1.58	0.61	4.73
N. chihuahua	1.61	1.38	1.66	0.49	0.51	1.15	0.45	3.45
N. chiliticus	1.61	1.28	1.28	0.50	0.53	1.18	0.45	3.88
L. chrysoceph.	2.36	2.12	2.32	0.58	0.66	1.86	0.67	5.16
L. cornutus	2.26	1.87	2.13	0.62	0.64	2.28	0.68	5.36
N. dorsalis	1.62	1.43	1.69	0.58	0.61	1.58	0.55	3.68
N. euryzomus	1.47	1.25	1.14	0.28	0.36	1.12	0.40	2.78
Ly. fumeus	1.41	1.18	1.30	0.25	0.24	0.92	0.48	3.11
C. galactura	2.13	1.67	1.74	0.53	0.59	1.52	0.58	4.17
N. girardi	1.44	1.37	1.78	0.50	0.52	1.60	0.46	2.84
N. greenei	1.55	1.30	1.41	0.39	0.44	1.44	0.44	4.32
N. heterodon	1.71	1.24	1.41	0.37	0.31	1.26	0.43	3.72
N. hudsonius	2.04	1.67	1.86	0.58	0.56	1.79	0.59	4.54
C. lepida	1.83	1.64	1.75	0.54	0.55	1.24	0.48	3.46
H. longirostris	1.57	1.44	1.62	0.54	0.55	1.41	0.46	3.04
C. lutrensis	1.88	1.84	2.06	0.52	0.55	1.74	0.51	3.58
N. nubilus	1.95	1.47	1.85	0.56	0.57	1.54	0.58	4.34
N. ornatus	1.67	1.51	1.59	0.49	0.55	1.46	0.44	2.96
N. ozarkanus	1.77	1.40	1.61	0.40	0.37	1.32	0.48	3.58
N. petersoni	1.48	1.26	1.48	0.33	0.29	1.25	0.47	3.36
L. pilsbryi	2.53	2.16	2.19	0.68	0.69	1.79	0.59	6.14
N. potteri	1.44	1.16	1.49	0.43	0.49	1.08	0.46	2.66
N. procne	1.49	1.21	1.36	0.48	0.44	0.98	0.40	3.60
C. proserpina	1.54	1.28	1.21	0.46	0.42	0.95	0.42	2.91
Ly. roseipinnis	1.70	1.53	1.73	0.27	0.22	1.39	0.48	4.00
N. rubellus	1.48	1.48	1.57	0.53	0.53	1.64	0.53	3.65
H. sabinae	1.62	1.46	1.66	0.53	0.60	1.18	0.51	2.98
N. snelsoni	1.20	1.08	1.20	0.29	0.31	0.83	0.42	2.73
C. spiloptera	1.68	1.47	1.52	0.50	0.45	1.52	0.50	3.49
N. stramineus	1.63	1.48	1.66	0.57	0.63	1.64	0.56	3.43
N. telescopus	2.11	1.61	1.82	0.45	0.46	1.40	0.50	5.47
N. texanus	1.71	1.42	1.70	0.43	0.42	1.05	0.43	3.51
N. topeka	1.54	1.28	1.31	0.32	0.36	1.31	0.46	3.13
Ly. umbratilis	1.54	1.32	1.31	0.27	0.26	1.41	0.48	3.39
undescr. sp.	1.64	1.43	1.50	0.54	0.53	1.20	0.50	3.49
C. venusta	1.96	1.86	2.11	0.46	0.48	1.42	0.55	3.90
N. volucellus	1.59	1.19	1.43	0.41	0.39	1.23	0.45	3.86
C. whipplei	1.68	1.38	1.37	0.44	0.50	1.33	0.49	3.67
N. xaenoceph.	1.80	1.22	1.34	0.45	0.37	1.62	0.48	4.26
L. zonatus	2.11	1.86	1.72	0.68	0.65	1.92	0.64	5.72

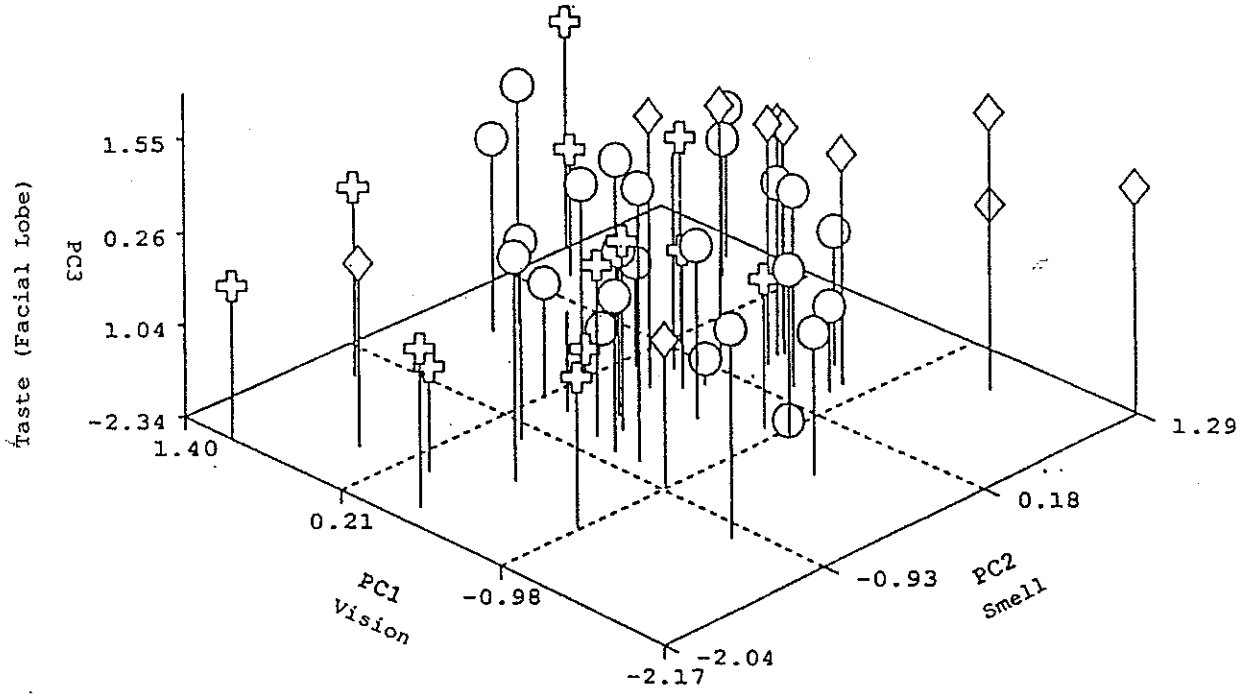

Fig. 2. 3-dimensional plot of species means of the scores on PC1, PC2, and PC3. Well developed sensory structures are characterized by high scores on PC1 for vision, PC2 for olfaction, and PC3 for taste. Plotting symbols represent species preferring turbid ◇, average ○, and clear ✣ habitats.

Table 4. Factor loadings of residuals of each variable on PC-axes following varimax rotation and variance explained by each axis (V). Abbreviations are Eigenvalue (EV), length (L), and width (W).

Structure	PC1	PC2	PC3	PC4
Olfactory bulb L.	−0.107	0.678	0.029	0.329
Olfactory bulb W.	−0.050	0.742	0.138	0.260
Telencephalon L.	0.508	−0.063	0.389	−0.042
Telencephalon W.	0.414	0.614	0.001	−0.311
Optic lobe L.	0.783	−0.072	−0.073	0.013
Optic lobe W.	0.783	−0.082	0.009	0.071
Cerebellum L.	0.675	0.465	0.083	0.136
Cerebellum W.	0.675	0.426	0.204	0.158
Facial lobe L.	−0.019	0.064	0.913	0.142
Facial lobe W.	0.043	0.164	0.890	0.122
Vagal lobe L.	−0.024	0.235	0.124	0.805
Vagal lobe W.	0.247	0.052	0.106	0.660
Eyediameter	0.532	−0.467	−0.204	0.172
EV	3.443	2.405	1.442	1.140
V	26.5%	18.5%	11.1%	8.8%

& Junger 1988). However, previous studies have suffered from one or more of the following problems: comparisons of distantly related taxa, comparisons of members of polyphyletic groups, comparisons of individuals of different size, and small sample size. Having reduced or avoided many of these difficulties, the results of this study strongly support the following two hypotheses: (1) species of minnows rely on different sensory modalities, which correlate with the physical parameters in their preferred habitat, and (2) the importance of a particular modality is reflected in the size of the corresponding neural structures.

The existence of two gustatory subsystems was demonstrated in ictalurid catfish species: a facial system, with an importance for the localization of a food source in the environment, and a glossopharyngeal-vagal system, which is critical for the ingestion of food placed into the mouth (Atema 1971). The present study supports this functional division in cyprinids, as habitat turbidity is correlated with the facial lobe but not with the vagal system.

The high concordance of the responses on the survey suggests that this approach provided an accurate estimate of preferred turbidity. PCA accounted for 65% of the variation among individuals. Further studies may help to account for the remainder by evaluating: (1) microhabitat use; (2) feeding habits; (3) territorial and non-territorial species; (4) schooling and solitary species; and (5) day and night feeders. A high correlation between size of cerebellum and visual structures (high loadings on PC1) suggests a functional association between these structures. Although this result may represent an effect of body size that remained after the regression on standard length, several alternative hypotheses should be considered. A visually oriented species, which can pursue faster moving prey, may require a more highly developed sense of motor coordination than a species relying on taste. In visually oriented species, more elaborate behavioral patterns may necessitate increased proprioceptive performance. Alternatively, Gatz (1979) and Felley (1984) suggested that 'swimming ability' is especially prominent in species inhabiting fast currents. Fast flowing habitats are often clear (Felley 1984), and swimming ability and vision may represent independent adaptations to this environment. Retinal fibers have been found that project to the cerebellum in at least some teleosts (Uchiyama et al. 1988) but it is unlikely that these would appreciably affect the size of the cerebellum.

Intersexual differences in the size of the olfactory bulb and cerebellum, and significant interaction

Table 5. Results of 2-way ANCOVAs of olfactory bulb, telencephalon, optic lobe, cerebellum, facial lobe, vagal lobe, with species and sex as treatment effects (standard length was used as covariate). Abbreviations are significance (p), and degrees of freedom (df), ns non-significant, $^{*}0.01 \leq p < 0.05$, $^{**}0.001 \leq p < 0.01$, $^{***}p < 0.001$.

Source	df	F	p
Olfactory bulb			
Covariate: standard length	1	90.908	***
Species	27	6.806	***
Sex	1	6.376	*
Species × sex	27	0.719	ns
Telencephalon			
Covariate: standard length	1	231.887	***
Species	27	13.833	**
Sex	1	0.246	ns
Species × sex	27	2.369	***
Optic lobe			
Covariate: standard length	1	324.602	***
Species	27	26.026	***
Sex	1	2.560	ns
Species × sex	27	3.560	***
Cerebellum			
Covariate: standard length	1	128.037	***
Species	27	15.772	***
Sex	1	7.477	**
Species × sex	27	3.429	***
Facial lobe			
Covariate: standard length	1	63.557	***
Species	27	22.295	***
Sex	1	0.920	ns
Species × sex	27	1.231	ns
Vagal lobe			
Covariate: standard length	1	54.528	***
Species	27	6.693	***
Sex	1	0.004	ns
Species × sex	27	1.772	*
Eye			
Covariate: standard length	1	420.409	***
Species	27	48.106	***
Sex	1	0.883	ns
Species × sex	27	2.904	***

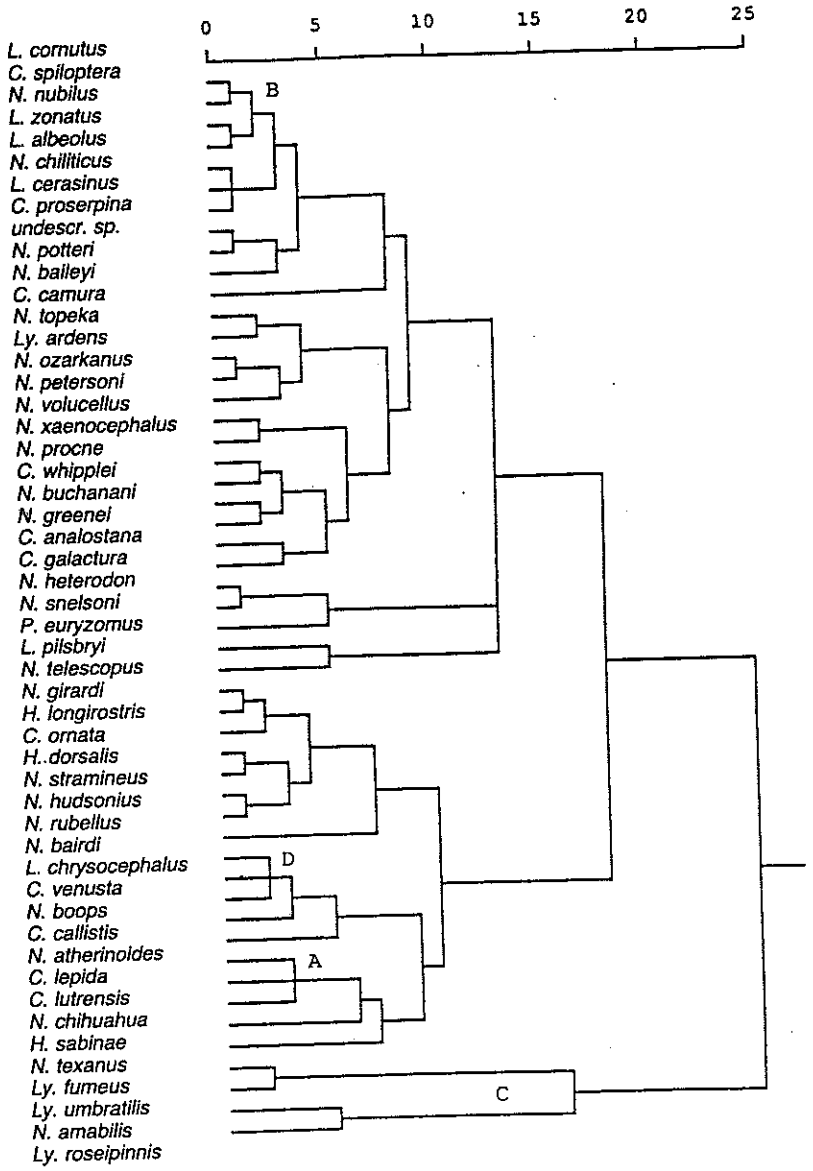

Fig. 3. Dendrogram of the size of olfactory bulb, telencephalon, optic lobe, cerebellum, facial lobe, vagal lobe, and eye in 51 species of the genera *Notropis, Pteronotropis, Cyprinella, Luxilus, Lythrurus,* and *Hybopsis.* Scale represents measures of phenetic dissimilarity.

terms between species and sex in the size of many structures suggests the existence of intersexual differences in ecology and behavior in this group of fishes.

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Appendix 1

Names and institutional affiliation of respondents.

John M. Aho – Savannah River Ecology Laboratory; Chris T. Amemiya – Showa Univ. Research Institute; Paul Angermaier – Virginia Polytechnic Institute; John A. Baker – Univ. Southern Mississippi; Hank Bart – Univ. Illinois; Kevin Bestgen – Univ. New Mexico; Albert Blair – Univ. Tulsa; Branley Branson – Eastern Kentucky Univ.; Noel Burkhead – Roanoke College; Miles M. Coburn – John Carrol Univ.; Frank B. Cross – Univ. Kansas Museum of Natural History; Don Distler – Wichita State University; Anthony A. Echelle – Oklahoma State Univ.; David Edds – Oklahoma State Univ.; David Etnier – Univ. Tennessee; William L. Fisher – Oklahoma Fish and Wildlife Service; Jeffrey W. Foltz – Clemson Univ.; A. John Gatz – Ohio Wesleyan Univ.; Gene Helfman – Univ. Georgia; Loren G. Hill – Univ. Oklahoma; Richard J. Horwitz – Acad. Natural Sciences, Philadelphia; Clark Hubbs – Univ. Texas at Austin; Donald C. Jackson – Mississippi State Univ.; Robert E. Jenkins – Roanoke College; K. Jack Kilgore – USCE Waterways Experiment Station; Flavius Killebrew – West Texas State Univ.; Edie Marsh – Angelo State Univ.; William J. Matthews – Univ. Oklahoma Biological Station; Richard L. Mayden – Univ. Alabama; Paul M. McKee – Beak Consultants Limited; David McNeely – Morehead State Univ.; Gary Meffe – Savannah River Ecology Laboratory; Edward F. Menhinick – Univ. North Carolina at Charlotte; William D. Pearson – Univ. Louisville; William J. Pflieger – Missouri Dept. Conservation; Jimmie Pigg – Oklahoma State Dept. Health; Gerald B. Pottern – North Carolina State Univ.; David L. Propst – New Mexico Dept. of Game and Fish; C. Richard Robins – Univ. Miami; Fred C. Rohde – North Carolina Div. Marine Fisheries; Isaac Schlosser – Univ. North Dakota; Richard H. Stasiak – Univ. Nebraska at Omaha.