Effects of turbidity on the neural structures of two closely related redfin minnows, *Pseudobarbus afer* and *P. asper*, in the Gamtoos River system, South Africa

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The neural structures of the sister species *Pseudobarbus afer* and *P. asper* were compared. *P. afer*, a redfin minnow which inhabits clear, perennial mountain streams, was found to have larger neural structures related to vision than *P. asper*, which inhabits turbid, intermittent streams of the Gamtoos River system. *P. asper* did not show any compensation to inhabiting a turbid environment. Overall, *P. afer* males had the largest neural structures, most notably the optic lobes and cerebella, and *P. asper* females had the smallest neural structures.

Die neuro-ekologie van die susterspesies *Pseudobarbus afer* and *P. asper* word vergelyk. Dit is bevind dat *P. afer*, 'n rooivlerkie wat skoon standhoudende bergstrome bewoon, beskik oor groter neurostrukture wat verband hou met gesigsvermoë as *P. asper*, wat die modderige strome van die Gamtoosriviersisteem bewoon. *P. asper* toon geen aanpassing vir die bewoning van modderige omgewings nie. In die algemeen beskik die manlike *P. afer* oor die grootste neurostrukture, mees opsigtelik die optiese lobbe en kleinharsings, en die wyfie *P. asper* beskik oor die kleinste neurostrukture.

Teleost studies have revealed that ecological characteristics are reflected in brain structures (e.g. Miller & Evans 1965; Davis & Miller 1967; Rao 1967; Kishida 1979; Kotrschal & Junger 1988; Huber & Rylander 1992a; Kotrschal & Palzenberger 1992). The assumption is that a larger size of a section of the brain means better performance of the functions controlled by that section. 'The environment may act upon the brain (and hence behaviour) through evolutionary forces as well as epigenetic changes' (Huber & Rylander 1992b, p. 250). Fish are useful for comparative studies, as the primary targets of sensory modalities are distinct divisions which can be measured in the intact brain (Huber & Rylander 1992a). Good correlations are evident between brain form and function in many fish species (Tuge, Uchihashi & Shimamura 1968).

In closely related vertebrates quantitative, comparative brain morphological techniques can reveal, within a group, trends of sensory diversification, and the findings can be interpreted in terms of ecology and evolution (Bullock 1983; Northcutt 1988; Goldschmid & Kotrschal 1989; Huber & Rylander 1992a; Kotrschal & Palzenberger 1992). One benefit of such studies is the understanding of sensory specializations at the species level (Miller & Evans 1965). Neuro-ecology can be used to elucidate and predict habitat types, radiations of vertebrate taxa and to generate novel evolutionary and functional hypotheses (Kotrschal & Palzenberger 1992).

Morphologically and meristically the main differences which separated *P. afer* from *P. asper* were scale size, length of gut and pigment pattern (Skelton 1988). Both species grow to the same maximum size (*c.* 80 mm SL; Cambray 1992). Since *P. asper* occurs in the highly turbid section of the Gamtoos River system and *P. afer* inhabits the clear flowing mountain streams, they are ideal candidates to investigate the relationship between brain morphology and turbidity preference. Patterns of brain morphological variation are correlated with the biology of *P. afer* and *P. asper* (Cambray 1992).

Larger eyes and optic lobes would be expected in *P. afer* because vision would possibly be superior to all other sensory modalities for evaluating the clear water environment. With an increase in turbidity other senses in *P. asper* may be better developed, such as taste, smell or touch, which would result in longer barbels and larger brain areas associated with these senses. These aspects were investigated in this study.

Methods

P. afer was collected in the Wit River, a clear, perennial stream found in the Cape Fold Mountains. *P. asper* was collected from the Groot River, a turbid, intermittent river flowing through the Karoo. Both rivers are tributaries of the Gamtoos River system in the eastern Cape and there is no physical barrier separating these two species (Cambray 1992). There are distinct differences in the water chemistry of the two sections of the river system (Table 1).

A collection of 85 *P. afer* (29,2–67,3 mm SL: 36 ♂♂) and 63 *P. asper* (27,7–71,6 mm SL; 30 ♂♂) was examined. An additional collection of 60 adult *P. afer* (30 ♂♂; 30 ♀♀)
and 60 adult *P. asper* (30 ♂♂; 30 ♀♀) between 54,0 and 57,0 mm SL was dissected and measured. It was assumed that fish in this narrow length group would have similar behaviour patterns and that there would be no functional shifts in sensory development within this length range. Males and females of *P. afer* and *P. asper* were analysed separately as there can be intersexual differences in the size of some brain structures.

The fish were fixed in 10% formalin and then preserved in buffered 5% formalin. They were dissected after at least six months preservation to allow for tissue shrinkage. Morphometric data were collected as suggested by Hubbs & Lagler (1947). Each specimen was sexed by examining the gonads and then measured to the nearest 0,5 mm SL. Standard length was used as body mass varies with seasonal gonad development and other physiological and nutritional factors. The eye diameter (along the nasal-temporal axis)

Table 1 Water analysis of the Wit and Groot Rivers giving the extreme ranges of the monthly readings during the period 22 February 1987 to 23 April 1989 (after Cambray 1992)

	Wit River	Groot River
pH	6,6 – 7,2	8,0 – 8,5
Electrical conductivity (mS/m)	7,7 – 10,94	118,0 – 1006,0
Total dissolved solids (mg/l)	44,0 – 159,0	763,0 – 5063,0
Turbidity (ntu)	0,2 – 3,0	1,7 – 36,0
Secchi disk (cm)	500 plus*	8 – 129

* Secchi disk was always visible to bottom of deepest pool

and length of barbel were measured to the nearest 0,05 mm. The fish were placed in a V-notched dissecting block on the stage of a dissecting microscope. The dorsal section of the neurocranium was dissected and removed leaving the brain exposed from the anterior olfactory bulbs to the rostral end of the spinal cord. The lobes were cleared of any tissue to improve accuracy of measurement. The length and width of the olfactory bulbs and lobes, optic, facial and vagal lobes, and cerebellum were measured to the nearest 0,05 mm at 10× magnification using a calibrated ocular micrometer. The length and width measurements of paired structures were taken from the structure on the right side of the brain (Figure 1). In some *P. asper* specimens longitudinal enlargements of the olfactory lobes covered part of the olfactory bulbs. The lobes were measured first and then lifted so that the bulbs could be measured. The size of each neural structure was estimated by the product of length and width of the structure (Huber & Rylander 1992a). These measurements provided a quantitative basis for comparison of the sizes of the various neural structures. The size of neural structures was related to the length of 85 *P. afer* (29,2–67,3 mm SL) and 63 *P. asper* (27,7–71,6 mm SL) using regression analyses. The two-sample *t*-test was used to analyse differences between the brain structures.

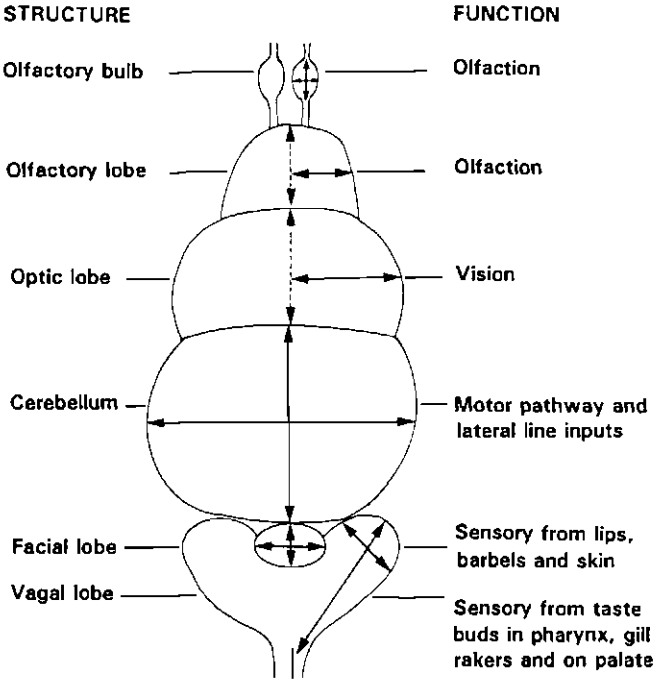

Figure 1 Schematic diagram of the dorsal view of a *P. afer* brain showing how the measurements were taken for paired and unpaired neural structures.

Results

Results of the regression analyses of neural structures related to length of the two species are given in Table 2. Males and females were combined as the smaller specimens were not sexed. There are good correlation coefficients (*r*) for all structures of both species with lengths at 95% confidence levels.

The lengths and widths of the structures are summarized in Table 3, together with the products of length times width for each of the neural structures. The trends are depicted in Figure 2.

The comparative statistics of the four groups analysed, ♂♂ and ♀♀ of *P. afer* and ♂♂ and ♀♀ of *P. asper*, indicated a significant enlargement of the optic lobes and cerebella of male *P. afer* compared with any of the other groups. Male *P. afer* had significantly larger optic lobes (t = 3,311; df = 29) and cerebella (t = 3,9015; df = 29) than female *P. afer*, whereas male *P. asper* had larger olfactory bulbs (t = 2,1905; df = 29) and cerebella (t = 2,1999; df = 29) than female *P. asper*. In a comparison of males, *P. afer* had larger olfactory bulbs (t = 4,084; df = 29), olfactory lobes (t = 4,8489; df = 29), optic lobes (t = 8,8165; df = 29), cerebellum (t = 8,0738; df = 29), eyes (t = 16,4756; df = 29) and longer barbels (t = 3,244; df = 29) than male *P. asper*. That is, the only two structures which were not significantly

Table 2 Linear regression analyses relating the size of the neural structures to length in *P. afer* (n = 85; 29,2–67,3mm SL) and *P. asper* (n = 63; 27,7–71,6mm SL) (where a and b are constants and r is the correlation coefficient)

Structure	a	b	*r*
P. afer			
Olfactory bulb	–0,39419	0,020482	0,942
Olfactory lobe	–0,87137	0,078884	0,969
Optic lobe	–0,57799	0,121911	0,967
Cerebellum	–1,39855	0,168248	0,922
Facial lobe	–0,49409	0,032313	0,926
Vagal lobe	–0,22134	0,113199	0,854
Eye diameter	1,2945	0,042496	0,960
Barbel length	–3,12038	0,113199	0,853
P. asper			
Olfactory bulb	–0,52324	0,022426	0,959
Olfactory lobe	–0,31624	0,053069	0,962
Optic lobe	0,07879	0,081623	0,953
Cerebellum	–0,55074	0,10184	0,971
Facial lobe	–0,18005	0,014088	0,954
Vagal lobe	–0,12068	0,034036	0,860
Eye diameter	1,50148	0,026256	0,949
Barbel length	–2,27093	0,080972	0,942

Table 3 Means and standard errors (*S.E.*) for the definitive brain morphology of *P. afer* and *P. asper*. All measurements are in millimetres (L = length, W = width; L × W (mm^2))

	P. afer		*P. asper*	
Neural structure	♂♂ *n* = 30	♀♀ *n* = 30	♂♂ *n* = 30	♀♀ *n* = 30
Olfactory bulb W	0,76	0,79	0,76	0,72
(*S.E.*)	(0,01)	(0,02)	(0,01)	(0,01)
Olfactory bulb L	1,11	1,07	0,91	0,85
(*S.E.*)	(0,03)	(0,02)	(0,02)	(0,03)
Olfactory bulb L × W	0,85	0,84	0,69	0,61
(*S.E.*)	(0,03)	(0,02)	(0,02)	(0,03)
Telencephalon W	1,26	1,27	1,21	1,15
(*S.E.*)	(0,02)	(0,01)	(0,01)	(0,1)
Telencephalon L	2,42	2,38	2,22	2,31
(*S.E.*)	(0,04)	(0,04)	(0,03)	(0,03)
Telencephalon L × W	3,05	3,01	2,69	2,65
(*S.E.*)	(0,06)	(0,06)	(0,04)	(0,05)
Optic lobe W	2,17	2,13	1,99	1,94
(*S.E.*)	(0,02)	(0,02)	(0,02)	(0,02)
Optic lobe L	2,84	2,71	2,57	2,57
(*S.E.*)	(0,03)	(0,03)	(0,03)	(0,02)
Optic lobe L × W	6,14	5,77	5,11	4,98
(*S.E.*)	(0,09)	(0,07)	(0,08)	(0,03)
Cerebellum W	3,01	2,9	2,68	2,56
(*S.E.*)	(0,03)	(0,03)	(0,03)	(0,04)
Cerebellum L	2,51	2,34	2,2	2,13
(*S.E.*)	(0,03)	(0,03)	(0,03)	(0,03)
Cerebellum L × W	7,56	6,8	5,93	5,48
(*S.E.*)	(0,15)	(0,13)	(0,14)	(0,15)
Facial lobe W	1,33	1,31	1,19	1,16
(*S.E.*)	(0,03)	(0,02)	(0,02)	(0,02)
Facial lobe L	1,0	0,95	1,07	1,04
(*S.E.*)	(0,01)	(0,01)	(0,01)	(0,02)
Facial lobe L × W	1,32	1,25	1,28	1,21
(*S.E.*)	(0,03)	(0,03)	(0,03)	(0,03)
Vagal lobe W	0,72	0,76	0,7	0,7
(*S.E.*)	(0,01)	(0,01)	(0,01)	(0,01)
Vagal lobe L	2,53	2,46	2,5	2,46
(*S.E.*)	(0,03)	(0,03)	(0,02)	(0,02)
Vagal lobe L × W	1,83	1,86	1,75	1,71
(*S.E.*)	(0,03)	(0,04)	(0,03)	(0,03)
Eye diameter	3,7	3,79	3,1	3,12
(*S.E.*)	(0,03)	(0,04)	(0,02)	(0,03)
Barbel L	2,7	2,55	2,36	2,31
(*S.E.*)	(0,1)	(0,09)	(0,04)	(0,05)

different were the facial (t = 1,052; df = 29) and vagal (t = 1,6533; df = 29) lobes. In a comparison of females, *P. afer* had larger olfactory bulbs (t = 6,7301; df = 29), olfactory lobes (t = 4,4277; df = 29), optic lobes (t = 7,3485; df = 29), cerebellum (t = 6,6952; df = 29), vagal lobes (t = 3,5831; df = 29) and eyes (t = 14,6728; df = 29) and longer barbels (t = 2,365; df = 29) than female *P. asper*. Male *P. afer* brains were significantly larger than female *P. asper* brains in all structures. Male *P. asper* brains and associated structures

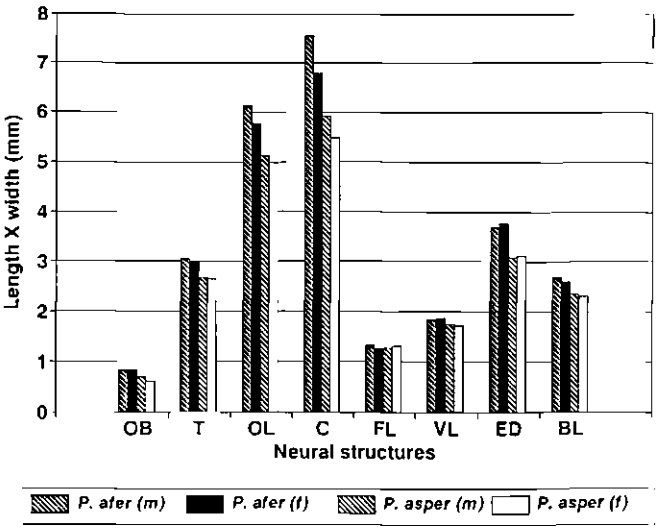

Figure 2 Comparative means for the product of length and width (mm^2) of seven neural structures and barbel length (mm) of *P. afer* (n = 30 ♂♂ and 30 ♀♀) and *P. asper* (n = 30 ♂♂ and 30 ♀♀). OB = olfactory bulb; T = telencephalon; OL = optic lobe; C = cerebellum; FL = facial lobe; VL = vagal lobe; ED = eye diameter; BL = barbel length (*S.E.* of means are too small to plot <0,1).

compared to the female *P. afer* structures were smaller in every respect except the facial lobe and barbel length. Overall, male *P. afer* had the largest brain and female *P. asper* the smallest.

Discussion

Some studies which have related brain morphology and ecological parameters of fish have a number of problems, such as small sample sizes and comparisons of: distantly related taxa, members of polyphyletic groups, different size ranges and different preservation methods (Huber & Rylander 1992a). In an ontogenetic study on cyprinid brain morphologies there were considerable differences which decreased with growth (Kotrschal & Junger 1988; Brandstätter & Kotrschal 1990). The potential effects of ontogenetic changes in neuro-anatomical studies are listed by Huber & Rylander (1992a). To avoid such ontogenetic variables the definitive brain form should be used (Miller & Evans 1965). Huber & Rylander (1992a) used only adults of a similar size ranging from 40 to 90 mm in length (although in minnow species 50 mm is a considerable difference). To overcome these problems, Huber & Rylander (1992a) used the residuals of a linear regression on standard length in their analysis of the brains of *Notropis* and related species. For meaningful conclusions to be drawn from quantitative interspecific comparisons of brain areas, the species should be closely related to ensure a high probability that the compared area would have a comparable functional role (Northcutt 1988; Goldschmid & Kotrschal 1989; Kotrschal & Palzenberger 1992).

The problems outlined above were avoided in this study because: *P. afer* and *P. asper* are sister species; a reasonably large sample of specimens of adult fish of about 55 mm SL was dissected; and all material was fixed and preserved in the same way.

Davis & Miller (1967) suggested that measurements of width rather than length of brain lobes were better indicators of habitat preference. They reasoned that longitudinal enlargements can displace adjacent lobes whereas lateral expansion is prevented only by available cranial space. Huber & Rylander (1992a) used both length and width measurements and this method was followed in this study. The relative lobe size in some species can be correlated with either hyper-development or degeneration of a specific afferent sensory system (Davis & Miller 1967).

The dorsal aspect of the gross brain morphology of the two redfin minnows is typical of cyprinid fish such as the false-goby minnow (*Pseudogobius esocinus*) depicted in Tuge *et al.* (1968). Both redfin minnows show a similar configuration but there are differences in the sizes of the various lobes.

Telencephalon

The olfactory bulbs were very similar for both sexes of *P. afer*, but male *P. asper* had larger bulbs than female *P. asper*. *P. afer* males and females had significantly larger olfactory bulbs than *P. asper* males or females. The olfactory lobes were similar in both sexes of *P. afer* and *P. asper*. The olfactory lobes of both sexes of *P. afer* were larger than both sexes of *P. asper*. Therefore, the telencephalon of *P. afer* is better developed than that of *P. asper*. The significantly larger olfactory bulbs and lobes of *P. afer* indicated that this clear water species has a better developed sense of olfaction than the turbid water species, *P. asper*. This may indicate that in clear water the olfactory bulb is used for social communication and is therefore more important than in species in turbid conditions.

Optic lobes and eyes

The larger visual centres of *P. afer* indicate that they are visual specialists compared with *P. asper*. *P. asper*, being the more derived species (Skelton 1980; 1988), has possibly undergone a reduction in the size of the optic lobes. Male *P. afer* had bigger optic lobes and eyes than *P. asper* males and females. The optic lobes of male *P. afer* were significantly larger than those of *P. asper* and this may be associated with their behaviour. Male *P. afer* have a brighter breeding colouration as well as larger nuptial tubercles (Skelton 1980; Cambray 1994) and the large optic lobe may be positively correlated with these features. Male *P. asper* are not as brightly coloured and have significantly smaller and fewer tubercles (Cambray 1994). One adaptation of fish to turbid waters is a reduction in the size of the eye to protect it from suspended particles (Nikolsky 1963). The reduced size of the eyes of *P. asper* may also be a protective adaptation to the high level of total dissolved solids in its habitat (Table 1).

Cerebellum

P. afer males have the largest cerebella and female *P. asper* the smallest. The large cerebellum might enable *P. afer* to: quickly and efficiently orientate to food items in the clear, flowing waters below riffles; maintain the high level of motor activity necessary for 'station-keeping' to resist being displaced in fast water currents; and allow for quick eye movements and the processing of information related to nuptial activities (suggested by the bigger optic lobes of *P. afer* males). In contrast, *P. asper* rarely inhabits fast-moving water, lives in a relatively food-rich environment and has less vivid colouration (Cambray 1992), which suggests that a relatively smaller cerebellum would be adequate.

Medulla oblongata

The facial lobes were similar for both redfin minnow species. The only significant difference occurred in the larger facial lobe in male *P. afer* compared with female *P. asper*. The swellings of the lobes of the vagal section of male and female *P. afer* was more developed than those of female *P. asper*. On a comparative basis, there is very little difference between the facial and vagal lobes of both species.

Barbels

The use of barbels in cyprinid taxonomy has stimulated considerable debate (Skelton 1988). Over a range of *P. afer*, Skelton (1980) found that the length of the posterior barbels showed considerable intraspecific variation. Barbel length variability within the *Pseudobarbus* species is probably influenced by local environmental conditions and is not genetically fixed. Schmidt (1983) suggested that barbels are not sound generic characters and should be used with caution at the species level. In some species barbel development may be a recent compensatory adaptation for reduced vision in turbid habitats (Hubbs & Ortenburger 1929). Contrary to the findings of this study, barbel size was longer in turbid water species of *Hybopsis* compared with clear water forms (Davis & Miller 1967). The males of *P. afer*, the clear water species, had significantly longer barbels than male *P. asper*, and female *P. afer* had longer barbels than female *P. asper*. The longer barbels of *P. afer* may be related to the need to locate hidden benthic prey quickly and efficiently in the oligotrophic, clear mountain stream (Cambray 1992). It is recommended that taste bud densities be investigated on *P. afer* and *P. asper* barbels. The density of taste buds may be more important than barbel length in locating food in the turbid environment of the Groot River.

Turbid versus clear water species

The sensory apparatus appears to be particularly sensitive to environmental variation (Huber & Rylander 1992b). The microscopic structure of the visual part of the optic tectum was better developed in minnow species which inhabited turbid water (Huber & Rylander 1991). In clear water species of *Notropis* and related genera, the primary optic structures and cerebellum were found to be larger (Huber & Rylander 1992a) and this relationship was also found in this study. In turbid water species of *Notropis* and related genera the olfactory bulb and facial lobe were larger. This suggests compensatory taste development when vision was impeded by high turbidity. In *P. afer* and *P. asper* the olfactory bulbs were larger in the clear water species and the facial lobes were of similar proportions. The differences in size of the neural structures are either the result of functional adaptations to respective habitats (clear mountain stream versus turbid Karoo stream) through evolution or by epigenesis

during development. The smaller neural structures of *P. asper* may reflect phenotypic plasticity between the sister species.

In American minnows, species which lived in both clear and turbid habitats had more variability in the brain lobe size than species which inhabited constant environments (Davis & Miller 1967). The correlation of brain morphology and turbidity in *Notropis* and related genera showed that the size of the brain structures concerned with vision, olfaction and gustation was correlated with habitat turbidity (Huber & Rylander 1992a). Habitat turbidity correlated with the size of the facial lobe but not with that of the vagal system. The facial lobe system is important for locating a food source in the environment, and the glossopharyngeal-vagal system is important for ingestion of food placed in the mouth (Atema 1971). Huber & Rylander's (1992a) study supported 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. Their analysis showed that neither similar turbidity preferences nor shared phylogeny were sufficient to explain the observed differences in brain morphology. In this study the two gustatory subsystems did not show the trend found in the American minnows.

In the American minnows a high correlation between size of cerebellum and visual structures suggested a functional association between these structures (Huber & Rylander 1992a). This study supports this finding for two African minnows. A visually orientating species which can pursue faster moving prey may also need better developed motor coordination than a species relying on taste (Huber & Rylander 1992a). In addition, swimming ability is more developed in species which inhabit fast currents which are frequently clear (Gatz 1979; Felley 1984). Therefore swimming ability and vision may be independent adaptations to a clear, fast-flowing stream environment (Huber & Rylander 1992a). *P. afer* are frequently seen in the swift water below riffles searching in the water column for prey (Cambray 1992). The larger areas of the brain of *P. afer* can possibly be explained by its adaptation to clear, perennial flowing mountain streams. In the turbid waters inhabited by *P. asper*, quick feeding movements would not be as advantageous.

Sight-feeding fishes usually have enlarged optic but small facial and vagal lobes, whereas fishes with enlarged vagal lobes are usually bottom feeders (Davis & Miller 1967). *P. afer* has enlarged optic lobes but the vagal lobes are similar to those of *P. asper* males. This may be because *P. afer* feeds both on the bottom of pools and in the water column below riffles (pers. obs.).

Intersexual differences

Male *P. afer* had larger optic lobes and cerebella than female *P. afer*, which may indicate a behavioural difference as was also suggested by the larger tubercles and brighter red nuptial fin colouration of male *P. afer* (Cambray 1994). The optic lobes of male and female *P. asper* are similar but males have larger cerebella than females. The cerebellum has many different functions (Demski 1983; Finger 1983). Male *P. asper* have larger telencephalons, olfactory bulbs and lobes than do female *P. asper*. In the turbid environment a larger telencephalon may be more important than larger optic lobes, which is the reverse of what was found for *P. afer* males and females. Olfactory bulbs play a role in social communication and therefore may be important in the turbid river, although these structures in *P. asper* are not significantly bigger than those in *P. afer*.

Taxonomic character

The morphology of neural structures, such as the valvula cerebella, can be used as a means of identification of otherwise morphologically closely related fish species (Tandon 1986). Attempts to use brain morphology as a taxonomic character have not always been successful (Lissner 1923 in Davis & Miller 1967) because ecological factors strongly influence the brain lobe proportions. Parallelisms in habitat preference and feeding behaviour may result in similar brain forms in different tribes of Catostominae (Davis & Miller 1967). Brain form should not be used alone as ecological factors influence brain morphology and may obscure phylogenetic relationships (Svetovidov 1953). Differences in the sizes of neural structures of the sister species *P. afer* and *P. asper* are probably due to ecological differences.

Summary

P. afer, which inhabits clear mountain streams, probably has better olfactory and optic senses and a considerably better developed locomotory centre (cerebellum) than its more derived sister species, *P. asper*, which inhabits the turbid section of the Gamtoos River system. The difference in relative size of the cerebellum was probably the result of a greater specialization of *P. afer* in the fast-flowing mountain streams. Certain neural structures of *P. asper*, such as the optic lobes and the eyes, were found to be comparatively smaller than those of *P. afer*. The size of brain structures, such as the vagal and facial lobes, which would compensate *P. asper* inhabiting a turbid environment, have not increased compared with those of *P. afer*.

There were intersexual and interspecies differences in some of the neural structures of *P. afer* and *P. asper*. The intersexual differences may be related to the ecology or behaviour of males and females. Overall, the largest brain occurred in male *P. afer* and the smallest in female *P. asper*. The interspecies differences may be related to the two distinct environments, one clear and one turbid. That *P. asper* has not developed relatively larger facial or vagal lobes to cope with turbidity may indicate that the morphological response is conservative in different ecological conditions.

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References

ATEMA, J. 1971. Structures and functions of the sense of taste in the catfish (*Ictalurus natalis*). *Brain Behav. Evol.* 4: 273–294.

BRANDSTÄTTER, R. & KOTRSCHAL, K. 1990. Life history of roach, *Rutilus rutilus* (Cyprinidae, Teleostei): a qualitative and quantitative study on the development of sensory brain areas. *Brain Behav. Evol.* 34: 35–42.

BULLOCK, T.H. 1983. Why study fish brains? In: Fish neurobiology, Vol. 1, (eds) R.G. Northcutt & R.E. Davis, pp. 361–368. Univ. of Michigan Press, Ann Arbor.

CAMBRAY, J.A. 1992. A comparative study of the life histories of the sister species, *Pseudobarbus afer* and *Pseudobarbus asper*, in the Gamtoos River system, South Africa. Unpub. Ph.D. thesis, Rhodes University, Grahamstown.

CAMBRAY, J.A. 1994. Seasonal occurrence, microwear and distribution of nuptial tubercles in two African minnows, *Pseudobarbus afer*, inhabiting clear water, and *Pseudobarbus asper*, inhabiting turbid water. *Ann. Cape prov. Mus. nat. Hist.* 19: 149–170.

DAVIS, B.J. & MILLER, R.J. 1967. Brain patterns in minnows of the genus *Hybopsis* in relation to feeding habits and habitat. *Copeia* 1967: 1–39.

DEMSKI, L.S. 1983. Behavioral effects of electrical stimulation of the brain. In: Fish neurobiology, Vol. 2, (eds) R.E. Davis & R.G. Northcutt, pp. 317–358. Univ. of Michigan Press, Ann Arbor.

FELLEY, J.D. 1984. Multivariate identification of morphological-environmental relationships within the Cyprinidae (Pisces). *Copeia* 1984: 442–455.

FINGER, T.E. 1983. Organization of the teleost cerebellum. In: Fish neurobiology, Vol. 1, (eds) R.G. Northcutt & R.E. Davis, pp. 261–284. Univ. of Michigan Press, Ann Arbor.

GATZ, A.J. 1979. Ecological morphology of freshwater stream fishes. *Tulane Stud. Zool. Bot.* 21: 91–124.

GOLDSCHMID, A. & KOTRSCHAL, K. 1989. Ecomorphology: developments and concepts. *Prog. Zool.* 35: 501–512.

HUBER, R. & RYLANDER, M.K. 1991. Quantitative histological studies of the optic tectum in six species of *Notropis* and *Cyprinella* (Cyprinidae, Teleostei). *J. Hirnforsch.* 32: 309–316.

HUBER, R. & RYLANDER, M.K. 1992a. Brain morphology and turbidity in *Notropis* and related genera (Cyprinidae, Teleostei). *Environ. Biol. Fishes* 33: 153–165.

HUBER, R. & RYLANDER, M.K. 1992b. Quantitative histological study of the optic nerve in species of minnows (Cyprinidae, Teleostei) inhabiting clear and turbid water. *Brain Behav. Evol.* 40: 250–255.

HUBBS, C.L. & LAGLER, K.F. 1947. Fishes of the Great Lakes region. *Cranbrook Inst. Sci. Bull.* 8: 1–95.

HUBBS, C.L. & ORTENBURGER, A.I. 1929. Further notes on the fishes of Oklahoma with descriptions of new species of Cyprinidae. *Univ. Okla. Biol. Surv.* 1(2): 15–43.

KISHIDA, R. 1979. Comparative study of the teleostean optic tectum. *J. Hirnforsch.* 20: 57–67.

KOTRSCHAL, K. & JUNGER, H. 1988. Patterns of brain morphology in mid-European Cyprinidae (Pisces, Teleostei): a quantitative histological study. *J. Hirnforsch.* 29: 341–352.

KOTRSCHAL, K. & PALZENBERGER, M. 1992. Neuro-ecology of cyprinids: comparative, quantitative histology reveals diverse brain patterns. *Environ. Biol. Fishes* 33: 135–152.

MILLER, R.J. & EVANS, H.E. 1965. External morphology of the brain and lips in catostomid fishes. *Copeia* 1965: 467–487.

NIKOLSKY, G.V. 1963. The ecology of fishes. Academic Press, New York.

NORTHCUTT, R.G. 1988. Sensory and other neural traits and the adaptationist program: mackerels of San Marco? In: Sensory biology of aquatic animals, (eds) J. Atema, R.R. Fay, A.N. Popper & W.N. Tavolga, pp. 869–883. Springer Verlag, New York.

RAO, P.D. 1967. Studies on the structural variations in the brain of teleosts and their significance. *Acta anat.* 68: 379–399.

SCHMIDT, R.E. 1983. Variation in barbels of *Rhinichthys cataractae* (Pisces: Cyprinidae) in south-eastern New York with comments on phylogeny and functional morphology. *J. Freshwat. Ecol.* 2: 239–246.

SKELTON, P.H. 1980. Systematics and biogeography of the redfin *Barbus* species (Pisces: Cyprinidae) from southern Africa. Unpub. Ph.D. thesis, Rhodes University, Grahamstown.

SKELTON, P.H. 1988. A taxonomic revision of the redfin minnows (Pisces, Cyprinidae) from southern Africa. *Ann. Cape prov. Mus. nat. Hist.* 16: 201–307.

SVETOVIDOV, A.N. 1953. Materials on the structure of the fish brain. 1. Structure of the fish brain of codfishes. *Trudy Zool. Inst. Akad. Nauk SSSR* 13: 330–419. (Ichthyological Lab. Translation No. 3).

TANDON, K.K. 1986. Valvula cerebelli and phylogenetic relationship (sic) in fishes. In: Indo-Pacific fish biology: Proc. of the 2nd Int. Conf. on Indo-Pacific fishes, (eds) T. Uyeno, R. Arai, T. Taniuchi & K. Matsuura, pp. 679–682. Ichthyological Society of Japan, Tokyo.

TUGE, H., UCHIHASHI, K. & SHIMAMURA, H. 1968. An atlas of the brains of fishes of Japan. Tsukiji Shokon, Tokyo.