Pseudotropheus callainos, a new species of mbuna (Cichlidae), with analyses of changes associated with two intra-lacustrine transplantations in Lake Malawi, Africa

Jay R. Stauffer, Jr. * and Eva Hert **

Pseudotropheus callainos, a new species of the P. zebra complex, is distinguished from other members of this complex by the blue color of the males, the blue and white color morphs of the females, and the absence of vertical bars. This species is native to the Nkhata Bay area of Lake Malawi, but has been transplanted into southern Lake Malawi. Multivariate analysis of variance (MANOVA) demonstrates that clusters formed by plotting the sheared second principal component (morphometric data) against the first factor score (meristic data) of the transplanted and native populations are significantly different (P<0.01) from each other. Furthermore, the northern (native) and southern (transplanted) populations of P. aurora are both morphologically and ecologically different.

Introduction

The rock-dwelling cichlids (mbuna) inhabit rocky shores and rock outcroppings of Lake Malawi and comprise a major portion of the haplochromine species flock that is endemic to the lake. These fishes are known for their explosive radiation, and many of the species are endemic to only one particular island within the lake or are geographically restricted to one part of the rocky shore along the lake (Ribbink et al., 1983; Stauffer, 1988, 1991; Stauffer & Boltz, 1989). Many of these fishes were described by Regan (1921) and Trewavas (1935) on the basis of anatomical features. Ribbink et al. (1983) emphasized that a revision of the mbuna, which takes coloration and behavioral features into account,

is necessary. Distributional surveys have documented that at least 12 species were transplanted to Thumbi West Island (Fig. 1) from other parts of the lake approximately 20 years ago; no documentation is available, however, concerning when or where translocations took place, or which fishes were involved (Ribbink et al., 1983; Trendall, 1988). Presumably, these transplantations were made by persons in the aquarium trade to reduce the time and expense required to travel to more remote portions of the lake. As a consequence of these transplantations, the island now has high species richness. The purposes of this paper are 1) to describe a new species from Nkhata Bay and 2) to compare the transplanted and native populations of the new species and Pseudotropheus aurora.

^{*} School of Forest Resources, The Pennsylvania State University, University Park, PA 16802, USA

^{* *} Max-Planck-Institut, Seewiesen, D-8130 Starnberg, Germany; present address: J. L. B. Smith Institute of Ichthyology, Private Bag 1015, Grahamstown 6140, Republic of South Africa

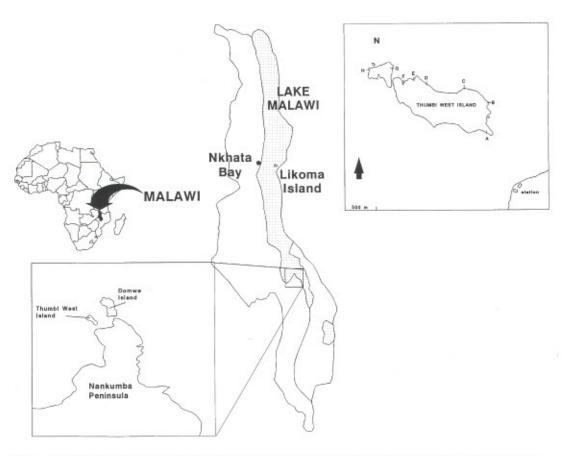


Fig. 1. Map of Thumbi West Island depicting areas where populations of Pseudotropheus aurora were observed.

Methods and Materials

External counts and measurements follow Barel et al. (1977). The number of scales in the lateral-line series do not include scales in the over-lapping portion of the lower lateral line; pored scales located posterior to the hypural plate were recorded separately. Standard length (SL) is used throughout. Except for gill raker meristics, all counts and measurements were made on the left side of the fish. Morphometric values are expressed as percent SL or percent head length (HL). Institutional abbreviations are: MFU, Malawi Fisheries Unit, University of Malawi, Zomba; PSU, Pennsylvania State University Fish Collection; USNM, National Museum of Natural History, Washington.

Body shapes of the native and transplanted populations of the new species and of *P. aurora* were compared using sheared principal component analysis in which the covariance matrix was factored (Humphries et al., 1981; Bookstein et al., 1985). This analysis ordinates factors independently of a main linear ordination (Reyment et al., 1984). Meristic differences were compared using principal component analysis in which the correlation matrix was factored and the population illustrated by plotting the sheared second principal component against the first meristic component. A multivariate analysis of variance (MANOVA) was used to test differences between the native and transplanted clusters generated by the above graphs.

Behavioral observations of P. aurora were made at Thumbi West Island (14°05'S 34°54'E; Fig. 1). Additional observations were made during an expedition to Likoma Island (12°00'S 34°55'E), located in the central part of the lake. All observations were made while SCUBA diving, except at Likoma Island, where a hookah diving system was used. Records were pencilled on PVC slates. This study concentrated on four

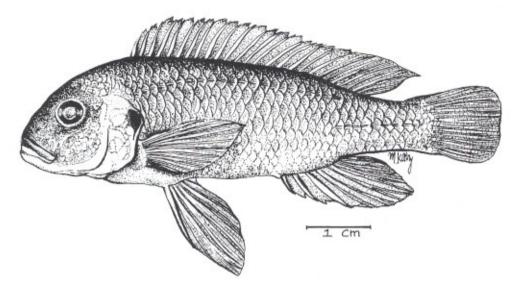


Fig. 2. Pseudotropheus callainos, holotype, PSU 2542.1, adult male, 76.3 mm SL.

different behaviors: chase heterospecific, chase conspecific male, chase conspecific female, and court conspecific female. Chasing was defined as attacking towards an intruding fish followed by pursuit to or beyond the territorial border; courting was defined as circling around with a female, which was sometimes interrupted by lateral displays.

Pseudotropheus callainos, new species (Figs. 2-5)

Pseudotropheus zebra 'cobalt', Ribbink et al., 1983: 165.

Holotype. PSU 2542.1, adult male, 76.3 mm, Nkhata Bay (11°35'S 34°41'E), Lake Malawi, Africa, 3-4 m, March, 1989. Collected by Stuart Grant.

Paratypes. PSU 2542.2 (6), MFU 2 (4), (60.5-68.3 mm) data as for holotype. - USNM 322426, 9 (64.7-80.1 mm), Nkhata Bay, Lake Malawi, Africa, 3-4 m, May 1988.

Diagnosis. A cichlid of the genus Pseudotropheus that is morphologically similar to members of the P. zebra complex as defined by Ribbink et al. (1983) in that it has a terminal mouth with several rows of teeth, the outer rows of which are bicuspid, with an occasional conical lateral tooth, and the inner rows of which are tricuspid. The overall blue color of the males, the blue and white color morphs of the females, and the complete absence of vertical bars in both sexes distinguish it from other members of the *P. zebra* complex (see Fryer, 1959; Fryer & Iles, 1972; McKaye, 1984).

Description. Morphometric ratios and meristics are presented in Table 1. Body moderately compact; jaws isognathous (Fig. 2). Teeth on lower jaw and premaxilla in 2-4 rows; most teeth in outer rows bicuspid, those in inner rows tricuspid; 11 teeth in outer row of left half of the lower jaw of holotype, and 11-17 in paratypes. Anal fin with 3 spines and 7 rays in holotype and in 18 paratypes, and 3 spines and 8 rays in one paratype; caudal fin emarginate. Lower pharyngeal bone of holotype triangular in outline; left posterior row with 23 pharyngeal teeth, left median row with 14. Scales along lateral side ctenoid; the holotype with 31 pored lateral line scales, and the paratypes with 30-32; pored scales posterior to hypural plate 1-3 (mode 2). The holotype and all paratypes with 4 scale rows on cheek. Gill rakers simple; first gill arch with 11-12 on the ceratobranchial, 1-3 on epibranchial, and one between epibranchial and ceratobranchial.

Lateral body coloration of males blue (Fig. 3) with green highlights on dorsal one-third; head blue with green highlights dorsally; gular white with blue highlights; black opercular spot;

Table 1. Morphometric characters and meristics of the holotype of *Pseudotropheus callainos* and the mean, standard deviation, and range of 19 paratypes, from Nkhata Bay and 13 specimens from Thumbi West Island.

J.	Holotype	P	Paratypes		Thumbi West Island		
		Mean	SD	Range	Mean	SD	Range
Standard length, mm	65.2	67.9	5.8	60.5-80.1	72.7	5.2	66.5-80.6
Head length, mm	20.4	20.8	1.7	18.3-23.8	21.8	1.4	20.2-23.9
Percent standard length							
Head length	31.3	30.6	0.7	29.2-31.6	30.4	0.7	29.1-31.8
Snout to dorsal	33.3	32.7	1.1	30.6-34.6	31.8	1.0	30.2-34.5
Snout to pelvic	38.6	36.8	0.7	35.7-38.2	36.9	0.7	35.9-38.1
Greatest body depth	31.0	31.4	1.3	28.8-33.5	32.7	1.4	30.4-34.9
Caudal peduncle length	15.0	14.8	0.8	13.1-15.9	14.9	0.6	13.9-15.7
Least caudal peduncle depth	11.8	12.0	0.4	11.5-13.0	12.0	0.5	11.6-13.5
Pectoral-fin length	27.0	25.7	1.6	21.9-28.6	25.0	1.5	23.4-27.5
Pelvic-fin length	26.2	30.5	3.7	24.0-35.5	29.8	3.6	25.0-37.7
Dorsal-fin base length	63.3	63.1	1.8	59.8-66.6	64.0	1.6	61.4-67.2
Percent head length							
Horizontal eye diameter	31.9	31.6	1.4	28.9-34.2	31.7	1.2	29.7-33.7
Vertical eye diameter	31.4	32.5	1.4	29.7-35.3	32.3	1.2	30.2-34.6
Snout length	30.9	32.7	2.5	28.8-37.0	32.5	1.6	28.9-36.0
Postorbital head length	41.7	40.4	1.4	37.8-42.6	40.0	1.0	38.2-41.2
Preorbital depth	22.5	22.7	1.4	20.1-25.0	23.2	1.2	21.6-24.9
Lower jaw length	35.3	37.0	1.6	34.9-39.9	38.0	1.1	36.4-40.2
Cheek depth	25.0	25.6	3.5	21.3-33.5	26.3	2.1	23.8-32.4
Head depth	85.3	93.1	8.6	63.2-103.9	99.4	4.7	92.7-110.2
Counts							
Lateral line scales	31	31.2	0.5	30-32	31.7	0.7	30-33
Pored scales posterior to hypural plat	e 1	2.1	0.5	1-3	1.4	0.6	0-2
Scale rows on cheek	4	4.0	0	4	4.2	0.4	4-5
Dorsal-fin spines	18	17.8	0.4	17-18	17.9	0.3	17-18
Dorsal-fin rays	9	8.7	0.5	8-9	8.9	0.5	8-10
Pectoral-fin rays	14	13.7	0.5	13-14	13.5	0.5	13-14
Anal-fin rays	7	7.1	0.2	7-8	7.1	0.5	6-8
Gillrakers on first ceratobranchial	11	11.2	0.4	11-12	10.7	0.7	10-12
Gillrakers on first epibranchial	2	2.3	0.6	1-3	2.3	0.5	2-3
Teeth in outer row of left lower jaw	11	14.2	1.3	11-17	12.8	2.6	5-15
Teeth rows on upper jaw	4	3.6	0.6	2-4	3.4	0.7	2-4
Teeth rows on lower jaw	4	3.9	0.2	3-4	3.8	0.4	3-4

dorsal-fin membranes light blue; pectoral-fin membranes clear with black rays; pelvic fins clear with white leading edge; anal fin white proximally, light blue distally, with 1-3 yellow ocelli. Some of the females similarly colored but not as intensely; ocellus absent from anal fin; other females white overall (Fig 4).

Remarks. Pseudotropheus callainos feeds on periphyton by orienting perpendicular to the substrate and scraping algae from the rocks (Holzberg, 1978). We also observed them feeding on zooplankton present in the water column. Schröder (1980) reported that the B morph (distinguished by the absence of black vertical bars and assumed to be P. callainos) was more aggressive than the BB morph (distinguished by possessing black vertical bars and assumed to be *P. zebra*) and made more attacks toward B and W (assumed to be the white color morph of *P. callianos*) morphs than toward BB morphs. Schröder (1980) concluded that the B and W color morphs were reproductively isolated from the BB morphs, since or because B and W females were only courted by B males and were never observed being courted by BB males. McKaye et al. (1984) documented genetic differences of *P. callianos* from sympatric BB forms, thus confirming reproductive isolation in this species.

Morphometric ratios and meristics of 13 specimens (PSU 2540.2) collected at Thumbi West Island (14°05'S 34°54'E), Cape Maclear in



Fig. 3. Pseudotropheus callainos, male, Thumbi West Island.



Fig. 4. Pseudotropheus callainos, female, white morph, Thumbi West Island.

Ichthyol. Explor. Freshwaters, Vol. 3, No. 3

Table 2. Size principal component and sheared second principal component (shape factor) of untransformed morphometric data for Pseudotropheus callainos from Nkhata Bay (n=20) and Thumbi West Island (n=13)

	Size	Sheared PC ₂
Standard length	0.165	-0.019
Head length	0.160	0.040
Snout length	0.231	0.202
Postorbital head length	0.150	0.081
Horizontal eye diameter	0.093	0.435
Vertical eve diameter	0.104	-0.069
Preorbital depth	0.247	0.113
Cheek depth	0.289	0.470
Lower-jaw length	0.168	0.068
Head depth	0.241	0.137
Body depth	0.201	-0.005
Snout to dorsal-fin origin	0.192	0.054
Snout to pelvic-fin origin	0.164	0.008
Dorsal-fin base length	0.182	-0.022
Least caudal-peduncle depth	0.197	-0.021
Caudal-peduncle length	0.147	0.078
Anterior dorsal to anterior anal	0.195	0.007
Posterior dorsal to posterior anal	0.193	-0.077
Anterior dorsal to posterior anal	0.182	-0.035
Posterior dorsal to anterior anal	0.167	-0.027
Posterior dorsal to ventral caudal	0.220	-0.011
Posterior anal to dorsal caudal	0.193	0.057
Anterior dorsal to pelvic-fin origin	0.211	0.073
Posterior dorsal to pelvic-fin origin	0.173	0.002
Pectoral-fin length	0.180	-0.237
Pelvic-fin length	0.307	-0.777

southern Lake Malawi are presented in Table 2. When the sheared second principal components (morphometric data) were plotted against the first factor components (meristic data), two clusters could be distinguished (Fig. 5). A MANOVA in conjunction with a Hotelling-Lawley trace demonstrated that the two clusters were significantly different (P < 0.01). The first principal component is interpreted as a size component and the sheared second component as shape, independent of size (Humphries et al., 1981; Bookstein et al., 1985). Size accounts for 80.5% of the total variance and after its effects are removed, the second principal component accounts for 27.1% of the remaining variance. The variables that have the highest loading on the sheared second principal component are cheek depth, horizontal eye diameter, snout length, pelvic-fin length, and pectoral-fin length (Table 3). The variables that have the highest standardized scoring coefficients on the meristic data are lateral-line scales, pored scales posterior to the lateral line, scale rows on cheek, and gill rakers on the first ceratobranchial (Table 4).

Etymology. The name callainos, from the Greek meaning 'turquoise', was chosen to reflect the blue ground color with green highlights of the territorial males.

Table 3. Standardized scoring coefficients on meristic data for *Pseudotropheus callainos* from Nkhata Bay(n=20) and Thumbi West Island (n=13)

	Factor 1
Dorsal-fin spines	-0.067
Dorsal-fin rays	0.126
Anal-fin rays	0.114
Pectoral-fin rays	0.142
Lateral-line scales	0.218
Pored scales posterior to lateral line	-0.311
Scale rows on cheek	0.299
Gill rakers on first ceratobranchial	-0.280
Gill rakers on first epibranchial	0.164
Teeth in outer row of left lower jaw	-0.054
Teeth rows on upper jaw	0.055
Teeth rows on lower jaw	0.033

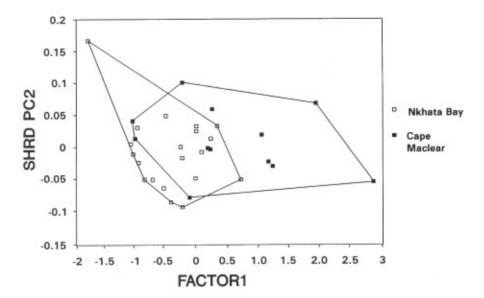


Fig. 5. Plot of the sheared second principal component (morphometric data) and the first factor score (meristic data) for the native (Nkhata Bay) and the transplanted (Cape Maclear) populations of *Pseudotropheus callainos*.

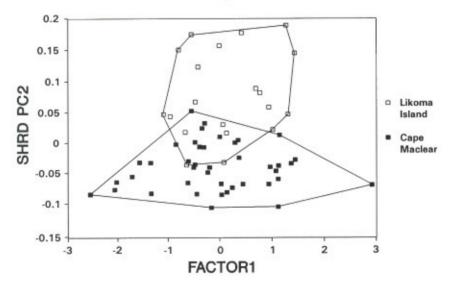


Fig. 6. Plot of the sheared second principal component (morphometric data) and the first factor score (meristic data) for the native (Likoma Island) and transplanted (Cape Maclear) populations of Pseudotropheus aurora.

Pseudotropheus aurora Burgess

Material examined. USNM 215292, holotype. -USNM 215293, 8 paratypes (see Burgess, 1976). -PSU 2545 (11 topotypes), Likoma Island, Lake Malawi, Malawi, Africa. - PSU 2540.1 (19), Thumbi West Island, Cape Maclear, Lake Malawi. - PSU 254l (22), Domwe Island, Cape Maclear, Lake Malawi.

Remarks. Morphometrics and meristics of the type series (n=9) and of 11 additional specimens collected from the type locality are presented in Table 5. The large eye (horizontal eye diameter

Table 4. Morphometric characters and meristics of the holotype and the mean, standard deviation, and range of 8 paratypes of and 11 typotypes Pseudotropheus aurora from Likoma Island, Malawi, Africa.

1	Holotype	Paratypes		Topotypes			
		Mean	SD	Range	Mean	SD	Range
Standard length, mm	80.8	76.0	5.1	69.5-83.5	73.5	5.5	59.0-80.1
Head length, mm	25.3	23.7	1.2	22.1-25.7	22.8	1.7	18.3-24.3
Percent standard length							
Head length	31.3	31.2	1.1	29.4-33.4	31.1	0.7	29.8-32.3
Snout to dorsal	33.8	34.3	1.0	32.6-36.0	34.4	1.0	32.9-36.1
Snout to pelvic	40.5	38.6	1.1	36.6-40.0	37.5	1.1	35.7-39.5
Greatest body depth	31.2	32.7	1.1	30.9-33.9	31.9	1.0	30.5-33.7
Caudal peduncle length	14.6	13.0	1.0	11.2-14.5	13.5	1.1	11.3-14.9
Least caudal peduncle depth	12.0	12.2	0.7	11.0-13.0	12.5	0.6	11.4-13.4
Pectoral-fin length	24.0	19.3	2.0	17.4-22.9	25.2	1.5	23.7-28.7
Pelvic-fin length	32.2	26.0	2.8	23.7-31.8	30.5	4.0	26.7-38.4
Dorsal-fin base length	62.1	61.3	0.6	60.7-62.2	62.5	1.0	60.7-63.6
Percent head length							
Horizontal eye diameter	36.4	38.0	1.2	35.8-39.7	37.6	1.2	36.0-39.9
Vertical eye diameter	37.5	38.9	0.9	37.0-39.9	37.5	1.5	34.7-39.9
Snout length	32.0	31.7	1.6	29.4-34.3	29.8	1.1	27.8-31.6
Postorbital head length	37.2	37.2	1.2	35.8-39.4	37.4	1.0	35.8-40.0
Preorbital depth	20.2	19.4	0.8	18.1-20.8	20.0	0.8	18.0-20.7
Lower jaw length	34.4	34.8	1.0	33.3-36.4	36.4	1.8	33.9-39.8
Cheek depth	24.5	25.0	1.4	23.2-27.2	24.3	1.4	21.3-26.1
Head depth	85.0	86.9	5.5	80.5-95.7	89.2	4.6	81.6-99.6
Counts							
Lateral line scales	31	31.8	0.5	31-32	31.8	0.6	31-33
Pored scales posterior to hypural plate	e 2	1.3	0.9	0-2	1.9	0.3	1.2
Scale rows on cheek	4	4.0	0	4	4.0	0	4
Dorsal-fin spines	17	17.9	0.4	17-18	18.0	0	18
Dorsal-fin rays	9	9.0	0.5	8-10	9.1	0.5	8-10
Pectoral-fin rays	13	13.2	0.5	13-14	12.9	0.3	12-13
Anal-fin rays	7	7.0	0	7	7	0	7
Gillrakers on first ceratobranchial	11	11.3	0.7	10-12	11.9	0.5	11-13
Gillrakers on first epibranchial	3	2.9	0.6	2-4	3.0	0.4	2-4
Teeth in outer row of left lower jaw	11	11.4	1.1	10-13	11.9	0.5	11-13
Teeth rows on upper jaw	4	4.0	0	4	3.9	0.3	3-4
Teeth rows on lower jaw	4	4.0	0	4	3.9	0.3	3-4

36.4-39.9% head length; vertical eye diameter 34.7-39.9% head length) distinguishes *P. aurora* from all other known *Pseudotropheus* species (Burgess, 1976).

Morphometric and meristic characters for the Cape Maclear populations (Thumbi West Island; Domwe Island) are summarized in Table 6. A plot of the sheared PC2 (representing body shape) and the first factor score (meristic data) indicate that the populations from Cape Maclear differ from those at Likoma Island (Fig. 6). A MANOVA in conjunction with a Hotelling-Lawley trace demonstrated that the two clusters were significantly different (P<0.01). The cluster formed by the type series was not significantly (P<0.01) different than that formed by the topo-

types. As stated previously, the first principal component is interpreted as a size component and the sheared component as shape, independent of size (Humphries et al., 1981; Bookstein et al., 1985). Size accounted for 68% of the total variance and after its effects were removed, the second principal component accounted for 39.3% of the remaining variance. The variables that have the highest loading on the sheared second principal component are pelvic-fin length, head depth, and cheek depth (Table 7). The variables that have the highest standardized scoring coefficients on the meristic data are number of dorsal-fin rays, number of gill rakers on the first ceratobranchial, and number of pectoral-fin rays (Table 8). The only observed

Table 5. Mean, standard deviation, and range of the morphometric and meristic characters of 19 specimens of Pseudotropheus aurora from Thumbi West Island and 22 specimens from Domwe Island, Malawi, Africa, collected in 1989.

	Thu	Thumbi West Island			Domwe Island		
	Mean	SD	Range	Mean	SD	Range	
Standard length, mm	77.0	2.9	71.2-81.8	73.7	5.5	64.8-82.3	
Head length, mm	24.0	0.9	22.1-25.5	23.5	1.6	20.6-25.9	
Percent standard length							
Head length	31.1	0.8	29.4-32.5	32.0	1.2	30.0-34.3	
Snout to dorsal	34.1	1.4	31.7-36.8	34.9	1.4	33.0-38.1	
Snout to pelvic	38.0	0.9	36.6-39.5	39.2	1.4	37.4-41.7	
Greatest body depth	35.1	1.8	29.2-37.1	36.3	1.3	34.3-38.5	
Caudal peduncle length	13.4	1.1	11.1-14.6	13.1	0.7	11.9-14.3	
Least caudal peduncle depth	12.4	0.5	11.1-13.0	13.1	0.5	12.3-14.1	
Pectoral-fin length	27.2	1.5	25.0-31.0	27.4	1.3	24.2-29.4	
Pelvic-fin length	36.2	3.9	27.6-41.8	34.5	4.0	28.2-42.0	
Dorsal-fin base length	62.0	1.6	59.4-65.1	62.5	1.6	59.3-65.5	
Percent head length							
Horizontal eye diameter	36.9	1.5	34.6-41.1	37.0	1.2	35.0-39.2	
Vertical eye diameter	37.1	1.6	34.1-39.8	37.3	1.5	35.0-40.2	
Snout length	32.1	1.3	29.4-34.0	31.1	1.6	28.6-34.6	
Postorbital head length	36.7	1.0	35.3-38.1	36.7	1.3	33.6-39.8	
Preorbital depth	19.6	0.9	18.2-22.0	19.5	1.4	16.9-22.0	
Lower jaw length	34.2	1.2	31.7-36.1	34.8	1.4	32.1-37.9	
Cheek depth	23.6	1.2	21.1-25.7	22.7	2.1	18.6-27.1	
Head depth	93.7	3.6	87.8-101.3	93.6	5.1	81.0-103.8	
Counts							
Lateral line scales	31.6	0.5	31-32	31.8	0.6	31-33	
Pored scales posterior to hypural plate	1.9	0.3	1-2	2.0	0.5	1-3	
Scale rows on cheek	4.0	0.3	3-5	4.0	0	4	
Dorsal-fin spines	17.8	0.5	17-19	17.8	0.4	17-18	
Dorsal-fin rays	9.1	0.6	8-10	8.7	0.5	8-10	
Pectoral-fin rays	12.8	0.4	12-13	12.9	0.5	12-14	
Anal-fin rays	7.3	0.5	7-8	7.2	0.5	6-8	
Gillrakers on first ceratobranchial	11.1	0.7	10-12	11.8	0.6	11-13	
Gillrakers on first epibranchial	2.8	0.4	2-3	2.9	0.4	2-4	
Teeth in outer row of left lower jaw	9.6	2.1	6-13	12.2	1.0	11-15	
Teeth rows on upper jaw	3.9	0.2	3-4	4.0	0.2	4-5	
Teeth rows on lower jaw	3.9	0.2	3-4	4.0	0.2	4-5	

difference within the transplanted populations involved egg spots on males' anal fins. The percentage of males with two or more egg spots on their anal fins is higher in the populations along the western portion of Thumbi West Island (Fig. 1, Areas D to H - 52.5%; n=476) than in populations that inhabit the eastern portion of Thumbi West Island (Fig. 1, Areas A to C, 34%; n=81), Otter Point (32%; n=82), and Likoma Island 32%; n=71).

Results and discussion

Pseudotropheus aurora has established reprod-

ucing populations at Otter Point, Thumbi West Island (Ribbink et al., 1983; Trendall, 1988), and Domwe Island, which is located approximately 2 km south of Thumbi West Island. Eighteen territorial males of *P. aurora* inhabited an area of 25 m² at Likoma Island, whereas, only 6-12 males established territories in an area of the same size at Thumbi West Island. Re-occupation of artificially emptied territories by conspecifics took longer at Likoma Island; of 18 territories, seven were re-occupied by heterospecifics, while five remained empty (Hert, 1990). Territorial *P. aurora* males of Likoma Island chased heterospecific intruders more frequently than did males of Thumbi West Island (t=2.38; df = 35; P < 0.05).

Table 6. Size principal component and sheared second principal component (shape factor) of the untransformed morphometric data for Pseudotropheus aurora from Likoma Island (n=20) and Cape Maclear (n=41).

	Size	Sheared PC ₂	
Standard length	0.172	0.080	
Head length	0.150	0.078	
Snout length	0.208	0.075	
Postorbital head length	0.159	0.107	
Horizontal eye diameter	0.145	0.122	
Vertical eye diameter	0.157	0.141	
Preorbital depth	0.260	0.129	
Cheek depth	0.288	0.269	
Lower-jaw length	0.186	0.142	
Head depth	0.210	-0.381	
Body depth	0.190	-0.124	
Snout to dorsal-fin origin	0.179	0.094	
Snout to pelvic-fin origin	0.167	0.084	
Dorsal-fin base length	0.186	0.049	
Least caudal-peduncle depth	0.180	0.015	
Caudal-peduncle length	0.209	0.082	
Anterior dorsal to anterior anal	0.187	0.066	
Posterior dorsal to posterior anal	0.190	0.053	
Anterior dorsal to posterior anal	0.194	0.061	
Posterior dorsal to anterior anal	0.201	0.009	
Posterior dorsal to ventral caudal	0.172	0.020	
Posterior anal to dorsal caudal	0.182	0.001	
Anterior dorsal to pelvic-fin origin	0.209	-0.041	
Posterior dorsal to pelvic-fin origin	0.183	-0.034	
Pectoral-fin length	0.183	-0.514	
Pelvic-fin length	0.257	-0.705	

There were no significant differences (P > 0.05) in the number of chases of conspecific males, or in interactions with females.

Although the Likoma Island population of *P. aurora* was more dense, re-occupation took longer and was incomplete. That heterospecifics were chased more frequently at Likoma Island could simply be due to the fact that heterospecifics intruded more frequently at Likoma Island. The five territories that remained empty may have been extremely unattractive to species other than *P. aurora* due to habitat specificity, and these territories might have become unattractive to *P. aurora* because of the presence of 'new' neighbors.

The translocated population of *P. callainos* has also diverged morphologically from the native population. Although other authors have reported hybridization of fishes other than cichlids following an introduction event (Nelson, 1973; Hocutt and Hambrick, 1973; Raesly et al., 1990), no evidence of hybridization had been recorded between *Pseudotropheus* species at Thumbi West Island prior to 1991. Video

recordings (PSU 2543) made during April, 1992 off Thumbi West Island showed several specimens that appeared to be hybrid BB P. zebra x P. callainos. These fish had pale blue sides with thin black vertical bars present on the middle two-thirds of the sides. These fish were not collected, because we did not possess 1992 collecting per-

Table 7. Standardized scoring coefficients on meristic data for *Pseudotropheus aurora* from Likoma Island (n=20) and Cape Maclear (n=41).

	Factor 1
Dorsal-fin spines	0.224
Dorsal-fin rays	-0.350
Anal-fin rays	0.040
Pectoral-fin rays	0.252
Lateral-line scales	0.199
Pored scales posterior to lateral line	-0.078
Scale rows on cheek	-0.042
Gill rakers on first ceratobranchial	0.266
Gill rakers on first epibranchial	0.238
Teeth in outer row of left lower jaw	0.207
Teeth rows on upper jaw	0.227
Teeth rows on lower jaw	0.059
40 7 C C C C C C C C C C C C C C C C C C	

mits for Lake Malawi National Park. Observations in the laboratory have shown that premating isolating mechanisms break down in aquaria, and that viable hybrids can be produced between P. callainos and other Pseudotropheus species (pers. obs.; Paulo, pers. comm. to Holzberg, 1978); thus it is conceivable that hybrids between native and translocated populations of the P. zebra complex could occur in the wild.

The morphological divergence between the transplanted and native populations of both *P. callainos* and *P. aurora* may have resulted from: (1) a founder event, in which only a small proportion of the total gene pool was represented by the initial inoculum (Mayr, 1963), (2) random drift or selection pressures that occurred after isolation, or (3) ecologically induced phenotypic plasticity (Chernoff, 1982; Meyer, 1987).

In conclusion, we strongly criticize the intralacustrine translocations of fishes within Lake Malawi. Transplanted species could potentially dilute gene pools of indigenous species and/or cause the extinction of native forms (Stauffer, 1984).

Acknowledgements

We thank the government of Malawi for providing the permits to make this research possible. L. W. Knapp arranged for shipment of specimens from Malawi to the USNM. The original line drawing of *P. callainos* was completed by M. Katz. B. Knauer prepared Figure 1. T. J. LoVullo and B. Hert provided valuable field assistance. This work was funded in part by the National Science Foundation (BNS86-06836) and the United States Agency for International Development (Grant No. 10.069; COM-5600-G-00-0017-00), Program in Science and Technology Cooperation, Office of Science Advisor.

Literature cited

- Barel, C. D. N., M. J. O. van Oijen, F. Witte & E. L. M. Witte-Maas. 1977. An introduction to the taxonomy and morphology of the haplochromine cichlidae from Lake Victoria. Part A. Text. Neth. J. Zool., 27: 333-389.
- Bookstein, F., B. Chernoff, R. Elder, J. Humphries, G. Smith & R. Strauss. 1985. Morphometrics in evolutionary biology. Academy of Natural Sciences of Philadelphia, Spec. Publ., 15: 1-277.

- Burgess, W. E. 1976. Studies on the family Cichlidae: 5. Pseudotropheus aurora, a new species of cichlid fish from Lake Malawi. Trop. Fish Hobby., 24 (9, May 1976): 52-56.
- Chernoff, B. 1982. Character variation among populations and the analysis of biogeography. Amer. Zool., 22: 425-439.
- Fryer, G. 1959. The trophic interrelationships and ecology of some littoral communities in Lake Nyasa with special reference to the fishes, and a discussion of the evolution of a group of rock-frequenting Cichlidae. Proc. Zool. Soc. London, 132: 153-281.
- Fryer, G. & T. D. Iles. 1972. The cichlid fishes of the Great Lakes of Africa. Their biology and evolution. Oliver & Boyd, Edinburgh, 641 pp.
- Hert, E. 1990. Factors of habitat partitioning in Pseudotropheus aurora (Pisces: Cichlidae) and introduced species to a species-rich community of Lake Malawi. J. Fish Biol., 36: 853-865.
- Hocutt, C. H. & P. S. Hambrick. 1973. Hybridization between the darters Percina crassa roanoka and Percina oxyrhyncha (Percidae, Etheostomatini), with comments on the distribution of Percina crassa roanoka in New River. Amer. Midl. Nat., 90: 397-405.
- Holzberg, S. 1978. A field and laboratory study of the behaviour and ecology of *Pseudotropheus zebra* (Boulenger), an endemic cichlid of Lake Malawi (Pisces: Cichlidae). Ztschr. Zool. Syst. Evolut. Forsch., 16: 171-187.
- Humphries, J. M., F. L. Bookstein, B. Chernoff, G. R. Smith, R. L. Elder & S. G. Poss. 1981. Multivariate discrimination by shape in relation to size. Syst. Zool., 30: 291-308.
- Mayr, E. 1963. Animal Species and Evolution. Harvard University Press, Cambridge, MA., 797 pp.
- McKaye, K. R., T. D. Kocher, P. Reinthal, R. Harrison & I. Kornfield. 1984. Genetic evidence for allopatric and sympatric differentiation among color morphs of a Lake Malawi cichlid fish. Evolution, 38: 215-219.
- Meyer, A. 1987. Phenotypic plasticity and heterochrony in Cichlasoma managuense (Pisces: Cichlidae) and their implications for speciation in cichlid fishes. Evolution, 41: 1357-1369.
- Nelson, J. S. 1973. Morphological differences between the teleosts Couesius plumbeus (lake chub) and Rhinichthys cataractae (longnose dace) and their hybrids from Alberta. J. Morph., 139: 227-238.
- Raesly, R. L., J. R. Stauffer & R. F. Denoncourt. 1990. Hybridization between two darters, Etheostoma zonale and Etheostoma olmstedi (Teleostei: Percidae), following an introduction event. Copeia, 1990: 584-588.
- Regan, C. T. 1921. The cichlid fishes of Lake Nyasa. Proc. Zool. Soc. London, 1921: 675-727.
- Reyment, R. A., R. E. Blackith & N. A. Campbell. 1984. Multivariate morphometrics. Academic Press, New York
- Ribbink, A. J., B. A. Marsh, A. C. Marsh, A. C. Ribbink & B. J. Sharp. 1983. A preliminary survey of the cichlid

- fishes of the rock habitats in Lake Malawi. South Afr. J. Zool., 18: 149-310.
- Schröder, J. H. 1980. Morphological and behavioural differences between the BB/OB and B/W colour morphs of Pseudotropheus zebra Boulenger (Pisces: Cichlidae) Ztschr. Zool. Syst. Evolut. Forsch., 18: 69-76.
- Stauffer, J. R. 1984. Colonization theory relative to introduced populations. Pp. 8-21 in: W. R. Courtenay & J. R. Stauffer (eds.), Distribution, biology, and management of exotic fishes. The John Hopkins University Press, Baltimore, MA.
- 1988. Descriptions of three rock-dwelling cichlids (Teleostei: Cichlidae) from Lake Malawi, Africa. Copeia, 1988: 663-668.

- 1991. Description of a facultative cleanerfish (Teleostei: Cichlidae) from Lake Malawi, Africa. Copeia, 1991: 141-147.
- Stauffer, J. R. & J. M. Boltz. 1989. Description of a rockdwelling cichlid (Teleostei: Cichlidae) from Lake Malawi, Africa. Proc. Biol. Soc. Washington, 102: 8-13.
- Trendall, J. R. 1988. The distribution and dispersal of introduced fish at Thumbi West Island in Lake Malawi, Africa. J. Fish Biol., 33: 357-369.
- Trewavas, E. 1935. A synopsis of the cichlid fishes of Lake Nyasa. Ann. Mag. Nat. Hist., (10) 16: 65-118.

Received 7 October 1991 Revised 8 May 1992 Accepted 15 June 1992