

# Using Population Parameters to Separate Fish Stocks in the Okavango Delta Fishery: A Preliminary Assessment

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## Abstract

Populations of three cichlid species from the upper and lower Okavango Delta were compared in terms of biological population parameters, in order to investigate whether the fish species of the Delta consist of one continuous, or two or more separate, stocks. Data were collected from the lower Delta and upper Delta using experimental fishing nets to ensure that representative samples were obtained. While no statistical tests for significance were conducted, the results show that the same species between the upper and lower Delta have different biological parameters. Therefore, it is concluded that these observed differences suggest that, for the three investigated species, there are at least two different populations in the Okavango Delta.

## Background

Biological (Begg, 1998), genetic, parasitological, morphometric, physical tagging and life history traits (Abaunza *et al*, 2000), and species' spatial and temporal distribution behaviour (Burmeister, 2000) are some of the methods used to identify fish stocks around the world. One of the simplest approaches widely used is applying biological population parameters (Begg, 1998), which are certain fixed parameters from which some aspects of population 'behaviour' can be predicted (Hilborn and Walters, 1992). These include age, growth rate, growth performance index, mortality rate and maturity (Sparre and Venema, 1998). Therefore, studying vital population parameters can assist in the identification of different unit stocks that exist in an area of interest. Fisheries management is normally based on the presumption of a unit stock in the area of interest, with growth and mortality constituting the main ingredients of fish stock assessment (Hilborn and Walters 1992; Sparre and Venema, 1998).

According to Hilborn and Walters (1992), a unit stock is a homogenous collection of fish that are all subject to the same opportunities for growth and reproduction and the same risks of natural and fishing mortality. Sparre and Venema (1998) define a unit stock as discreet groups of animals that show little mixing with adjacent groups. An essential characteristic of a unit stock is that its growth and mortality parameters remain constant throughout its area of distribution (Sparre and Venema, 1998). Based on the definition above, it follows that a comprehensive management of a fishery can only be achieved on the basis of a well defined unit stock. While recent stock assessments (Mosepele, 2000; Mosepele and Kolding, 2003) showed that the fishery in the Okavango Delta is underutilised, it assumed that the fishery is characterized by a homogenous fish stock. Therefore, Mosepele's (2000) conclusion that fishing efforts in the fishery can be doubled without danger of biological over-exploitation can be wrong if indeed there is more than one fish stock in the Delta.

The Okavango Delta is not a uniform system where fish of all species are distributed and breeding evenly all over it. Instead, fish species aggregate at distinct places, at distinct times, for distinct purposes of feeding, breeding, migration and nursery area protection (Jackson, 1986). Merron (1991) established that the annual flood regime is important in maintaining fish populations. He argued that since the seasonal flooding of the Delta coincides with winter, the life history strategies of the fish populations in the lower Delta and the upper Delta may differ.

Merron and Bruton (1988) observed populations of 'dwarfed' three-spot tilapia (*Oreochromis andersonii*) in small flood plains connected to lagoons, compared to fish in the more stable permanent waters of the panhandle and larger oxbow. Tweddle *et al* (2003) highlighted the possibility of *K* strategists in the upper Delta and *r* selected species in the lower Delta. *K* selected species, which are normally found in stable ecosystems, are characterized by delayed maturation, longer life cycles, relatively low numbers of offspring and marked trophic specialisation. Conversely, *r* selected species occur in ephemeral conditions, and are characterized by rapid growth to maturity and high individual fecundity resulting in the maximum number of young ones (Begon and Mortimer, 1986; Lowe-McConnell, 1987; Hilborn & Walters, 1992).

The aim of this study is to compare growth and mortality of upper and lower Delta populations of three fish species, in order to evaluate whether the species consists of one continuous or at least two separate populations in the Delta. The results are assessed in terms of their implications for fisheries management. We assume that vital population parameters like growth and mortality are population specific.

## Materials and Methods

### Study Area

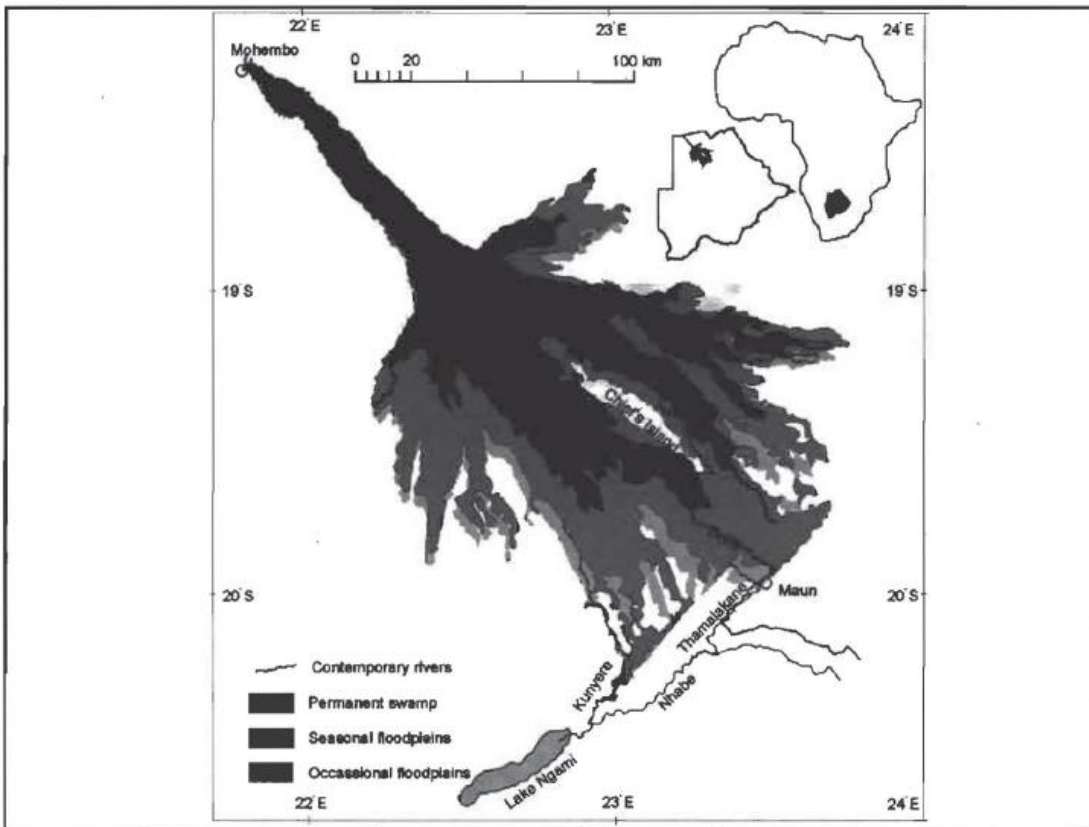


Figure 1. Map showing the Okavango Delta. Experimental fishing was conducted in the panhandle area or the upper Delta while the lower Delta habitat was around Chief's Island.

### Materials

Similar experimental fishing gear and gear setting procedures were used in both the upper Delta (UD) and lower Delta (LD) habitats. Standard experimental fishing methods with multi-panel, multi-mesh monofilament (gear code L) and multifilament experimental (gear code N) nets were used in this study. The L nets were made up of 12 panels, each 3 m long of different meshes with the meshes arranged geometrically from 10, 13, 16, 20, 25, 31, 39, 48, 58, 70, 86 and 110 mm stretched mesh. The N nets had 9 different panels, each 10 m long, with mesh sizes of 22, 28, 35, 45, 58, 73, 93, 118 and 150 mm stretched mesh. The construction of the experimental fishing net validated the assumption that most fish in the population had an equal probability to be sampled.

The nets were set overnight for approximately 12 hours and removed the following morning. When the allocated setting time lapsed, the nets were removed from the water and placed in separate containers with maximum care taken to ensure that the catch from different mesh sizes did not mix. Data from the different meshes were pooled later for analysis. Total length measurements of all specimens were taken to the nearest millimetre from the tip of the snout to the tip of the caudal fin for all the study fish species. Data was collected from both the upper and lower Delta as shown in Figure 1, while data sources are summarized in Table 1 below.

Table 1. Summary of the different data sources used in this study.

	Period	Gear Code	Mesh Range	Data Type	Habitat	N
<i>O.andersonii</i>	2001- 2004	N	22 - 150	Length, weight	UD	42
<i>O.andersonii</i>	2003- 2005	N	22 - 150	Length, weight	LD	36
<i>O.macrochir</i>	1999-2001	L	10 - 110	Length, weight	UD	53
<i>O.macrochir</i>	2003-2005	L	10 - 110	Length, weight	LD	50
<i>T.rendalli</i>	1999-2001	L	10 - 110	Length, weight	UD	114
<i>T.rendalli</i>	2003-2005	L	10 - 110	Length, weight	LD	355

### Data Analysis

Data were then entered into a computer using the PASGEAR (Kolding 1989-2002) computer software programme.

Data for each study species were then corrected for selectivity because gill nets generally select against small and big fish. The gill net selectivity corrected catches were then exported into FiSAT for derivation of vital population parameters.

### Growth

Several assumptions were made to derive growth parameters ( $L_{\infty}$  and K) from the VBGF implemented in ELEFAN 1 as highlighted by Gayanilo and Pauly (1997):

- Samples are representative of the population;
- All length differences are attributed to differences in age; and
- Growth is similar from one year to the next.

Growth parameters were then derived using ELEFAN 1 through the following process:

1. Estimating  $L_{max}$  (maximum length) from FiSAT and inputting this as a seed value for  $L_{\infty}$ . This value was then used to scan for K values. The selected K value corresponded to the most optimum value of goodness of fit index or Rn (where  $0 < Rn < 1$ ).
2. An automatic search routine in FiSAT was used with the seeded  $L_{\infty}$  and K values on the length frequencies of the study species. These values were then incremented/decremented until the best (highest) Rn value was obtained.
3. The growth parameters were then fitted onto an unreconstructed length frequency of the study species and were accepted when high Rn values were obtained.

For all species the ELEFAN I module implemented in FiSAT was used to calculate parameters for the generalized von Bertalanffy growth function (VBGF) (Pauly, 1982):

$$L_t = L_{\infty} \left( 1 - e^{-K(t-t_0)} \right) \quad (1)$$

Where

$L_{\infty}$  is the mean length of very old fish (asymptotic length).

K is a curvature parameter that determines the rate at which a fish approaches  $L_{\infty}$

In ELEFAN I the parameter  $t_0$  is replaced by starting points defined by a starting sample (SS) number and a starting length (SL), with both coordinates defining a size at which some non-zero frequencies are observed (Gayanilo and Pauly, 1997). These points are used to fix the curve onto a time scale.

### **Mortality**

#### **Total Mortality (Z)**

Several assumptions were made as according to Gayanilo and Pauly (1997) for the construction of the length converted catch curve:

- Z is the same in all age groups used in the plot;
- The recruitment fluctuations for all age groups used in the plot were small and random;
- All age groups used in the plot were equally vulnerable to the sampling gear; and
- The sample used was representative of the average population structure over the time period considered.

$$\ln \left( \frac{C_i}{\Delta t_i} \right) = a + b \cdot t_i \quad (2)$$

Where

$C_i$  is the number of fish in various length classes i

$\Delta t_i$  is the time needed to grow through length class i

$$\Delta t_i = \left( \frac{1}{K} \right) \cdot \ln \left[ \frac{L_{\infty} - L_{i+1}}{L_{\infty} - L_i} \right] \quad (3)$$

and

$$t_i' = \left(\frac{1}{K}\right) \cdot \ln \left[ 1 - \left(\frac{L_i}{L_\infty}\right) \right] \quad (4)$$

$L_i$  is the midpoint of length class  $i$   
the value of  $b$  with the sign changed then provides an estimate of  $Z$ .

**Natural mortality ( $M$ )**

Natural mortality rate of the study species was estimated from Pauly's (1982) empirical formula:

$$M = -0.0066 - 0.279 \log(L_\infty) + 0.6543 \log(K) + 0.463 \log(T) \quad (5)$$

Where

$M$  is natural mortality

$L_\infty$  and  $K$  are growth parameters from the VBGF

$T$  is the annual mean temperature. 25°C was used as the mean water temperature for the Okavango Delta.

**Growth Performance Index ( $\phi'$ )**

Growth performance index (Pauly and Gayanilo, 1997) for the study species was estimated from the following equation:

$$\phi' = \text{Log}(K) + 2 \text{Log}(L_\infty) \quad (6)$$

Where

$K$  and  $L_\infty$  are growth parameters from VBGF.

The derived vital population parameters,  $L_\infty$ ,  $K$  and  $M$  were then tested onto a hypothetical stock modelled in a Microsoft Excel spreadsheet, starting with an initial population size of 1000 fish. Vital population parameters were then accepted if the hypothetical population decreased to less than 20 individuals when length approached  $L_\infty$ .

**Length at Maximum Possible Yield ( $L_{opt}$ )**

The length at maximum possible yield (Froese and Binohaln, 2000) was calculated from the empirical relationship:

$$L_{opt} = 10^{(0.044 + 0.98411 \cdot \text{LOG}_{10}(L_\infty))} \quad (7)$$

Where

$L_\infty$  is a growth parameter from VBGF

**Length at Maturity ( $L_m$ )**

Length at first maturity was calculated from Froese and Binohaln's (2000) empirical relationship:

$$L_m = 10^{0.8979 \cdot \text{LOG}_{10}(L_\infty) - 0.0782} \tag{8}$$

Where

$L_\infty$  is a growth parameter from VBGF

**Results**

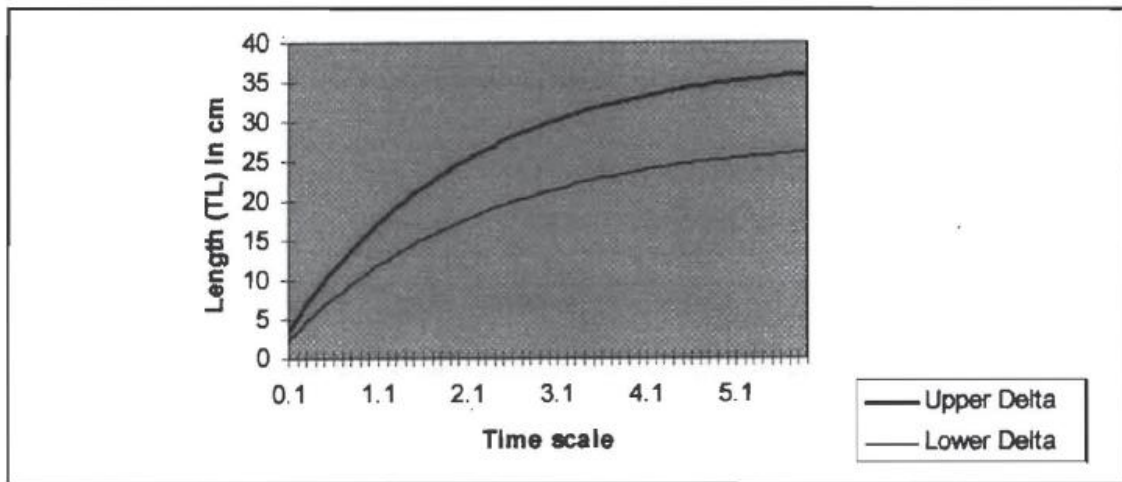


Figure 2. Growth curves for *Oreochromis macrochir* from the upper and lower Delta.

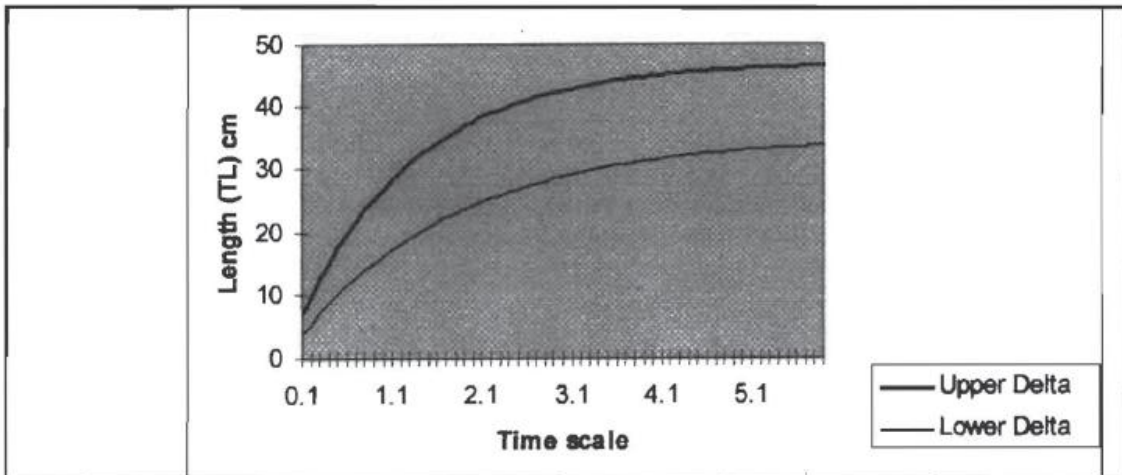


Figure 3. Growth curves for *Tilapia rendalli* from the upper and lower Delta.

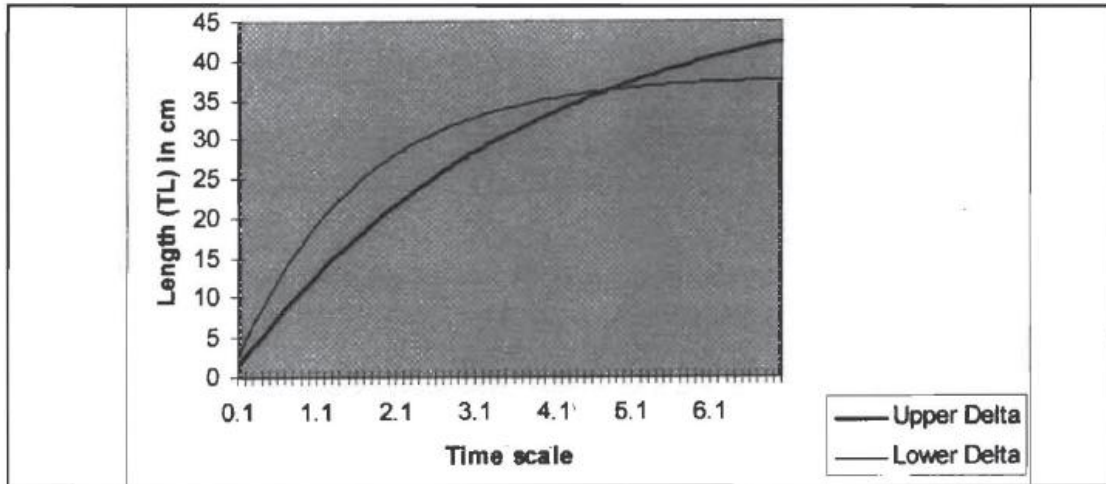


Figure 4. Growth curves for *Oreochromis andersonii* from the upper and lower Delta.

Figures 2, 3 and 4 show that *Tilapia rendalli*, *Oreochromis macrochir* and *O. andersonii* grow faster and reach bigger sizes in the upper Delta while the same species from the lower Delta grow more slowly and reach smaller sizes.

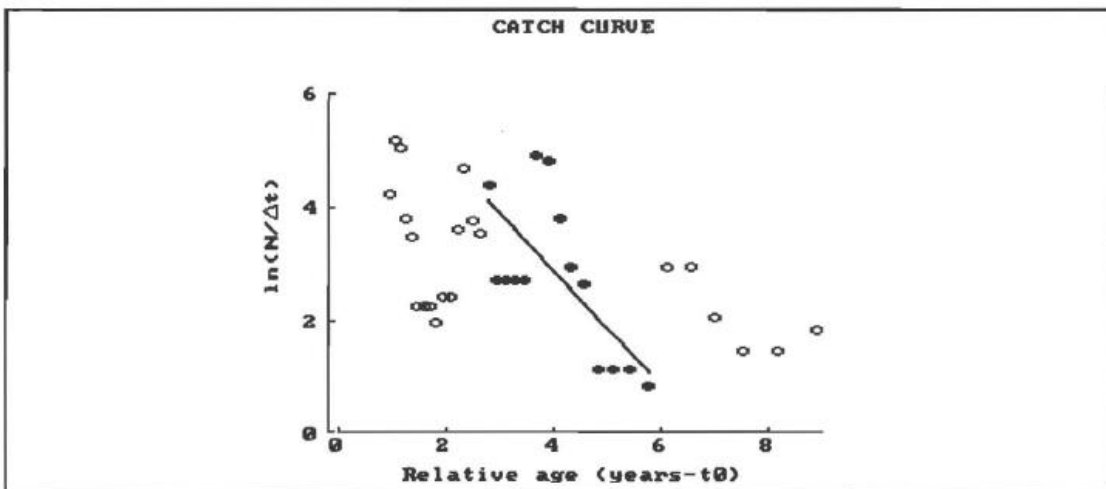


Figure 5. Total mortality ( $Z$ ) length-converted catch curve for *O. andersonii* from the upper Delta.

Figures 5-10 illustrate the length-converted catch curve for the study species in both the upper and lower Delta. Generally, the figures show a similar demographic structure of both the upper and lower Delta populations of *O. andersonii* and *O. macrochir*. However, the curves show that only the younger size classes for the upper Delta *Trendalli* populations were sampled (i.e. ages 0 to 2 years) while a broader range of age classes were sampled for the lower Delta *Trendalli* populations (i.e. ages 0 to 4 years).

Table 2 shows that the upper Delta populations have a higher growth performance, have higher total mortalities ( $Z$ ), and mature later than the lower Delta populations. Moreover,  $L_{opt}$  values (length at maximum possible yield) for the upper Delta populations are much higher than for the lower Delta populations.

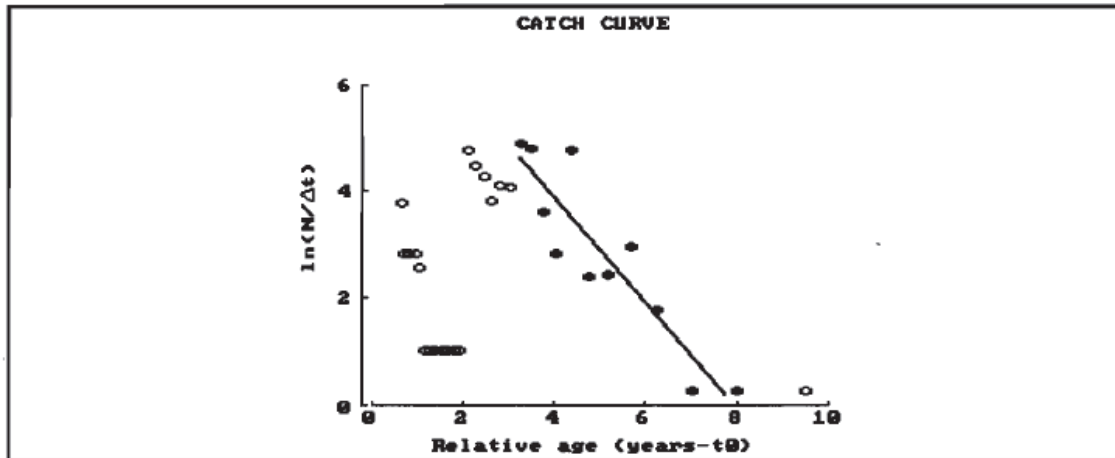


Figure 6. Total mortality (Z) length-converted catch curve for *O. andersonii* from the lower Delta.

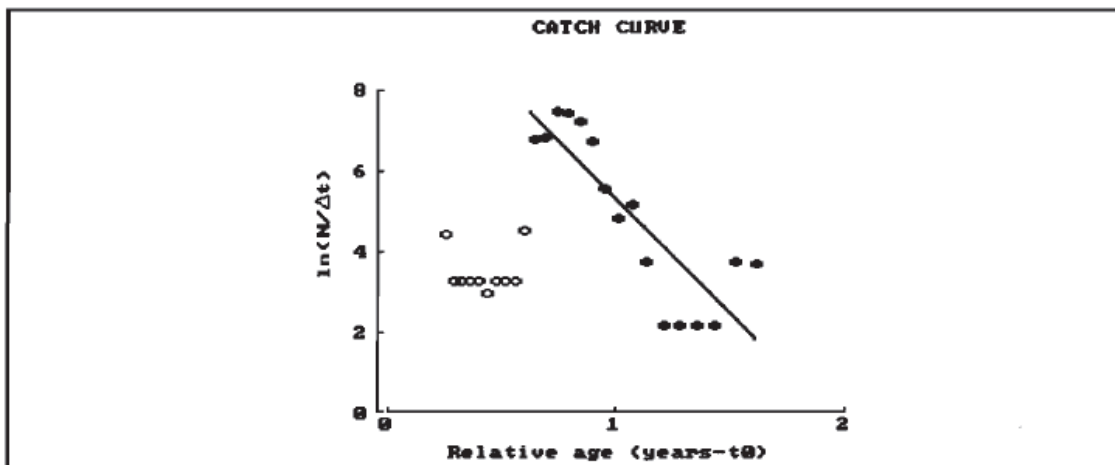


Figure 7. Total mortality (Z) length-converted catch curve for *T. rendalli* from the upper Delta.

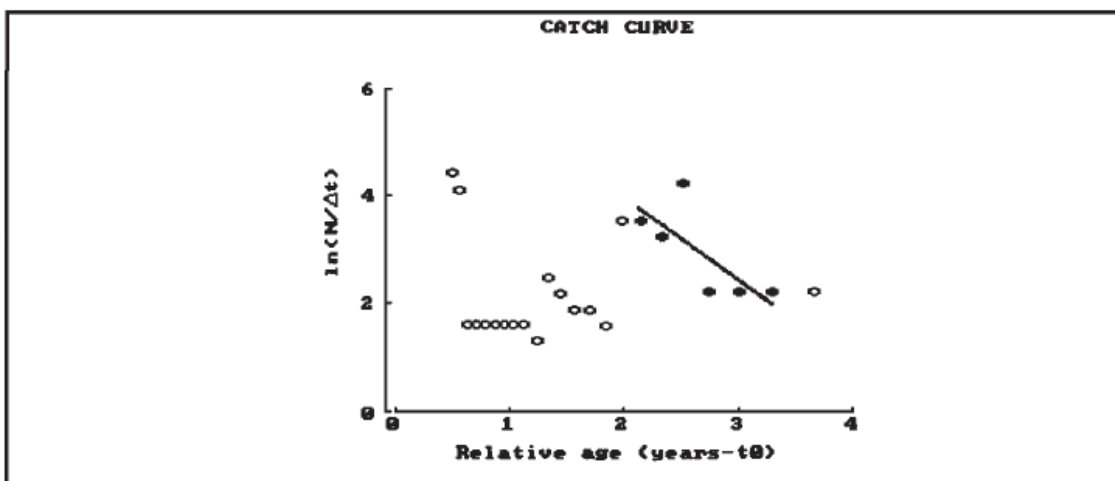


Figure 8. Total mortality (Z) length-converted catch curve for *T. rendalli* from the lower Delta.



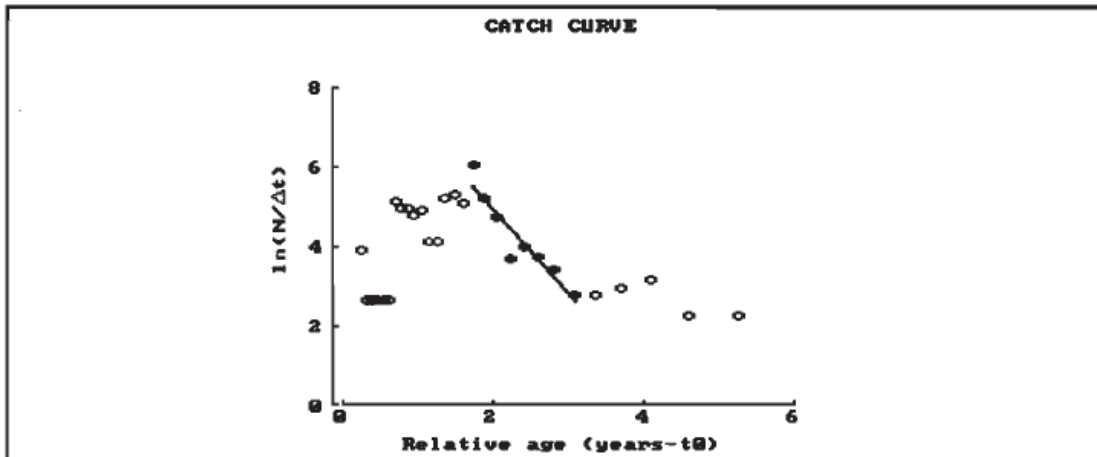


Figure 9 Total mortality (Z) length-converted catch curve for *O. macrochir* from the upper Delta.

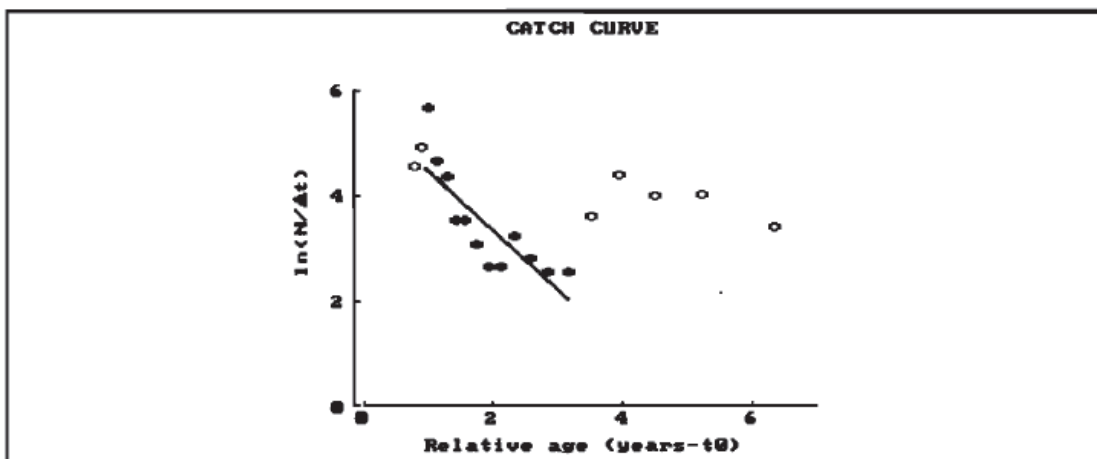


Figure 10 Total mortality (Z) length-converted catch curve for *O. macrochir* from the lower Delta.

Table 2 shows that  $L_{\infty}$  is higher for all the selected species from the upper Delta compared to those from the lower Delta. Moreover,  $L_{opt}$  values (length at maximum possible yield) for the upper Delta species are much higher than for the lower Delta species.

### Discussion

Various techniques have been used to determine or evaluate fish 'unit stocks' (Haddon, 2001; Begg, 1998; Austin, 1998; Sparre and Venema, 1992; Gabche and Hockey, 1995; Lai *et al* 1996). However, an approach similar to Begg (1998) was adopted in this study where differences in growth curves were used to identify fish stocks, without conducting any statistical tests for significance as suggested by Haddon (2001) and Lai *et al* (1996). Gabche and Hockey (1995) also simply compared  $L_{\infty}$  values, without any statistical tests, to determine stock separation of *Sardinella maderensis*. Stearns (1992) also compared growth curves without statistical tests for significance to illustrate growth rate as a function of mortality. Therefore, a

Table 2. Summary of vital population parameters for the study fish species for both the lower Delta and the upper Delta.

Species	Parameters	Upper Delta	Lower Delta
<i>O. andersonii</i>	$L_{\infty}$	50	38
	K	.27	.34
	M	.62	.78
	$L_m$	28.00	21.90
	$L_{opt}$	31.40	23.60
	Z	1.00	.97
	F	.38	.19
	$\emptyset'$	2.83	2.69
<i>O. macrochir</i>	$L_{\infty}$	35	23
	K	.50	.46
	M	1.03	1.04
	$L_m$	20.30	16.60
	$L_{opt}$	21.60	17.10
	Z	2.18	1.16
	F	1.15	.12
	$\emptyset'$	2.79	2.56
<i>T. rendalli</i>	$L_{\infty}$	47	35
	K	.77	.56
	M	1.26	1.11
	$L_m$	26.50	20.30
	$L_{opt}$	29.40	21.60
	Z	5.74	1.48
	F	4.48	.48
	$\emptyset'$	3.23	2.84

similar approach was adopted in this study, where growth curves were compared qualitatively without any statistical tests. In this study, all the study species show different growth curves, which suggest different populations growing at different growth rates. The results show that upper Delta *T.rendalli* and *O. macrochir* populations' grow faster and attain larger sizes, while lower Delta species have slower growth rates and reach smaller maximum ( $L_{\infty}$ ) sizes. This observation agrees with Mosepele (2000) who observed that lower Delta populations have slower growth rates compared to upper Delta populations. Conversely, upper Delta *O.andersonii* populations grow slower and reach bigger sizes while lower Delta populations grow faster and attain smaller maximum sizes. Other studies in the Okavango Delta have also pointed out that growth rates for fish populations in the upper Delta are slower than for the lower Delta (Merron and Bruton, 1988; Booth *et al*, 1995; Booth and Merron, 1996; Tweddle *et al*, 2003), which agrees with observations made for *O. andersonii*.

Spatial differences in fishing mortality can account for differences in growth rates between upper and lower Delta populations. The results show that the estimated total mortality (Z) for the study species is higher in the upper Delta than the lower, and there is a corresponding higher fishing mortality for the upper Delta populations than the lower Delta. Therefore, the high growth rates (for the upper Delta *T.rendalli* and *O. macrochir* populations) might be

attributed to higher fishing mortality compared to the lower Delta (Mosepele, 2000). According to Lowe-McConnell (1987), cichlids respond to high mortality (fishing pressure in this case) by progressively changing their life history strategies from *K* to *r*-selected strategists, illustrating what Stearns (1992) calls 'reproductive compensation'. Since fishing pressure is higher in the upper Delta than lower (Mosepele, 2000, 2001), it can therefore be assumed that the cichlids (i.e. *Trendalli* and *O.macrochir*), as the principal target species in the commercial fishery (Mosepele, 2002), have progressively increased their growth rates to counterbalance the effects of fishing pressure.

Natural mortality is caused by any causes other than fishing (Beverton and Holt, 1957; Gayanilo and Pauly, 1997). Sparre and Venema (1989) discuss that the same species might have different natural mortalities in different habitats depending not only on the ambient system, but also on the density of predators and competitors whose abundance might be influenced by fishing pressure. Stergiou and Papaconstantinou (1993) also observed that natural mortality is area specific due to different environmental conditions. Therefore, the differences in natural mortalities for the study species could be related to any of these factors. It is clearly evident from the results that the three cichlid species face different environmental conditions, which may account for the differences in natural mortalities. *Trendalli* could be under higher predation pressure in the upper Delta than in the lower Delta, the opposite might be true for *O.andersonii*, while conditions for *O.macrochir* might be generally similar in either habitat.

Spatial differences in fish community structure, especially as it relates to abundance and composition, might result in spatial differences in inter- and intra-specific competition. This observation is based on Merron and Bruton's (1988) observation that there is a higher abundance of *H.vittatus* (a top piscivorous predator), *C.gariepinus* (a top omnivore) and *O.andersonii* in the upper Delta, while *S.intermedius* and *H.odoe* dominate the lower Delta fish community structure. Moreover, there is lower species diversity in the lower Delta than in the upper Delta (Merron, 1991; Tweedle *et al*, 2003; Kolding *et al*, 2003). This essentially agrees with the stated observation that the same species face different pressures in different habitats in the Delta.

Gayanilo and Pauly (1997) point out that comparing tropical fish growth is difficult because of the unreliability of some of the methods used. Therefore they proposed a growth performance index based on empirical observations. Mosepele (2000) subsequently used the method to compare fish growth between the Okavango Delta and Bangweulu Swamps. This approach was also used in this study to compare fish growth between upper and lower Delta. The results show that upper Delta fish populations have a higher growth performance index than the lower Delta fish populations. This, according to Gayanilo and Pauly (1997), suggests that there are better growth conditions in the upper Delta than the lower.

Although the differences in biological parameters in this study were not tested for statistical significance, there is sufficient reasoning to postulate that the life history strategies of the same species (i.e. the study species) in two habitats (i.e. upper Delta vs. lower Delta) differ enough to suggest the possible existence of two separate populations. Begg (1998) used a similar approach and managed to identify different stocks of haddock (*Melanogrammus aeglefinus*) in the Northwest Atlantic Ocean. Notwithstanding, genetic methods have also been used extensively to separate fish stocks (Abaunza *et al*, 2000), although this has not yet been done for the Okavango Delta fishery. Nonetheless, the observed differences in the life history strategies, especially growth rates and maturity, testify to the possible existence of different fish populations between the lower Delta and upper Delta. Several other studies have alluded to the existence of at least two fish populations in the Okavango Delta fishery (Merron and Bruton,

1988; Merron, 1991; Mosepele, 2000; Tweddle, 2003). However, these differences do not necessarily conform to the  $r$  and  $K$  selected paradigms, as observed by the life history parameters of the cichlids species in this study. There appears, therefore, to be a coterie of other factors that is shaping and regulating fish stock in the different habitats (i.e. upper and lower Delta), both density dependent and density independent. The management implications of the possible existence of at least two fish populations in the Okavango Delta fishery are fully discussed in Mosepele and Mosepele (2005). However, one of the most important implications of this study to fisheries management is illustrated by the results in Table 2. They show that maximum possible yield is obtained at bigger sizes for upper Delta populations and smaller sizes for lower Delta populations. Therefore, this suggests that different gear need to be used in the two habitats in order to gain maximum benefit from the fishery.

There are several possible sources that may have introduced error or bias into the observed results. The sampling gear used was not absolutely non-selective. Therefore, it is very possible that one of the assumptions used in the derivation of the growth parameters would have been violated and would have caused error in the derived growth parameters. Moreover, preferred habitat for juvenile fish was not sampled systematically (in either the upper or lower Delta), and this would have resulted in an over-representation of older age classes. The derived growth parameters would subsequently reflect growth of older fish, which is generally slower than that of younger fish. This observation is more evident in the length converted catch curves shown in the results, which show that there are some differences in the sampled demographic structure of the two populations (i.e. upper and lower Delta populations). The sampled population structure for *O. andersonii* as illustrated by the length-converted catch curve is similar for both habitats (i.e. lower and upper Delta). Therefore, this might explain the reason why the observations made for this species differs from the other species.

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#### References

- Abaunza, P., Murta, A., Teja, A., Molloy, J., Nascetti, G., Mattiucci, S., Cimmaruta, R., Magoulas, A., Sanjuan, A., MacKenzie, K., Iversen, S., Dahle, G., Gordo, L., Zimmerman, C., Stransky, C., Santamaria, M.T., Ramos, P., Quinta, R. and Campbell, N. (2000) *HOMSIR: An international project on horse mackerel stock identification research in the ICES area and in the Mediterranean Sea*, p. 7. Working document for the ICES Working Group of the Assessment of Mackerel, Horse Mackerel, Sardine and Anchovy. Copenhagen, 14-23 September, 2000.
- Austin, H.M. (1998) Morphometric separation of annual cohorts within mid-Atlantic bluefish, *Pomatomus saltatrix*, using discriminant function analysis. *Fish. Bull.* 97: 411 – 420.
- Begg, G.A. (1998) A review of stock identification of haddock, *Melanogrammus aeglefinus*, in the Northwest Atlantic Ocean. *Marine Fisheries Review*, 60 (4): 1-15.
- Begon, M. and Mortimer, M. (1986) *Population ecology; a unified study of animals and plants*. Oxford: Blackwell Scientific Publications.

- Beverton, R.J.H. and Holt, S.J. (1957) *On the Dynamics of Exploited Fish Populations*. New York: Chapman and Hall.
- Booth, A.J. and Merron, G.S. (1996) The age and growth of the greenhead tilapia, *Oreochromis macrochir* (Pisces: Cichlidae) from the Okavango Delta, Botswana. *Hydrobiologia*, 321: 29-34.
- Booth, A.J., Merron, G.S. and Buxton, C.D. (1995) The growth of *Oreochromis andersonii* (Pisces: Cichlidae) from the Okavango delta, Botswana, and a comparison of the scale and otolith methods of ageing. *Environmental Biology of Fishes*, 43: 171-178.
- Burmesiter, L. (2000) Is there one stock of *Merluccius paradoxus* da Franca in the Benguela region? Mphil thesis. Bergen: Norway: University of Bergen.
- Froese, R. and Binohlan, C. (2000) Empirical relationships to estimate asymptotic length, length at first maturity, and length at maximum yield per recruit in fishes, with a simple method to evaluate length frequency data. *Journal of Fish Biology*, 56 (4): 758-773.
- Gabche, C.E. and Hockey, H.-U.P. (1995) Growth, mortality and reproduction of *Sardinella maderensis* (Lowe, 1841) in the artisanal fisheries off Kribi, Cameroon. *Fisheries Research*, 24: 331-344.
- Gayanilo, F.C. and Pauly, D. (1997) *The FAO-ICLARM stock assessment tools (FiSAT)*. Reference manual. Rome: FAO.
- Haddon, M. (2001) *Modeling and quantitative methods in fisheries*. New York: Chapman and Hall.
- Hilborn, R. & Walters C.J. (1992) *Quantitative Fisheries Stock Assessment; Choice, Dynamics & Uncertainty*. New York: Chapman and Hall Publishers.
- Jackson, P.B.N. (1986) Report on Okavango visit, In: Merron, G.S., and Bruton, M.N. (eds.) Results from two expeditions to the Okavango delta, pp. 28-31. Grahamstown: JLB Smith Investigative Report, (18).
- Kolding J., Bills, I.R., Mosepele, K., Mmopelwa, T. and Nengu, S. (2003) Fisheries and Fish Biodiversity in the Okavango delta, Botswana; A rapid assessment, In: Mosepele, K. and Mosepele, B.(Eds) *AquaRAP II: Rapid Assessment of the Aquatic Ecosystems of the Okavango Delta, Botswana*; Preliminary Report, pp. 30-46 Maun: Conservation International, Okavango Programme.
- Kolding, J. (1989-2002) PASGEAR: A data-base for experimental or artisanal fishery data from passive gears. Bergen: University of Bergen.
- Lai, H.L., Galucci, V.F. and Gunderson, D.R. (1996) Age determination in fisheries: Methods and applications to stock assessment, In: Galucci, V.F., Saila, S.B., Gustafson, D., Rothschild, B.J. (Eds) *Stock Assessment; quantitative methods and applications for small-scale fisheries*, pp. 82-178 New York: Lewis Publishers.
- Lowe-McConnell, R.H. (1987) *Ecological studies in tropical fish communities*. Cambridge: Cambridge University Press.
- Lowe-McConnell, R.H. (1979) Ecological aspects of seasonality in fishes of tropical waters. *Symp. Zool.Soc.London.*, 44: 219-241.
- Merron, G.S. (1991) The ecology and management of the fishes of the Okavango Delta, Botswana with particular reference to the role of seasonal floods. PhD thesis. Grahamstown: Rhodes University.
- Merron, G.S. and Bruton, M.N. (1988) The ecology and management of the fishes of the Okavango Delta, Botswana, with special reference to the role of the seasonal flood, *Investigational Report No. 29*, Grahamstown: J.L.B Smith Institute of Ichthyology.

- Mosepele, K. (2000) Preliminary Length Based Stock Assessment of the Main Exploited Stocks of the Okavango Delta fishery. MPhil Thesis. Bergen: University of Bergen.
- Mosepele, K. (2001) *Description of the Okavango Delta fishery*. Technical Report to the Fisheries Section. Gaborone: Ministry of Agriculture.
- Mosepele, K. and Kolding, J. (2003) Fish Stock Assessment in the Okavango Delta, Botswana - preliminary results from a length based analysis, In: Bernard, T., Mosepele, K. and Ramberg, L. (Eds) *Proceedings of an "Environmental Monitoring of Tropical and Subtropical Wetlands"* Conference held 4-6 December 2002, Maun. pp. 363-390. Maun: Harry Oppenheimer Okavango Research Centre.
- Mosepele, K. and Mosepele, B. (2005) Spatial and temporal variations in the fishery and fish community structure in the Okavango Delta, Botswana: Preliminary Analysis. *Botswana Notes and Records*. (Submitted)
- Mosepele, K. (2002) *Trends in Fisheries Development and Fish Utilization in the Okavango Delta*. <<http://www.okavangochallenge.com/>>
- Pauly, D. (1982) *Studying single-species dynamics in a tropical multi-species context*, Manila: International Centre for Living Aquatic Resource Management.
- Sparre, P. and Venema, S.C. (1998) Introduction to tropical fish stock assessment. Part 1: Manual. Rome: FAO Technical Paper No. 306/1.
- Stergiou, K.I. and Papaconstantinou, C. (1993) Natural mortality of red bandfish, *Cepola macrophthalma* (L.), in the Aegean Sea (Greece): comparison of direct and indirect estimation methods. *Fisheries Research*, 16: 347-361.
- Tweddle, D., Bills, R., Van der Waal, B., Skelton, P., Kolding, J. and Nengu, S. (2003) Fish diversity and fisheries in the Okavango Delta, Botswana, In: Alonso, L.E. and Nordin, L. (Eds) *A rapid biological assessment of the aquatic systems of the Okavango Delta, Botswana: High water survey*, RAP Bulletin of Biological Assessment 27: 97-110. Washington D.C.: Conservation International.