

## A SEMINAL STUDY OF THE DYNAMICS OF A MUDSKIPPER (*PERIOPHTHALMUS PAPILIO*) POPULATION IN THE CROSS RIVER, NIGERIA \*

LAWRENCE ETIM, THOMAS BREY and WOLF ARNTZ

**KEYWORDS:** Population dynamics; mudskipper; *Periophthalmus papilio*; Cross River; Nigeria.

### ABSTRACT

A seminal study was conducted in which the population dynamics (growth, mortality and recruitment) of the mudskipper (*Periophthalmus papilio*) in the Cross River, Nigeria, was elucidated for the first time using length frequency data and the ELEFAN software. The allometric relationship was:  $\text{Weight} = 0.012(\text{Length})^{2.940}$ ,  $n = 415$ ,  $r^2 = 0.939$ ,  $P < 0.0005$ . The seasonalized Von Bertalanffy growth parameters were  $L_{\infty} = 19.39$  cm,  $K = 0.51 \text{ y}^{-1}$ ,  $C = 0.3$ , and  $WP = 0.4$ . The instantaneous total mortality coefficient  $Z$  was  $2.208 \text{ y}^{-1}$  while the instantaneous natural mortality coefficient was  $1.341 \text{ y}^{-1}$ . The instantaneous fishing mortality coefficient of  $0.867 \text{ y}^{-1}$  yielded the expectedly low exploitation rate  $E$  of 0.393. Our estimate shows that the species could reach an average maximum life span of about 6 years in the Cross River system. These results are used in quantitative elucidation of the state of exploitation of the population and will serve as input for the proper and scientific management of the fish resource.

### INTRODUCTION

The mudskipper or mudhopper is an extremely euryhaline teleost fish whose habitats range from muddy intertidal banks of rivers through brackish to oceanic environments. There is acute paucity of scientific research on this amphibious fish. For example, literature search using ASFA reveals that between 1978 and 1995 only 54 papers were published on mudskippers worldwide. Out of this, only three (BERTI *et al.*, 1992; 1994; COLOMBINI *et al.*, 1995) were done in Africa.

The dearth of studies on this ammoniotelic fish especially in Africa may well be due to the fact that it is not a widely accepted food fish. Consequently, mudskipper fishery is almost in-existent or entirely subsistent. However, the mudskipper is of both ecological and economic importance. It occupies a unique niche in its habitat

and is invariably the best known example of resident intertidal fish. It is a traditional delicacy of some riverine ethnic groups in South Eastern Nigeria. According to CLAYTON (1993) mudskipper is also eaten in China, Taiwan, and in India, where it provides an alternative fishery during the monsoon. In Taiwan, it is extensively cultured and in Malaysia aphrodisiac values are attributed to its raw flesh. It is utilized by some Nigerian artisanal fishermen as baits in exploiting other commercially important species.

In this study, the population dynamics (growth, mortality, recruitment) of the mudskipper *Periophthalmus papilio* in the Cross River system were investigated in order to quantify the basic fishery parameters which are necessary as input in the quantitative elucidation of the state of exploitation of the population. Proper understanding of the latter is necessary for the scientific management of stock.

\* Alfred Wegener Institute Contribution nr. 1090.

**MATERIAL AND METHODS**

From February to June 1994, samples of *P. papilio* were obtained at monthly intervals from the Esuk River at the Esuk Nsidung, Calabar (8° 3' E, 5" N) through the help of artisanal fishermen. Flood has the most profound effect on the hydrology and limnology of the river system. During the flood an enormous amount of run-off water with a heavy load of debris is brought into the river system causing a tremendous rise in the level of the water. Salinity ranges between 4.4‰ in the rainy season and 21‰ in the dry season. Spatial and vertical variation in temperature is negligible but seasonal variation has been recorded. A peak temperature of about 33.3°C is observed in April while a minimum about 26°C is observed in July. The mean water transparency is 0.57 m, of pH 6.8, of nitrate 1.02 mg l<sup>-1</sup>, of phosphate 0.017 mg l<sup>-1</sup>, and of silicate 0.17 mg l<sup>-1</sup>. The phosphate values for the bottom and surface are the same. For silicate, the bottom values are higher than the surface values.

The fish was caught by means of a simple trap. A cylindrical hole of about 15 to 20 cm deep dug in the ground and covered with a plant leaf through which a bait is placed. When the mudskipper jumps on the leaf for the bait, the leaf gives way under the weight of the mudskipper and it falls into the pit from where it cannot escape. The total length and total weight of each specimen were measured with callipers (to the nearest 0.1 cm) and weighed (to the nearest 0.1g).

**Weight-length relations**

A power function of the form

$$\text{Weight} = a(\text{Length})^b \quad (1)$$

was fitted iteratively to the length-weight data through the Simplex algorithm (PRESS *et al.*, 1986) employing the user-specified procedure available in SYSTAT (1992). Here a and b are the intercept on the y-axis and the slope of the regression line, respectively.

**Length-at-age analysis**

The ELEFAN software (BREY *et al.*, 1988; GAYANER *et al.*, 1989) was used for the analysis.

Growth in fishes is commonly described by the VON BERTALANFFY (1938) growth function (VBGF)

proposed by PAULY and GASCHUTZ (1979) and later modified by SOMERS (1988) takes the form

$$L_t = L_\infty [ (1 - \exp -(K(t - t_0) - CK/2\pi (\sin 2\pi (t - t_s) - \sin 2\pi (t_0 - t_s))) ) ] \quad (3)$$

Expression (3) was used to parametrize individual growth of *P. papilio*.  $L_\infty$  is the asymptotic length, K the Von Bertalanffy growth coefficient,  $L_t$  the length at age t, C the indicator of the intensity of growth oscillations,  $t_0$  the 'age' of the fish at zero length (granted the fish had been growing according to the VBGF) and  $t_s$  the beginning of the sinusoidal growth oscillation with respect to  $t = 0$ . To facilitate biologically meaningful computation,  $t_s$  was replaced by WP (Winter Point) which is  $t_s + 0.05$ . By definition WP is the period of the year (expressed as a fraction of the year) when growth is slowest.

To obtain a first estimate of  $L_\infty$ , the WETHERAL (1986) method, as modified by PAULY (1986) was used. It is a steady-state model and applies when population mortality follows a single negative exponential model (see below) with a stable age distribution. The method entails regressing  $L_m - L'$  against  $L'$  according to the linear regression equation

$$L_m - L' = a + bL'; L_\infty = a/b \quad (4)$$

where  $L_m$  is the mean length computed from  $L'$  upward in the length frequency sample, while  $L'$  is the limit of the first length class used. The sequentially arranged length frequency data set was restructured to enable an objective definition (or identification) of peaks which could be confidently assumed to correspond to 'cohorts' (BREY *et al.*, 1988). Then, using the first estimate of  $L_\infty$  as a seeded value, and a combination of various K values, growth curves were fitted to the restructured data beginning from the base of each peak and projecting backward and forward in time to meet all other samples of the same set. The curve(s) that passes through the highest number of peaks and avoided the highest number of troughs yields the best parameter estimate.

**Mortality estimate**

The size-converted catch curve (PAULY, 1983) was used to estimate the total mortality coefficient Z of the single negative exponential mortality model:

at time  $t$ ,  $Z$  was computed from pooled size-frequency data with monthly samples  $N$ /size class converted to  $\%N$ /size class. This conversion conferred the desired effect of equal weight to each sample (BREY *et al.*, 1988):

$$(N_i/\Delta t_i) = N_0 e^{-Zt_i}, \quad (6)$$

hence

$$\Delta t_i = (-1/K) \ln(L_\infty - L_{i2}/L_\infty - L_{i1}) \quad (7)$$

$N_i$  is the number of mudskippers in size class  $i$ ,  $L_{i1}$  and  $L_{i2}$  are the upper and lower limits of the size class  $i$ ,  $\Delta t_i$  is the time required to grow through this size class and  $t_i$  is the relative age of the mid-size of class  $i$  as estimated from the inverse form of the Von Bertalanffy equation

$$t_i = \ln(1 - L_t/L_\infty) / K. \quad (8)$$

By plotting  $\ln(N_i/\Delta t_i)$  against  $t_i$ , a straight descending right arm was obtained and  $Z$  was computed from the linear regression

$$\ln(\%N_i/\Delta t_i) = a + bt_i, \quad (9)$$

where  $Z = -b$ . The growth of any fish is not linear. So the division of  $\%N$  by  $\Delta t_i$  in eq. (9) serves to correct for the nonlinearity of the growth of the mudskipper. In addition,  $Z$  was also estimated from the mean length of the fish in the catch using the BEVERTON and HOLT (1956) method

$$Z = [K(L_\infty - L_m)] / (L_m - L'), \quad (10)$$

where  $L_m$  is the mean length of all fish which is equal to or longer than  $L'$ , the latter being the smallest length fully represented in the length frequency data. The coefficient of instantaneous natural mortality  $M$  was estimated from two models, *viz.*: the empirical relationship proposed by PAULY (1980):

$$\begin{aligned} \log M = & -0.006 - 0.279 \log L_\infty \\ & + 0.654 \log K + 0.463 \log T, \end{aligned} \quad (11)$$

where  $T$  is the mean annual environmental temperature in degrees Centigrade (here 30°C), and the model of TAYLOR (1960):

$$M = 2.9957/(t_0 + 2.9957/K), \quad (12)$$

where  $2.9957/K$  is the estimator of longevity of

the mudskipper. Since  $Z$  is equal to the sum of the instantaneous natural mortality coefficient  $M$  and instantaneous fishing mortality coefficient  $F$ , the latter was then calculated from the relationship  $F = Z - M$ ; and the exploitation rate  $E$  was estimated as  $F/Z$ .

### Probability of capture

The probability of capture  $P$  of each size class  $i$  was calculated from the ascending, left arm of the length-converted catch curve following the method of PAULY (1984). This entails dividing the numbers actually sampled by the expected numbers (obtained by projecting backward the straight portion of the catch curve) in each length class in the ascending part of the catch curve. By plotting the cumulative probability of capture against mid length a resultant curve was obtained from which the length at first capture  $L_c$  was taken as corresponding to the cumulative probability at 0.5 (50%).

### Recruitment pattern

The procedure used here first corrects the length frequency data for nonlinear fish growth, then projects it back to a one-year time scale to obtain a graphical representation of the recruitment pattern (PAULY, 1987).

### Yield per recruit

The relative yield per recruit and biomass per recruit were estimated from the model of BEVERTON and HOLT (1966):

$$\begin{aligned} (Y/R)' = & EU^m \{1 - (3U)/(1+m) + (3U^2)/(1+2m) \\ & - (U^3)/(1+3m)\}, \end{aligned} \quad (13)$$

where  $E = F/Z$  = the exploitation rate (*i.e.* the mortality of the mudskipper caused by the fishermen),  $U = 1 - L_c/L_\infty$ , which is the fraction of growth to be completed by the mudskipper after entry into the exploitation phase, and  $m = (1 - E)/(M/K)$ , which is equal to  $K/Z$ . The other parameters were already defined.

## RESULTS

The length-weight regression (Fig. 1) was:  $\text{Weight} = 0.012(\text{Length})^{2.940}$ ,  $n = 415$ ,  $r^2 = 0.939$ ,  $P < 0.0005$ . Estimated values of  $L_\infty$  and  $Z/K$  as obtained from the modified Wetheral plot (Fig. 2) were 19.39 cm and 3.989, respectively. The run of ELEFAN with  $L_\infty = 19.39$  cm as the seeded value produced the seasonalized growth

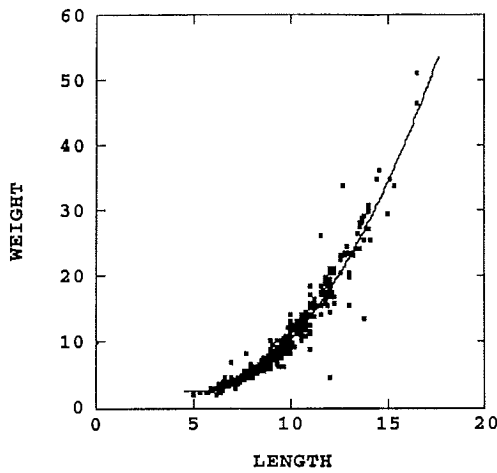


Fig. 1. Length-weight relationship of *Periophthalmus papilio* in the Cross River system. Weight (g) = 0.012 (Length in cm)<sup>2.94</sup>, n = 415, r<sup>2</sup> = 0.939, P < 0.0005.

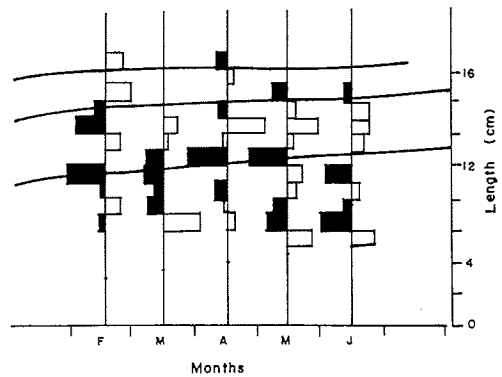


Fig. 3. Seasonalized Von Bertalanffy growth curve (parameter values:  $L_{\infty} = 19.39$  cm,  $K = 0.51$  y<sup>-1</sup>,  $C = 0.3$ , and  $WP = 0.4$ ) superimposed on the restructured length frequency histogram of *Periophthalmus papilio* in the Cross River system. The black and white bars are positive and negative deviations from the 'weighted' moving average.

curve depicted in Fig. 3 as superimposed on the restructured length frequency histograms. The curve is characterized by the following seasonalized Von Bertalanffy parameters  $L_{\infty} = 19.39$  cm,  $K = 0.51$  y<sup>-1</sup>,  $C = 0.3$ ,  $WP = 0.4$ . Incidentally,  $L_{\infty}$  values from the modified Wetheral and ELEFAN methods were the same. Up to four peaks could be identified in this diagram (see Fig. 3, April sample) and they are taken to correspond to separate cohorts.

The length-converted catch curve procedure (Fig. 4) yielded an instantaneous total mortality

coefficient  $Z = 2.208$  y<sup>-1</sup> while a value of 2.283 y<sup>-1</sup> was obtained from the mean length analysis. The instantaneous fishing mortality rate and instantaneous natural mortality coefficient were 0.867 y<sup>-1</sup> and 1.341 y<sup>-1</sup>, respectively, giving a current exploitation rate  $E = 0.393$ . The analysis of probabilities of capture shows that the length at first capture was 7.6 cm (Fig. 5).

We computed relative yield per recruit using two different sets of assumptions and inputs. In assuming knife edge selection (Fig. 6) we obtained

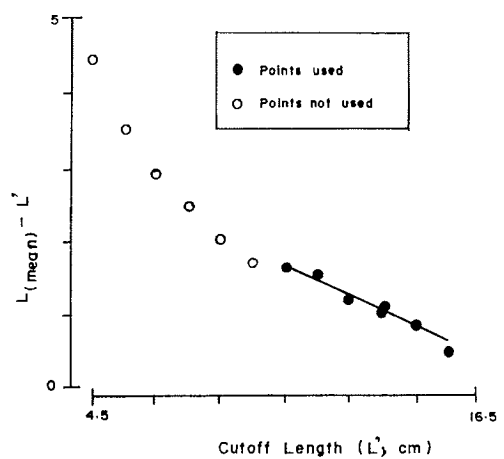
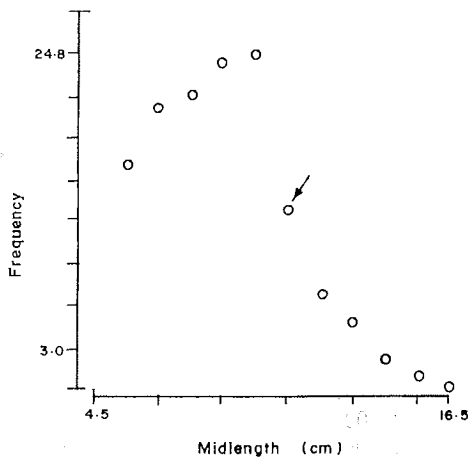


Fig. 2. Modified Wetheral plot for *Periophthalmus papilio* in the Cross River system. The arrow in the left graph indicates the first selected point. The points used in the right graph are described by the equation  $Y = 3.89 - 0.201 X$ ,  $r = 0.989$ . Estimated  $L_{\infty} = 19.39$  cm,  $Z/K = 3.99$ .

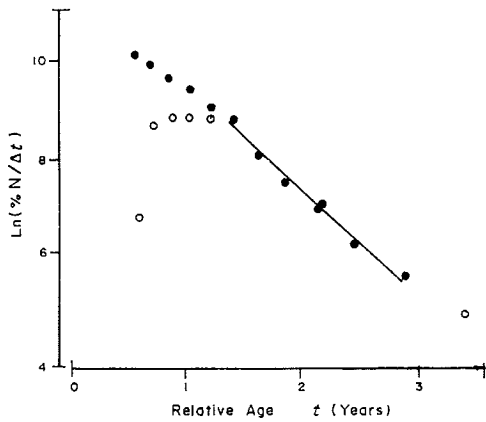


Fig. 4. Length-converted catch curve for *Periophthalmus papilio* in the Cross River. Range of lengths 4.95 cm to 16.95 cm. Dots indicate points included in the regression:  $Y = 10.9 - 2.208 X$ ,  $r = 0.95$ ,  $n = 7$ .

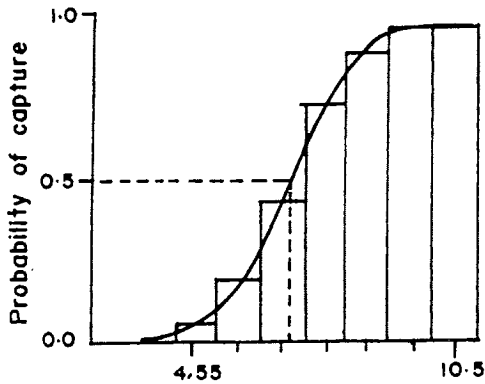


Fig. 5. Probability of capture of *Periophthalmus papilio* as derived from the length-converted catch curve. Broken line indicates mean length at first capture ( $L_{0.5}$ ), which is 7.6 cm.  $L_{0.25} = 6.7$  cm, and  $L_{0.75} = 8.5$  cm.

the following summary statistics for the optimum level of exploitation :  $E_{max}$  as 0.69, but using selection ogive or probability of selection procedure (Fig. 7) a value of  $E_{max} = 0.52$  was obtained. As shown in Fig. 8 the recruitment pattern displayed two peaks. The longevity or the average life span of the species in the Cross River was about 5.9 years.

**DISCUSSION**

From the extant scientific literature, it is clear that this is the first time in which the po-

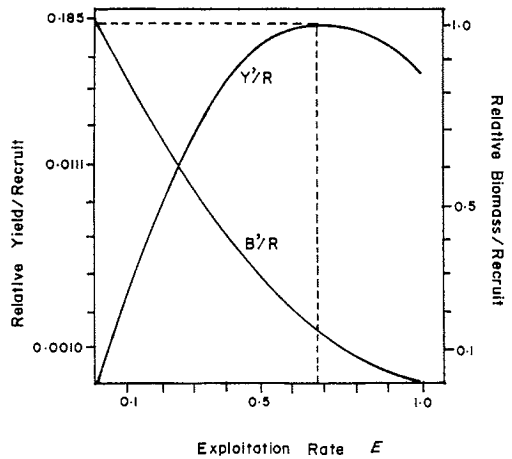


Fig. 6. Relative yield per recruit ( $Y/R$ ) and relative biomass per recruit ( $B/R$ ) of *Periophthalmus papilio* as computed with the knife edge selection procedure. The optimum exploitation rate ( $E_{max}$ ) of 0.69 is indicated by the broken line.  $E_{0.1} = 0.6$  and  $E_{0.5} = 0.3$ .

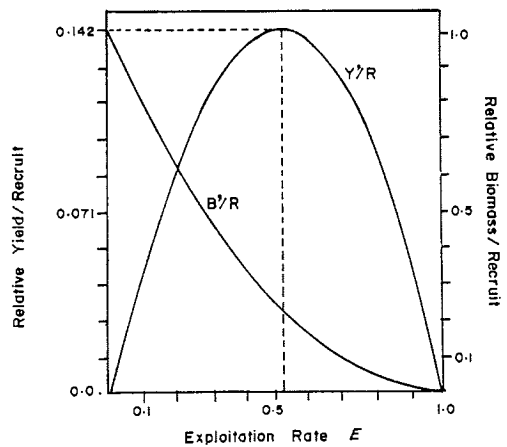


Fig. 7. Relative yield per recruit ( $Y/R$ ) and relative biomass per recruit ( $B/R$ ) of *Periophthalmus papilio* as computed with the probability selection procedure. The optimum exploitation rate of 0.52 is indicated by the broken line.  $E_{0.1} = 0.45$  and  $E_{0.5} = 0.3$ .

pulation dynamics of any species of mudskipper has been reported. Thus, our result, apart from being seminal, will serve as a springboard for further research in this field. The power function of the type we used in equation 1 is usually fitted to data through the least square procedure using the following linearized version

$$\log(\text{Weight}) = \log a + b \log(\text{Length}). \quad (14)$$

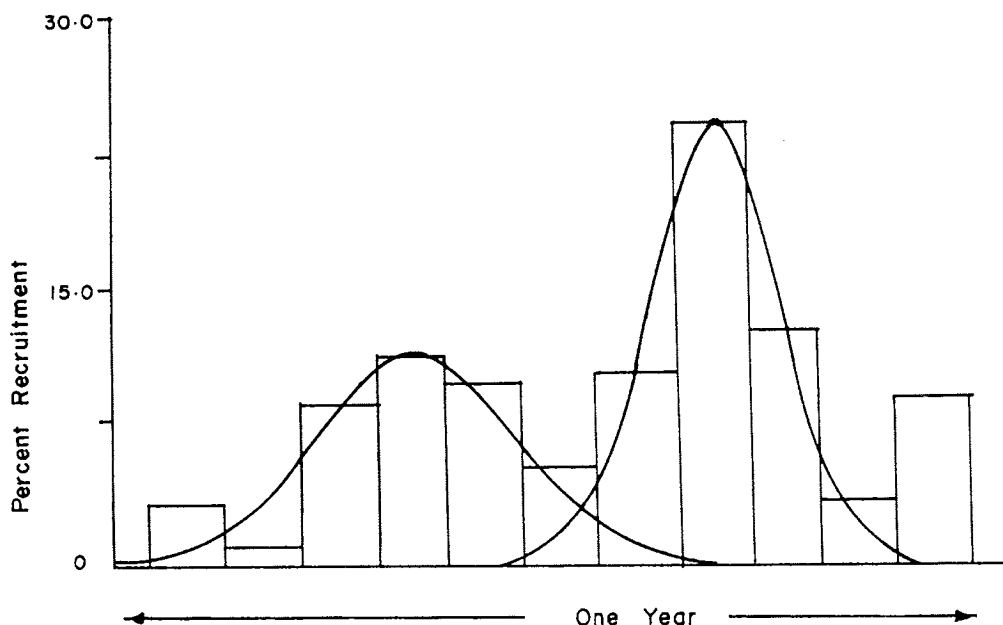


Fig. 8. Recruitment pattern of *Periophthalmus papilio* in the Cross River system.

According to SPRUGEL (1983) this kind of transformation introduces a systematic bias into the calculation, which should be eliminated by multiplying with a correction factor (CF):

$$CF = \exp(SEE^2/2) \quad (15)$$

and

$$SEE = \sqrt{[\sum (\log y_i - \log y^{\wedge})^2 / (N-2)]} \quad (16)$$

SEE is the standard error of estimate,  $\log y_i$ 's are the log-transformed values of the dependent variable,  $\log y^{\wedge}$ 's are the corresponding predicted values from eq. (14). The SEE must be converted to base e (by multiplying by 2.303) before being used in eq. (15). The logarithmic correction factor is a simple and straightforward statistical tool to remove systematic bias. Although such error could be as high as 10% (SPRUGEL, 1983), this procedure is scarcely adopted by scientists. In our analysis, we fitted the model iteratively to the data, consequently the parameters were free of this kind of transformation-related bias. The resultant length-weight model could explain up to 88.2% of the variation of length on weight of the mudskipper.

To facilitate future comparisons of growth performance of other populations, we will use the PAULY and MUNRO (1984) equation

$$\phi' = \log K + 2 \log L_{\infty} \quad (17)$$

to quantify growth performance  $\phi'$  as 2.28. Generally,  $\phi'$  values are species specific parameters and have been shown to be narrowly distributed around a mean which is characteristic of the species, whether shellfish (VAKILY, 1992) or finfish (MOREAU, 1986).

Our data are limited to the five-month dry season period because during the peak of the rains the muddy intertidal portions of the river are permanently flooded and the mudskippers were not found. Mudskippers have been described as one of the most terrestrial of the amphibious fishes. *P. koelreuteri* has been observed to carry out multiple terrestrial excursions for feeding without a return to water (SPONDER and LAUDER, 1981) but it is not known how far or how long *P. papilio* could wander landward. However, some species of mudskippers do build complex burrows (CLAYTON, 1993) and studies have shown that they are particularly capable of existing in sustained hypoxic conditions in their natural habitats (LOW *et al.*, 1992).

From a study of otolith rings of *Boleophthalmus dentatus* (= *B. dussumieri*) at the West coast of the Indian continent, SONI and GEORGE (1986) showed that a 13.0 cm total length fish is 2 years old. Our non-seasonalized Von Bertalanffy growth function (eq. (1)) yields a comparable value of 2.176 years for a 13.00 cm fish, granted the value of  $t_0$  is zero. Axiomatically, this

provides a good validation of the length-based ELE-FAN procedure used in this analysis.

The K value generally expresses the rate at which a species grows towards its asymptotic size, which is the theoretical maximum size attainable by the species in that particular habitat, given the ecological peculiarities of the environment under consideration. Our K value of  $0.51 \text{ y}^{-1}$  shows that the species in the Cross River is relatively fast growing. Our qualitative observation revealed that there seems to be a gradation in maximum size of the mudskipper with habitat. Thus the larger sized individuals are common towards the oceanic environment, while the smaller sized ones are common in the riverine environments. It is not certain whether this difference is due to differences in fishing pressures on the different stocks or merely to a consequence of ecological adaptation. Our results show that the pressure on the fishery as indicated by the exploitation rate of 0.35 is low and quite below the predicted optimum of 0.69 based on knife edge selection, or 0.52 based on assumption of probability selection. Within this context, stepping up fishing mortality or bringing down the size at first capture may lead to higher yields for the fishermen without real danger to the fishery. Moreover, in small tropical fisheries like this the maximization of yield may require high F values.

The mudskippers' extreme ability to manoeuvre over the muddy environment, difficult of access for man, implies that they are not easy to catch. Although various catching techniques and devices have been used, CLAYTON (1993) pointed out that specimens caught by blowpipe, weighted hook and air riffle are often not of use for further scientific studies. Fish caught by traps, nets or lassos are obviously more preferable. The probability of capture for the fishing method employed here shows that the length at first capture is 7.6 cm and that the probability of the device capturing a fish equal

to or greater than 10.5 cm in length is unity. Although our computation puts the estimated maximum age of the species at about 6 years, yet our restructured length - frequency diagram could only account for four cohorts. The whereabouts of the other two could probably be accounted for by selectivity of the gear.

The Chinese mudskipper *P. cantonensis* exhibits reproductive behaviour of nesting and courtship in the months of June to August (IKEBE and OISHI, 1992) but nothing is reported about the pattern of its recruitment. Conceptually, a recruitment pattern can be represented by a graph whose peaks and troughs reflect the seasonality of recruitment to the stock in question. The overlapping nature of the pattern (Fig. 8) implies a continuous recruitment, while the two peaks denote that there are two recruitment pulses in a year. If so, this is different from the bivalve *Egeria radiata* (ETIM, 1993; ETIM and BREY, 1994) which spawns once a year in the same river but similar to the croaker *Pseudolithus elongatus* (ETIM *et al.*, 1994) which exhibits two recruitment peaks in a year, also in the Cross River. For the recruitment pattern to indicate the exact time of spawning,  $t_0$  must be known. But obtaining this from length frequency data is not feasible.

#### ACKNOWLEDGEMENTS

Dr. Etim (Institute of Oceanography, University of Calabar, Nigeria) is sponsored by the Alexander von Humboldt (AvH) Foundation, Bonn during his research tenure at the Alfred Wegener Institute (AWI). Thanks are extended to AvH Foundation for sponsorship, AWI for support, Mr Ernest Ayegboku for help in field sampling and laboratory measurements, and Dr. Edak Umoh for supervising the cartographic work.

#### REFERENCES

- BEVERTON, R.J.H. and S.J. HOLT, 1956. A review of methods for estimating mortality rates in fish populations, with special references to sources of bias in catch sampling. Rapp. P.-V. Réun. Cons. Int. Explor. Mer. 140: 67-83.
- BEVERTON, R.J.H. and S.J. HOLT, 1966. A manual of methods for fish stock assessment. Part 2. Tables of yields functions. FAO Fish Technic. Pap. 38 Rev. 1: 67.
- BERTI, R., L. CHELAZZI, I. COLOMBINI and A. ERCOLINI, 1992. Direction finding ability in a mudskipper from the delta of the Tana River (Kenya). Trop. Zool. 5: 219-228.
- BERTI, R., L. CHELAZZI, I. COLOMBINI and A. ERCOLINI, 1994. Directional orientation in Kenyan populations of *Periophthalmus sobrinus* Eggert: Experimental analysis of the operating mechanisms. J. Exp. Mar. Biol. Ecol. 181: 135-141.

- BREY, T., M. SORIANO and D. PAULY, 1988. Electronic length frequency analysis. A revised and expanded users guide to ELEFAN 0, 1 and 2 (2nd edition.) Ber. Inst. Meereskunde (Kiel), 1-31.
- CLAYTON, D.A., 1993. Mudskippers. In: A.D. Ansel, R.N. Gibson and M. Barnes, Eds., Oceanography and Marine Ecology - An Annual Review. 31. UCL Press London, p. 507-577.
- COLOMBINI, I., A. BERTI, A. ERCOLINI, L. NOCITA, and L. CHELAZZI, 1995. Environmental factors influencing the zonation and activity patterns of a population of *Periophthalmus sobrinus* Eggert in a Kenyan mangrove. J. Exp. Mar. Biol. Ecol., 190: 135-149.
- ETIM, L., 1993. Comparison of condition indices and their seasonal variation in the freshwater clam *Egeria radiata* (Lamarck) (Tellinacea: Donacidae) from the Cross River, Nigeria. Aquacult. Fish. Managem. 24: 603-612.
- ETIM, L. and T. BREY, 1994. Growth, productivity and significance for fishery of the bivalve *Egeria radiata* (Donacidae) in the Cross River, Nigeria. Arch. Fish Mar. Res. 42: 63-75.
- ETIM, L., B.U. UWE-BASSEY and T. BREY, 1994. Population dynamics of the West African croaker *Pseudotolithus elongatus* in the Cross River estuary, Nigeria. Sci. Mar. 58: 315-321.
- GAYANILO Jr, F.C., M. SORIANO and D. PAULY, 1989. A draft guide to the Complete ELEFAN International Centre For Living Aquatic Resource Management (ICLARM). Manila, Philippines, 1-70.
- IKEBE, Y and T. Oishi, 1992. Diurnal change of behaviour pattern in the Chinese mudskipper *Periophthalmus cantonensis* (Abstract only), Zool. Sci., 9:1296.
- LOW, W.P., S.F. CHEW and Y. KIP, 1992. Difference in electrophoretic patterns of lactate dehydrogenases from the gills, hearts and muscles of three mudskippers. J. Fish Biol. 40: 975-977.
- MOREAU, J., C. BAMBINO and D. PAULY 1986. Indices of overall fish growth performances of 100 *Tilapia* (Cichlidae) populations. In: J. L. Maclean, L. B. Dizon and L. V. Hosillos, Eds., First Asian Fisheries Forum, Manila, Asian Fisheries Society, p. 201-206.
- PAULY, D., 1986. On improving the operation and use of ELEFAN programs. Part 1. Improving the estimation of L-infinity. Fishbyte 4: 18-20.
- PAULY, D. and G. GASCHUTZ, 1979. A simple method for fitting oscillating length data, with a program for pocket calculators. ICESCM 1979/24. Demersal Fish Committee.
- PAULY, D., 1980. On the interrelationships between natural mortality, growth parameters and mean environmental temperatures in 175 fish stocks. J. Cons. Int. Explor. Mer. 39: 175-192.
- PAULY, D., 1983. Length-converted catch curves. A powerful tool for fisheries research in the tropics (Part 1). ICLARM Fishbyte 1: 9-13.
- PAULY, D., 1987. A review of the system for analysis of length data in fish and invertebrates. In: D. Pauly and G.R. Morgan, Eds., Length based methods in fisheries research. ICLARM Conf. Proc. ICLARM, Manila 13: 7-34.
- PAULY, D. and J.L. MUNRO, 1984. Once more on the growth comparison in fish and invertebrates. Fishbyte 2: 17-19.
- PRESS, W.H., B.P. FLANNERY, S.A. TEUKOLSKY and W.T. VETTERLING, 1986. Numerical recipes: The art of scientific computing. Cambridge University Press, Cambridge.
- SOMERS, I.F., 1988. On seasonally oscillation growth function. Fishbyte 6: 8-11.
- SONI, V.C. and B. GEORGE, 1986. Age determination and length-weight relationship in the mudskipper *Boleophthalmus dentatus*. Indian J. Fish., 33: 321-324.
- SPONDER, D.L. and G.V. LAUDER, 1981. Terrestrial feeding in the mudskipper *Periophthalmus* (Pisces: Teleostei). A cineradiographic Analysis. J. Zool., 193: 517-530.
- SPRUGEL, D.G., 1983. Correcting for bias in log-transformed allometric equations. Ecology 64: 209-210.
- SYSTAT, 1992. Statistics. Version 5.2 Edition. Systat Inc., Evanston, IL.
- TAYLOR, C.C., 1960. Temperature, growth and mortality - the Pacific cockle. J. Cons. Int. Explor. Mer 26: 117-124.
- VAKILY, J.M., 1992. Determination and comparison of growth in bivalves with emphasis on the tropics and Thailand. ICLARM Tech. Rep., 36: 1-125.
- VON BERTALANFFY, L., 1938. A quantitative theory of organic growth. Hum. Biol. 10: 181-213.
- WETHERAL, J.A., 1986. A new method for estimating growth and mortality parameters from length-frequency data. ICLARM Fishbyte 4: 12-14.

**Address of the authors:**

Alfred Wegener Institute for Polar and Marine Research, Postfach 120161, D-27515 Bremerhaven, Germany.