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Maximum observed length as an indicator of growth rate in tropical fishes

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ABSTRACT

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A positive linear relationship between maximum observed length (MOL) and growth rate is shown for 69 marine, fresh- or brackishwater African fish species in the natural environment and for six cultured species. When accurate data on growth are missing, the MOL appears to be one of the most useful criteria for the preselection of candidate fish species for aquaculture.

INTRODUCTION

As an introduction to his work on environmental factors and fish growth, Brett (1979) notes that, although readily observed and easily measured, growth is one of the more complex activities of the organism. It represents "the net outcome" of a general metabolic system involving internal and external (biotic and abiotic) factors.

The variability of the growth process (at the individual, population, species level) and the multiplicity of the interactive controlling factors considerably increase the difficulty of the experimental approach and limit the significance of its results. Many workers have thus tried to estimate growth rate in nature with a set of methods mainly based on age (size) frequency distribution and/or marks on scales and bones. Detailed reviews of these methods have been given by Tesch (1968), Weatherley (1972), Daget and Le Guen (1975), Ricker (1979) and Weatherley and Gill (1987).

The description of the general pattern of growth is generally made by means of a few widely known biomathematical models (see Ricker, 1979, for re-

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view). Based on the Pütter equation[1] (Pütter, 1920), the Von Bertalanffy growth formula[2] (Von Bertalanffy, 1938) in the notation of Beverton and Holt (1959) has been widely used in fisheries science because of its supposed virtue of including terms that represent metabolic properties of assimilation (the somewhat uncritical use of asymptotic growth curves has been commented upon by Ricker, 1979). However, many growth analyses are unable to directly utilize curves of this sort, because varying environmental factors cause fish growth patterns to diverge more or less widely from idealized growth forms.

Age and growth determination has been considered to be more difficult in tropical than in temperate fishes (De Bont, 1967; Weatherley and Gill, 1987; De Merona et al., 1988) although Pauly (1983) considered that problems had generally been over-emphasized, especially for small tropical fishes. In order to circumvent these difficulties (practical as well as theoretical) some authors (e.g. De Merona, 1983) proposed a model for rapid estimation of growth.

However, in spite of many basic studies on fish growth, there is no clear confirmation of the idea that the greater the maximum length of a particular species, the greater its growth potential. To our knowledge, this (simple) hypothesis has never really been tested. The aim of the present paper is to show the validity and practical limitations of the maximum observed length (MOL) as an indicator of growth rates, for different species of African fishes of continental, estuarine or marine origin. The practical implication of these findings is that the MOL appears to be one of the most useful criteria for preselection of candidate fish species for aquaculture.

MATERIAL AND METHODS

The study was based on growth data collected from fish in their natural environment and, for a limited number of species, on results obtained in culture conditions.

In the natural environment, the relationship between the MOL and growth rates was analysed using the relationship between the MOL and the estimated length at 1 ($L1$) and 2 ($L2$) years of age. Lengths at more advanced ages were not taken into consideration because:

- it is generally agreed upon that small fishes have a shorter lifespan than

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[1] $\mathrm{d}w/\mathrm{d}t = Hw^m - Dw^n$ where H and D are coefficients of rates of anabolism and catabolism, w = body weight, $m = 2/3$, $n = 1$.

[2] $Lt = L\infty\ (1 - \mathrm{e}^{-K(t-t_0)})$ where Lt is the length at time t, $L\infty$ is the maximum size towards which the length of the fish is tending (asymptotic length), K is a measure of the rate at which the length approaches $L\infty$, t_0 indicates the (hypothetical) time at which the fish would have had zero length.

[illegible]

those of a larger size; small species tend to achieve their maximum length more quickly;

- it is not realistic, from an aquaculture point of view, to consider a growth cycle of more than 2 years with fish raised in tropical zones.

Taken from the literature, 58 pairs of values (MOL–*L*1 and MOL–*L*2) were used, corresponding to 47 species of continental or estuarine origin of which growth rates were studied in different environments (Table 1). Considering that a given species is likely to show great variability in growth rate and maximum length, depending on its environment, only reports allowing estimations of growth rates and maximum lengths in the same location were considered. Depending on the case, the MOL refers either to the value given by the authors or to the length of the largest individual caught in the samples when they were considered sufficiently varied and abundant. The lengths *L*1 and *L*2 were taken from age–length tables, graphic interpretation of growth curves, or from parameters of the Von Bertalanffy equation.

A similar procedure was followed for 22 marine species the growth rates of which were studied in the eastern part of the tropical Atlantic. In all, 26 pairs of values (MOL–*L*1 and MOL–*L*2) were used (Table 2). The MOL corresponds to the value given by the authors or, in a few cases, by Fisher et al. (1981).

In culture conditions (Table 3), the average length and weight reached at the age of 12 months for the six species tested by the Abidjan Oceanographic Research Center (A.O.R.C.) at the Layo Aquaculture station (Ebrié Lagoon, Ivory Coast) were used. After the hatchery phase and fry rearing in ponds, growout was performed in cage-enclosures or enclosures in the lagoon, with stocking rates of from 5 to 20 individuals per m^2. The fish were fed with a pelleted feed containing 30 to 35% crude protein. The MOL are those measured in the Ebrié Lagoon (Albaret, 1991) except for *Heterobranchus longifilis*, the largest specimen of which was captured in the Agneby River near its Ebrié Lagoon outlet.

Though different according to authors or species considered (Tables 1 to 3), the type of length (fork length, standard length) remains homogeneous in each pair of values and therefore had no effect on the observed relationships.

RESULTS

In the natural environment, a positive adjustment of the reduced major axis is obtained in all cases (continental and estuarine species, Fig. 1; or marine species, Fig. 2). The relationship between the MOL and the lengths at the ages of 1 and 2 years is highly significant, with correlation coefficients (r) between 0.812 and 0.959 ($P<0.001$; Table 4).

In culture conditions, the results obtained for the six species tested confirm these observations and also show a significant correlation ($P<0.01$; Fig. 3

TABLE 1

Maximum observed length (MOL) and lengths at the ages of 1 and 2 years for 47 species of African fish from fresh and brackish waters

Species	MOL (mm)	Length at 1 year (mm)	Length at 2 years (mm)	Type of length	Location	Reference
Alestes baremoze	420	129	234	SL	Niger	Hopson, 1975*
Alestes baremoze (F)	305	130	196	SL	Chad	Durand and Loubens, 1969
Alestes baremoze (F)	284	154	199	SL	Ivory Coast	Paugy, 1978
Alestes baremoze (M)	282	124	180	SL	Chad	Durand and Loubens, 1969
Alestes baremoze (M)	266	128	175	SL	Ivory Coast	Paugy, 1978
Bagrus docmak	875	230	350	TL	Niger, Benue	Motwani, 1970
Bagrus meridionalis	970	100	190	TL	Lake Malawi	Tweddle, 1975
Brycinus imberi	189	98	126	SL	Lake McIlwaine	Marshall and Van der Heiden, 1977
Brycinus macrolepidotus	501	195	285	TL	Niger, Benue	Motwani, 1970
Brycinus nurse	201	90	130	SL	Ivory Coast	Paugy, 1980
Brycinus nurse	213	109	158	SL	Niger	Daget, 1952
Chrysichthys maurus	257	156	236	TL	Lekki Lagoon	Ikusemiju, 1976 (*)
Chrysichthys nigrodigitatus	700	180	240	FL	Ebrie Lagoon	Dia, 1975
Citharinus citharus	803	202	312	TL	Niger, Benue	Motwani, 1970
Clarias anguillaris	795	332	477	SL	Lake Kossou	Jocque, 1977
Clarias gariepinus	679	193	298	TL	Egypt	El Bolock, 1972 (*)
Clarias gariepinus	770	280	450	TL	Oubangui	Micha, 1973
Distichodus rostratus	1020	231	367	TL	Niger, Benue	Motwani, 1970
Ethmalosa fimbriata	300	145	190	FL	West Africa	Charles-Dominique, 1982
Gymnarchus niloticus	1450	370	590	TL	Niger, Benue	Motwani, 1970
Hemisynodontis membranaceus	443	180	280	TL	Niger, Benue	Motwani, 1970
Heterobranchus longifilis	1300	290	500	TL	Niger, Benue	Motwani, 1970
Heterotis niloticus	988	345	590	TL	Niger, Benue	Motwani, 1970
Hippopotamus discorhynchus	576	77	111	SL	Lake Kariba	Balon and Coche, 1974 (*)
Hydrocynus forskalii	780	126	206	SL	Chad	Srinn, 1974 (*)

Hydrocynus forskalii	820	230	355	TL	Niger, Benue	Motwani, 1970
Ichthyborus besse besse	210	140	175	SL	Chad	Lek and Lek, 1978
Labeo altivelis	434	79	129	SL	Lake Kariba	Balon and Coche, 1974 (*)
Labeo coubie	825	230	345	TL	Niger, Benue	Motwani, 1970
Labeo pseudocoubie	925	224	350	TL	Niger, Benue	Motwani, 1970
Labeo senegalensis	480	139	225	TL	Lake Kainji	Blake and Blake, 1978
Labeo senegalensis	485	180	310	TL	Niger, Benue	Motwani, 1970
Lates mariae	720	155	285	FL	Lake Tanganyika	Coulter, 1976
Lates niloticus	1636	242	363.	SL	Chari	Loubens, 1974
Lates niloticus	1700	320	520	TL	Niger, Benue	Motwani, 1970
Micralestes acutidens	65	43	57	SL	Lake Kariba	Balon and Coche, 1974 (*)
Mormyops deliciosus	1100	227	375	TL	Niger, Benue	Motwani, 1970
Oreochromis andersonii (F)	360	139	208	FL	Kafue, Zambia	Dudley, 1974
Oreochromis andersonii (M)	450	136	211	FL	Kafue, Zambia	Dudley, 1974
Oreochromis lidole	380	130	230	L	Lake Malawi	Lowe, 1952 (*)
Oreochromis macrochir (M)	330	117	191	FL	Kafue, Zambia	Dudley, 1974
Oreochromis mossambicus	236	80	120	TL	Lake Sibaya	Bruton and Allonson, 1974
Oreochromis saka	340	120	220	L	Lake Malawi	Lowe, 1952 (*)
Oreochromis shiranus	290	100	180	L	Lake Malawi	Lowe, 1952 (*)
Oreochromis squamipinnis	330	90	170	L	Lake Malawi	Lowe, 1952 (*)
Petrocephalus bovei	110	70	90	SL	Ivory coast	De Merona, 1980
Polypterus senegalus	315	162	210	SL	Chari	Daget et al., 1965 (*)
Sarotherodon galilaeus	370	91	206	TL	Syria	El Bolock and Koura, 1961 (*)
Schilbe (Eutropius) niloticus	389	170	270	TL	Niger, Benue	Motwani, 1970
Schilbe (Schilbe) mystus	223	64	95	SL	Lake Kariba	Balon and Coche, 1974 (*)
Schilbe mystus	267	115	160	SL	Ivory Coast	Leveque and Herbinet, 1980
Synodontis nebulosus	150	44	64	SL	Lake Kariba	Balon and Coche, 1974 (*)
Synodontis zambesensis	272	80	105	SL	Lake Kariba	Balon and Coche, 1974 (*)
Tilapia rendalli (M)	400	138	220	FL	Kafue, Zambia	Dudley, 1974
Tilapia zillii	210	72	127	TL	Syria	El Bolock and Koura, 1961 (*)
Tilapia zillii (M)	250	95	158	SL	Niger	Daget, 1956 (*)
Tylochromis bangwelensis	277	68	103	FL	Lake Bangweulu	Griffith, 1977
Tylochromis jentinki	390	126	170	FL	Ebrie Lagoon	Amon Kothias, 1982

TL, total length; SL, standard length; FL, fork length; F, females; M, males.
*References in De Merona and Ecoutin (1979).

TABLE 2

Maximum observed length (MOL) and lengths at the ages of 1 and 2 years for 22 species from the tropical East Atlantic

Species	MOL (mm)	Length at 1 year (mm)	Length at 2 years (mm)	Type of length	Location	Reference
Balistes carolinensis	400	153	231	FL	Senegal	Caverivière et al., 1981
Brachydeuterus auritus	240	130	166	TL	Ivory Coast	Barro, 1976
Brachydeuterus auritus	220	129	184	FL	Congo	Fontana and Bouchereau, 1976
Brotula barbata	740	150	250	TL	Senegal	Levenez and Potier, 1983
Cynoglossus canariensis	540	264	340	TL	Ivory Coast	Chauvet, 1972
Dentex angolensis	350	160	200	FL	Congo	Cayre and Fontana, 1981
Dentex angolensis	350	136	181	FL	Ivory Coast	Konan, 1977
Epinephelus aeneus	1150	242	430	TL	Senegal	Cury and Worms, 1982
Epinephelus aeneus	900	180	242	TL	West Africa	Cadenat, 1935
Euthynus alletteratus	1000	311	389	FL	Senegal	Cayre and Diouf, 1980
Galeoides decadactylus	450	162	208	FL	Congo	Samba, 1974
Katsuwonus pelanis	1000	380	495	FL	Tropical Atlantic	Cayre et al., 1988
Pagelus coupei	302	109	179	TL	Ghana	Rijavec, 1973
Pagrus ehrenbergi	550	166	270	TL	Ghana	Rijavec, 1973
Pentanemus quinquarius	230	95	160	FL	Congo	Fontana and Baron, 1976
Pomadasys jubelini	520	150	230	TL	Congo	Longhurst, 1963
Pomatomus saltator	1060	209	375	TL	Senegal, Mauritania	Champagnat et al., 1983
Pseudotolithus senegalensis	630	231	318	TL	Congo	Troadec, 1971
Pseudotolithus senegalensis	520	195	263	TL	Senegal	Sun, 1975
Pseudotolithus typus	870	253	350	TL	Congo	Poinsard, 1973
Pseudupeneus prayensis	355	155	222	FL	Senegal	Chabanne, 1987
Pteroscion peli	230	121	186	TL	Congo	Fontana and Baron, 1976
Sardinella maderensis	310	154	214	FL	Congo	Gheno and Fontana, 1981
Sardinella aurita	330	180	233	FL	Congo	Gheno and Fontana, 1981
Thunnus albacares	2100	527	686	FL	Tropical Atlantic	Cayre et al., 1988
Thunnus obesus	2200	444	701	FL	Tropical Atlantic	Cayre et al., 1988

TL, total length; FL, fork length.

TABLE 3

Maximum observed length (MOL) in the wild and length or mean weight at the age of 12 months for the species cultured at the Layo Aquaculture station (Ebrié Lagoon, Ivory Coast)

Species	MOL (mm)	Weight at 12 months (g)	Length at 12 months (mm)	Type of length	Reference
Tilapia guineensis	315 (a)	85	165	FL	Legendre et al., 1991
Sarotherodon melanotheron	334 (a)	115	180	FL	Legendre et al., 1989
Chrysichthys maurus	403 (a)	70	165	FL	A.O.R.C., unpubl. data
Chrysichthys nigrodigitatus	700 (a)	170	230	FL	Anonymous, 1987
Trachinotus teraia	724 (a)	400 (c)	255 (c)	FL	Trebaol, pers. commun.
Heterobranchus longifilis	1200 (b)	900	490	TL	Legendre, 1991

TL, total length; FL, fork length.
(a) In the Ebrié Lagoon; (b) in the Agneby River, near its lagoon outlet; (c) estimates based on the duration of hatchery and nursery rearing phases (up to 20 g) obtained with *Trachinotus carolinus.*

and Table 4) between the MOL found in the natural environment and the lengths reached under culture conditions after 12 months.

The relationships obtained for continental and marine species in nature were compared two-by-two, at 1 and 2 years of age respectively, using the t-test which applies to the comparison of two reduced major axes (Mayrat, 1966). In the first case (MOL–$L1$) as well as in the second case (MOL–$L2$), no significant difference was found between the slopes or the intercepts for the two environments ($P > 0.1$).

The ratios $L1$/MOL and $L2$/MOL show that African fishes, both of continental and marine origin, on average reach approximately one-third and one-half of their maximum length at the end of their first and second years, respectively. However, a close examination of the relationships between the ratios $L1$/MOL, $L2$/MOL and the MOL shows that the simplest relation that can be fitted to the group of points is in the form $y = ax^b$, where $b < 0$ (Fig. 4, using as an example the marine species at the age of 2 years).

DISCUSSION

The present results show a clear strong positive linear relationship between the MOL and the lengths reached after 1 or 2 years of age for several African fish species. On average, therefore, in the first 2 years, species with a greater MOL reveal faster absolute growth rates than species with a smaller MOL.

This observation is in contrast to the short-cut model for the rapid estimation of fish growth proposed by De Merona (1983); this author indicates that at the age of 1 or 2 years, all species reach a more or less equivalent length, regardless of their maximum length. As the present approach was simple and

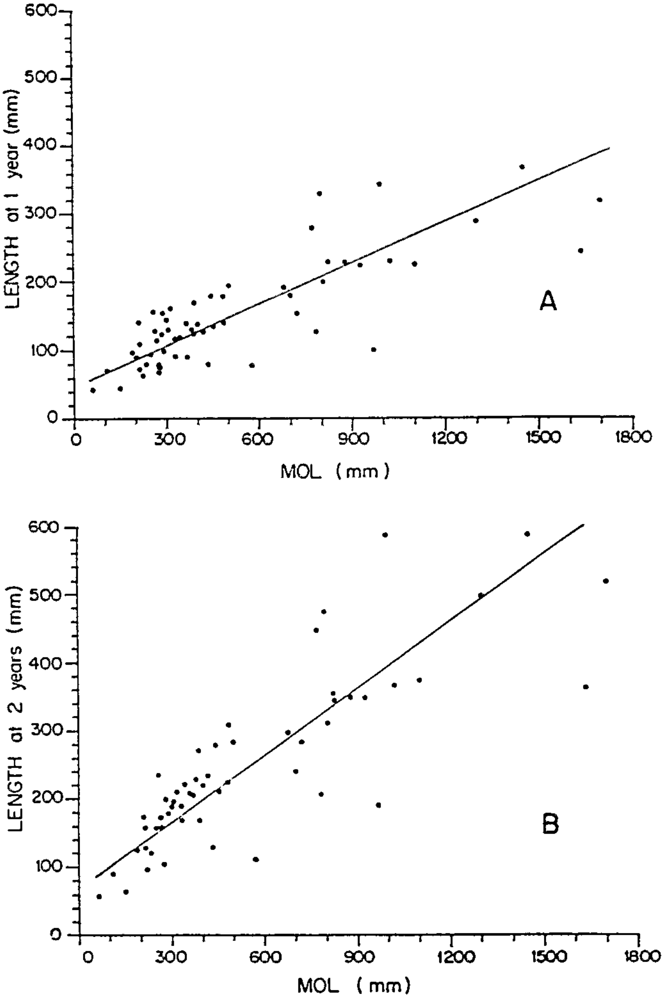

Fig. 1. Relationship between the maximum observed length (MOL) and the length at 1 year (A) and 2 years (B) for 47 species of African fish from fresh and brackish waters.

direct, this difference probably results from the approximations made by De Merona to establish his model.

No significant differences were found between the relationships obtained for marine and continental species at the age of 1 or 2 years. This suggests that fishes of both environments roughly follow the same rules of growth and that the observed relationships are valid. A similar comparison with species from temperate or cold water would be very useful in order to clarify the global incidence of climatic conditions on growth. In fact, it is a commonly held opinion that, in tropical conditions, organisms grow faster than in temperate

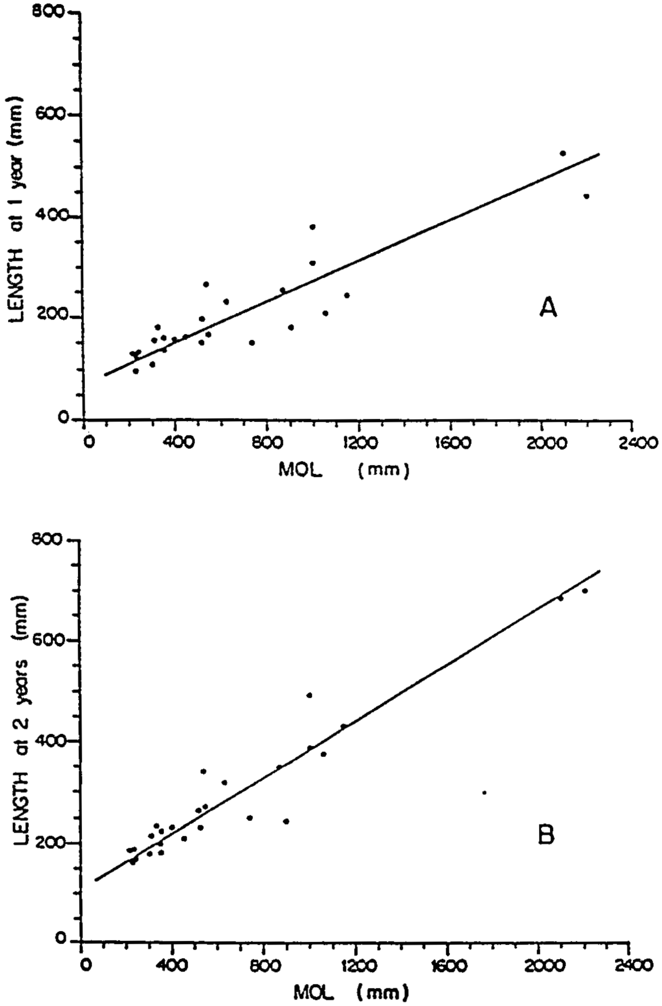

Fig. 2. Relationship between the maximum observed length (MOL) and the length at 1 year (A) and 2 years (B) for 22 species from the tropical East Atlantic.

conditions. But, in the case of fish, the recent observations by De Merona et al. (1988), tend to invalidate this principle.

The form of the relationship found between the relative growth (ratios *L*1/MOL and *L*2/MOL) and the MOL is in good agreement with the results of De Merona (1983), showing the existence of a similar relationship between the infinite length and the growth coefficient (*K*) of Von Bertalanffy's equation. Therefore, if the relative growth of a species tends to be as slow as its maximum length is great (which is accompanied by a greater longevity), this

TABLE 4

Statistical relationships between the maximum observed length (MOL) and the length at the ages of 1 year ($L1$) and 2 years ($L2$) for different species of African fishes in the wild or in culture. In all cases, adjustment of the relationships was made using the least rectangles method (reduced major axis)

Origin		N	Relationship	r
Wild	Continental or estuarine	58	$L1=0.205\,\mathrm{MOL}+45.57$	0.812^{***}
		58	$L2=0.333\,\mathrm{MOL}+63.86$	0.835^{***}
	Marine	26	$L1=0.202\,\mathrm{MOL}+70.72$	0.905^{***}
		26	$L2=0.280\,\mathrm{MOL}+107.16$	0.959^{***}
Culture	Lagoon	6	$L1=0.367\,\mathrm{MOL}+22.85$	0.960^{**}

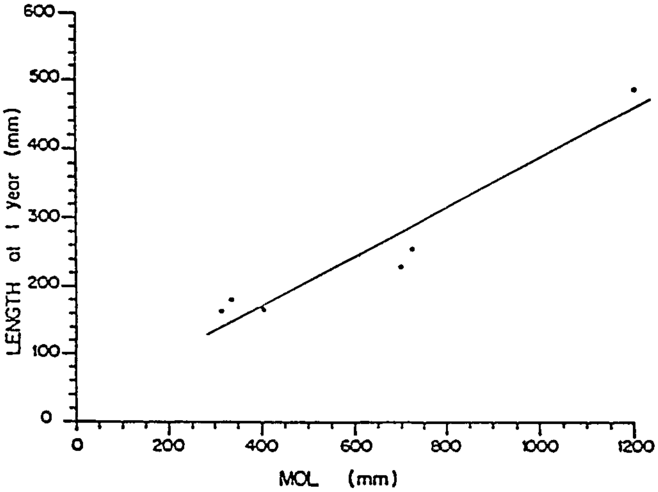

Fig. 3. Relationship between the maximum observed length (MOL) in the wild and the length at 1 year for the species raised at the Layo Aquaculture station.

is not incompatible with the fact that species of greater size on average show the fastest absolute growth rates.

However, the purpose of the present paper is not just to over-simplify such a complex phenomenon as fish growth. For example, in the wild and more particularly for fish of continental origin (Fig. 1), a high interspecific variability is observed among lengths at different ages for species of similar MOL. Although at least a part of this variability could be inherent to the different methods used in the original investigations, it is clear that the observation of maximum length cannot, by itself, be substituted for a precise growth study when accurate estimates are necessary. However, the present results confirm that the MOL is a useful tool for a rapid evaluation of growth rates in the

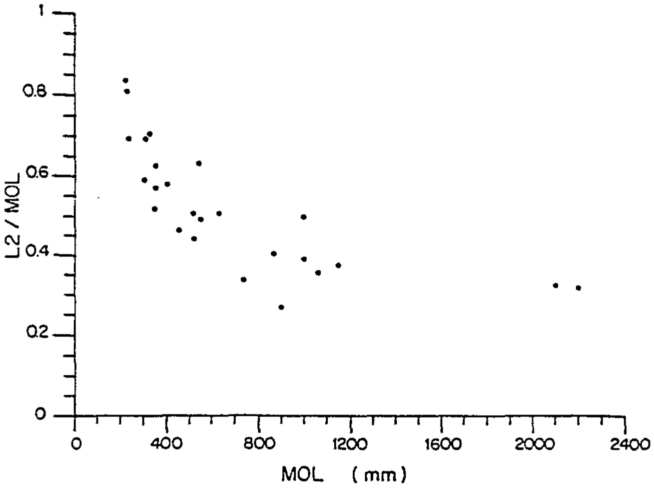

Fig. 4. Relationship between the maximum observed length (MOL) and the relative growth at the age of 2 years ($L2$/MOL ratio) for 22 species of the tropical East Atlantic.

absence of basic data and represents, as such, an interesting criterion for the preselection of species of potential interest for aquaculture.

Application to the preselection of species of interest for aquaculture

The potential for aquaculture of indigenous species of many aquatic tropical environments is still poorly known. This is particularly the case for West African brackishwater areas where aquaculture is a recent practice with acute problems in choosing appropriate species. This choice depends directly on biological and ecological characteristics of the species and on the environment, as well as on the economic and social context of the countries concerned.

In order to identify fish species of potential interest for aquaculture in Ivorian lagoons, a two-stage procedure was proposed (Legendre and Albaret, 1984):

(1) On the most objective biological and economic criteria, a preliminary screening, the *preselection* stage, retains those species that, among the entire local ichthyofauna, present the greatest potential for a given type of aquaculture.

(2) Then, in the *selection* stage, an evaluation of the aquaculture performances of the preselected species is made by means of culture trials.

Among the biological preselection criteria, indication of rapid growth constitutes an important element in the evaluation of the duration of the growing cycle and its potential profitability. In fact, growth capacity is obviously a major economic characteristic for culture, but accurate data on the growth of tropical fish, especially African species, are still scarce.

In this context, the MOL can be used as a criterion for a hierarchic classification of species with otherwise similar biological characteristics of reproduction, feeding habits or hardiness. Species of greater length should then be chosen because they have the highest probability of rapid growth in culture. But more than the growth in length, it is generally the gain in weight that matters in aquaculture. In fact, at equivalent MOL, and therefore at similar lengths after a given growout period, individual weights of the produced fish can differ noticeably. This is particularly so in the case of *C. nigrodigitatus* and *T. teraia*, species with similar MOL where the average weight after 12 months is two times greater in the latter than in the former (Table 3). Therefore, when preselecting for species of aquacultural interest based on their MOL, it seems useful to take into consideration the allometry of growth, which can easily be done using length–weight relationships.

Finally, in spite of the limited amount of data from culture conditions, it is interesting to note that the comparison between the MOL–$L1$ relationships obtained in culture and in the wild (Table 4) tends to confirm that aquacultural techniques lead effectively towards an optimisation of growth rates.

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