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# Does overfishing lead to a decrease in catches and yields? An example of two West African coastal lagoons

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**Abstract** The factors affecting fish yields in lagoons were studied through the stability, species composition and size structure of the yields at high and low fishing intensities, respectively, in Togo and the Ivory Coast. Heavy fishing was followed by the development of a plateau phase resulting from a reorganization of species assemblage. In such a state, exploitation produced only a few dominant species for which average catch lengths were small; which were generally herbivorous and exhibited a continuous reproduction, sometimes a lowering of the age at first sexual maturity, permitting a faster turnover. Even if total catches did not collapse, fish biomass and catch per unit effort decreased when fishing effort increased. One option for management could be to locate the level of fishing effort on the plateau such that fishermen can be at least financially independent and provide sufficient fish for local subsistence.

KEYWORDS: adaptation, fish population structure, inland fisheries management, lagoon fisheries, overfishing, West Africa.

## Introduction

The current approach to fisheries management is largely based upon the utilization of global models (Schaefer 1967), analytic models (Beverton & Holt 1957) and stock-recruitment models (Ricker 1954; Beverton & Holt 1957) which require expensive data sets comprising total catch, fishing intensity and biological characteristics of exploited stocks. These models, which were developed for fisheries in temperate waters, proved difficult to apply, especially to tropical multispecies and multigear artisanal fisheries in continental areas. Their ultimate aim is to predict maximum sustainable yield (MSY), arguing that below and above the corresponding fishing effort, total catches decrease.

More empirical relationships can be used in lakes for predicting yields from the morphoedaphic index (Ryder, Kerr, Loftus & Regier 1974; Henderson & Welcomme 1974; Ryder 1982; Schlesinger & Regier 1982; Bernacsek & Lopes 1984; Marshall 1984), surface area (Youngs & Heimbuch 1982; Crul 1992), phytoplankton primary productivity (Melack 1976) or total phosphorus (Hanson & Legget 1982). In tropical river-floodplain ecosystems, a positive correlation was found between fish catches and river length or basin area (Welcomme 1985; Payne, Crombie, Halls & Temple 1993) or the intensity of flooding (Welcomme 1986; Payne

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& Harvey 1989; Lae 1992a). This type of relationship is based upon the hypothesis that the fishing intensity is sufficient to produce a maximum yield which depends essentially upon the characteristics and carrying capacity of the ecosystem. These relationships probably have some predictive utility because numerous fully exploited fisheries exist for tropical aquatic ecosystems. However, fishing effort must be taken into account because it is the most important variable explaining yields among lakes, floodplains and coastal lagoons (Bayley 1988).

The relationships concerning lagoon ecosystems remain imprecise because datasets are established without any distinction between closed, semi-closed and open lagoons; different sampling methodologies are juxtaposed and yields and explanatory variables are typically difficult to measure accurately or are poorly defined. For example, in the same fishery, catches for local consumption can be twice those of commercial fisheries which are often the only ones sampled in big trade centres. Similar problems exist with fishing effort because of the use of many types of gear, and generally it is defined as the number of fishermen km$^{-2}$. This kind of fishing index can be criticized and must at least take into account both full- and part-time fishermen. Furthermore, large errors can result when using this fishing effort over a long time period or between places where the fishing technologies have developed differently.

These empirical analyses can be useful in broader predictions over time or space (e.g. sets of fisheries), but they only define maximum yields without giving attention to the biological properties of the ecosystem. As a consequence, the dynamics of species and the interspecific relationships are only exceptionally accounted for (Andersen & Ursin 1977). These aspects can be discussed in theoretical studies (Lévêque 1995) where the role of biodiversity is examined with hypotheses on the bottom-up control (LeCren & Lowe-McConnell 1980) or the top-down control (Werner 1986; Northcote 1988), but the impact of fishing on the variability and resilience of fish stocks is never approached.

In the Togolese lagoons, fishing is an inland activity for mainly local consumption: fishing gear costs can be low but the associated fishing activity can be substantial. Consequently, these lagoons constitute an extreme case of exploited fisheries and can be used to test model assumptions relating to yield trends and to obtain a better understanding of factors affecting yields. The stability, species composition and size structure of the yields were studied at high and low fishing intensities in Togo and Ebrie lagoons.

## The Togo and Ebrie lagoons in West Africa

This study was based on the survey of two coastal lagoons in the Gulf of Guinea (West Africa): Lake Togo in Togo and the Ebrie lagoon in the Ivory Coast. Results for these two lagoons were reported by Laë (1992a, 1994), Ecoutin (1992) and Ecoutin, Durand, Laë & Hie Daré (1994). The Togolese lagoons whose freshwater input comes from three coastal rivers: Sio, Haho and Boko (Fig. 1), have a surface area of 64 km$^2$. During the flood season, in the absence of a natural outlet, the water level rises rapidly and requires a canal to be cut between the lagoon and the sea to avoid flooding the city of Aneho. In the context of the current drought that has characterized Africa for the last 20 years, this connection has occurred only five times from 1976 to 1995, as opposed to 10 times from 1960 to 1975. The interruption in the exchanges between sea and lagoon waters resulted in a progressive decrease in the lagoon water salinity from 16 ‰ to 4 ‰ in Agbodrafo (Laë 1994). In 1984 (Millet 1984; Laë 1992a),

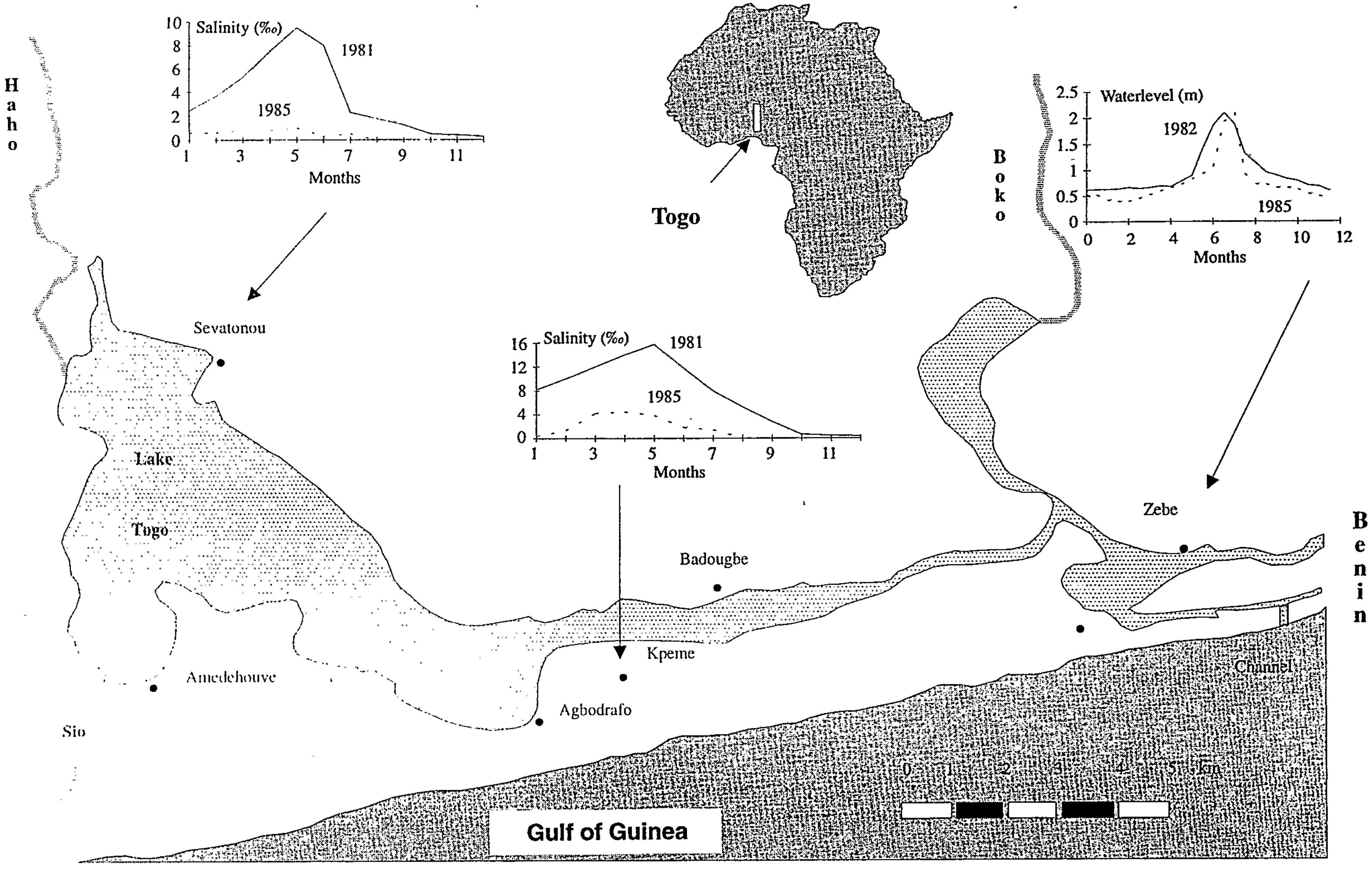

**Figure 1.** The Togo lagoons.

the lagoon had been closed for four years and had low salinity. Fishing was very active and involved an estimated 1800 fishermen for an estimated yield of 960 t (Table 1) or 150 kg $ha^{-1}$ $year^{-1}$. The artisanal fishery utilized a wide variety of gears to target a fish assemblage that varies seasonally and by location. Cast nets were the most important gear (494 t), followed by gill nets (261 t), unbaited multihook lines (101 t), bow nets (83 t) and traps (21 t).

The freshwater input for Ebrie lagoon comes from a tropical transition regime river, the Comoe, and two forest rivers, the Me and the Agneby (Fig. 2). It has a surface area of 566 $km^2$ and has been permanently connected to the sea since the opening of the Vridi canal in 1943. Studies on the hydroclimate and the primary production defined six sectors (Durand & Skubich 1982). The constant access to the sea produces typical estuarine characteristics at least for the sectors located near the canal (III, II and IV). Sectors V and VI, in the western part of the lagoon, represent nearly 50% of the total area and are quite stable and homogeneous zones with low salinity water (maximum at 5 ‰). Resemblances among these two sectors are based on physical and chemical variables and on fish community composition: species richness is 22 in sector V and 23 in sector VI (Albaret 1994). Fishing in the Ebrie lagoon is characterized by two distinct periods: one before 1982 with collective (beach seines, purse seines) and individual (cast nets, gill nets, lines, bow nets) fishing activities, the other since 1982 with only individual fishing activities (Ecoutin *et al.* 1994). The average fish yields were about 150 kg $ha^{-1}$ $yr^{-1}$ before 1982 but the fish production was enhanced in sector III (300–600 kg $ha^{-1}$ yr) by the regular immigration of fish from outside of the lagoon (*Sardinella* and *Anchovis* species).

Yields from Ebrie and Togo lagoons are not directly comparable because of the permanent connection with the sea in Ivory Coast. Therefore, sectors V and VI are similar to the Togolese lagoons and the fishing activities are the same after 1982. Thus, it is possible to correlate

**Table 1.** Fish species comprising 83% of total catches in Ebrie and Togo lagoons

| | Ebrie (V & VI) 1978 | | Ebrie (V & VI) 1984 | | Lake Togo 1984 | |
|---|---|---|---|---|---|---|
| Species | t | % of total | t | % of total | t | % of total |
| *Ethmalosa fimbriata* | 2148 | 45.2 | 769 | 36.2 | | |
| *Elops lacerta* | 953 | 20.0 | 289 | 13.6 | | |
| *Liza falcipinnis, L. grandisquamis* | 166 | 3.5 | 44 | 2.1 | | |
| *Polynemus quadrifilis* | | | 52 | 2.4 | | |
| *Chrysischthys nigrodigitatus, C. maurus* | 319 | 6.7 | 267 | 12.5 | 141 | 14.7 |
| *Gerres nigri, Eucinostomus melanopterus* | 210 | 4.4 | | | | |
| *Sarotherodon melanotheron, Tilapia guineensis* | | | 214 | 10.1 | 481 & 68 | 50.1 & 7.0 |
| *Tylochromis jentinki* | 263 | 5.5 | 63 | 3.0 | | |
| *Trachinotus teraia* | | | 66 | 3.1 | | |
| *Penaeus duorarum* | | | | | 55 | 5.7 |
| *Callinectes latimanus* | | | | | 49 | 5.1 |
| Total | 4757 | | 2127 | | 960 | |
| Number of species (representing 83% of catches) | 9 | | 11 | | 6 | |
| Yield (kg $ha^{-1}$) | 164.6 | | 70.1 | | 150 | |
| Fisherman $km^{-2}$ | 9.6 | | 5.5 | | 28.1 | |

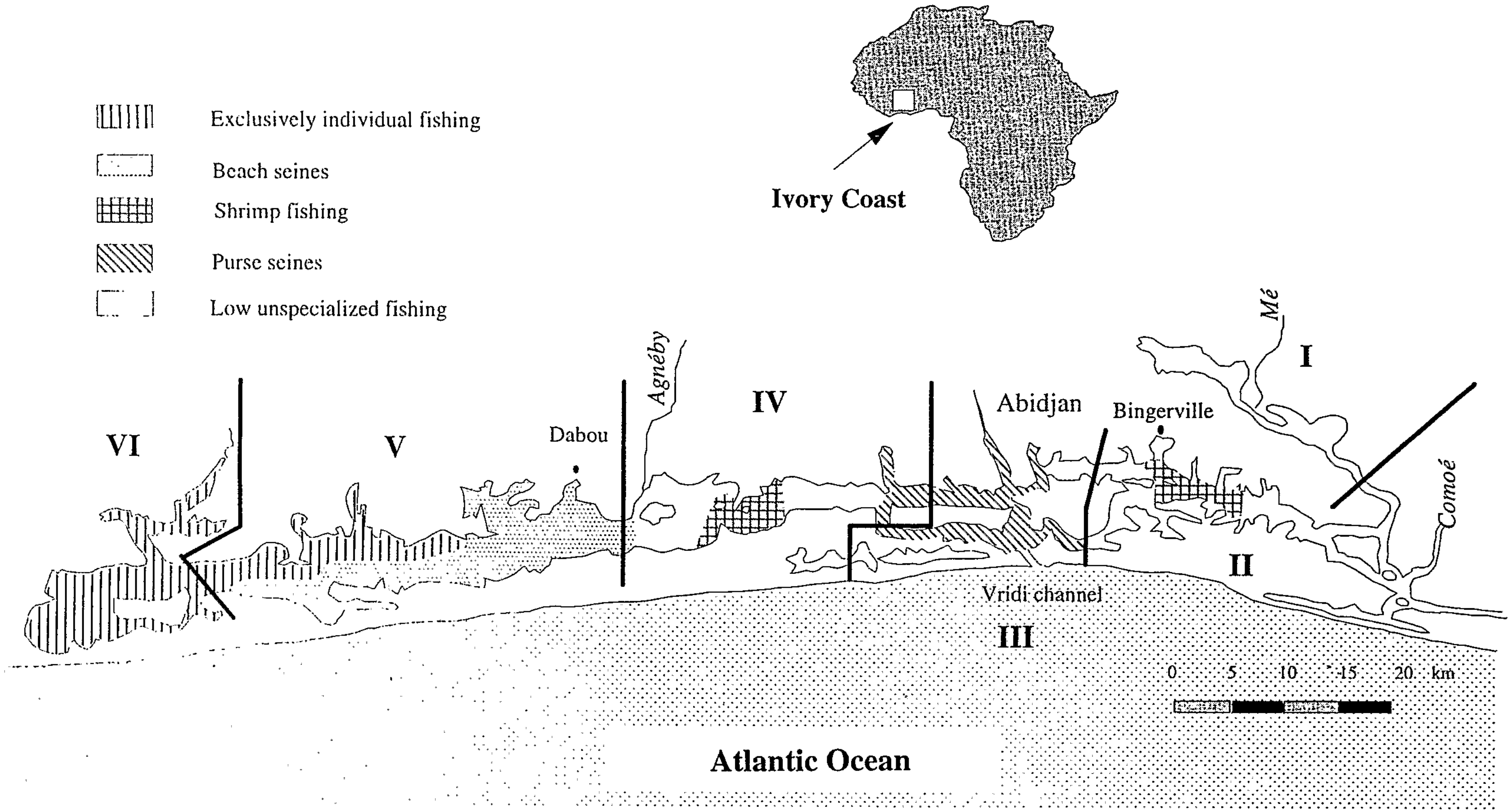

**Figure 2.** The Ebrie Lagoon: Fishing activities before 1982. In sectors V and VI which are oligohaline (characterised by low salinity water), beach seines were forbidden in 1982.

yields against different levels in fishing effort from these sectors in 1978 and 1984 with yields in lake Togo in 1984.

## Results

### Specific composition

Yields observed in sectors V and VI of the Ebrie lagoon in 1978 (165 kg $ha^{-1}$) and in Togo in 1984 (150 kg $ha^{-1}$) were similar (Table 1). In both lagoons fishing effort, defined as the number of full- and part-time fishermen $km^{-2}$, was intensive but was higher in lake Togo (28.1 fishermen $km^{-2}$) than in Ebrie (9.6 fishermen $km^{-2}$). In 1984, estimated yields in the Ivory Coast were lower (70 kg $ha^{-1}$) than in 1978 but over the same period, resulting from the ban on the use of seines, the fishing pressure decreased to 5.5 fishermen $km^{-2}$. Catch compositions from both lagoons were markedly different. In the Ebrie, *Ethmalosa fimbriata* (Bowdich) was the main species (45% of total landings in 1978 and 36% in 1984) while tilapias dominated in Togo (57% of total catches). Furthermore, in Togo six species comprised 83% of total landings in 1984 while in Ebrie there were nine in 1978 and 11 in 1984 (Table 1).

### Length composition

In Togo, catches were mostly represented by two groups based on maximum observed lengths: the larger, more abundant group included all species with maximum observed lengths from 30 to 40 cm (60.4% of total catches) and the second one all species with maximum lengths from 60 to 70 cm (18.7% of total catches). Nevertheless, the length frequency distributions of catches of all species combined showed most fish caught were small, being between 6 and 20 cm (Fig. 3). The average lengths at capture for the nine main species fished were always

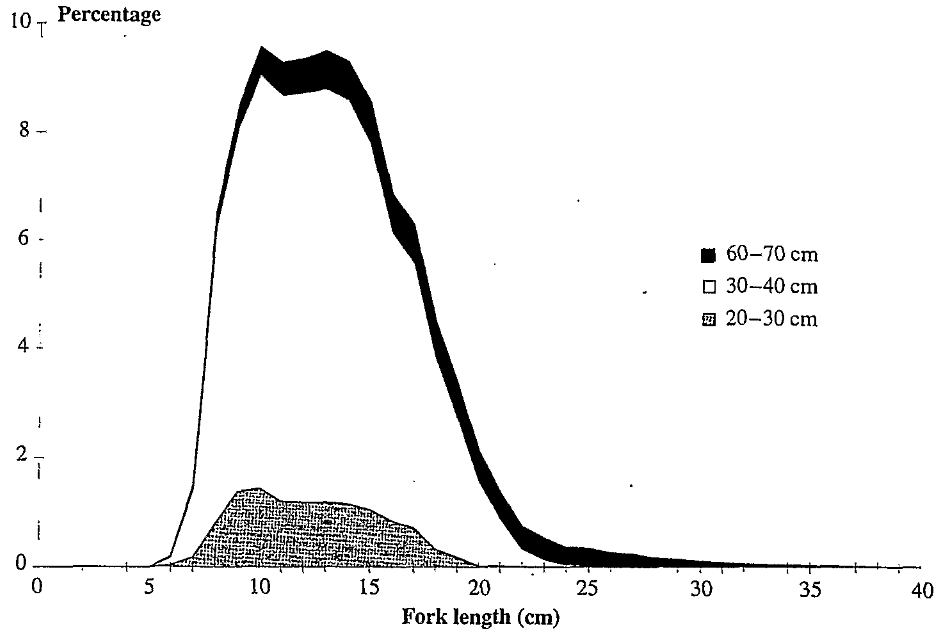

**Figure 3.** Overall precentage length frequency distribution of catches in Togo by classes of maximum observed length of species.

much lower in Togo than in the Ivory Coast (Fig. 4). Differences were found to be highly significant ($P = 0.01$ for most species, especially the tilapias & *Chrysichthys*).

## Growth

Laë (1994) suggested that *Sarotherodon melanotheron* (Bleeker) in Togo had a slow growth, but more recent studies, using sclerochronology methods, showed that the fish were not stunted (Laë unpublished data) and had a comparable growth rate with fish from rearing enclosures in nearby Ebrie (Legendre & Ecoutin 1989). There were no studies of growth for *Sarotherodon* in Ebrie lagoon but maximum observed lengths seemed to be similar in both lagoons, as they were for the other main species fished. In consequence growth rates in both lagoons would not be very different.

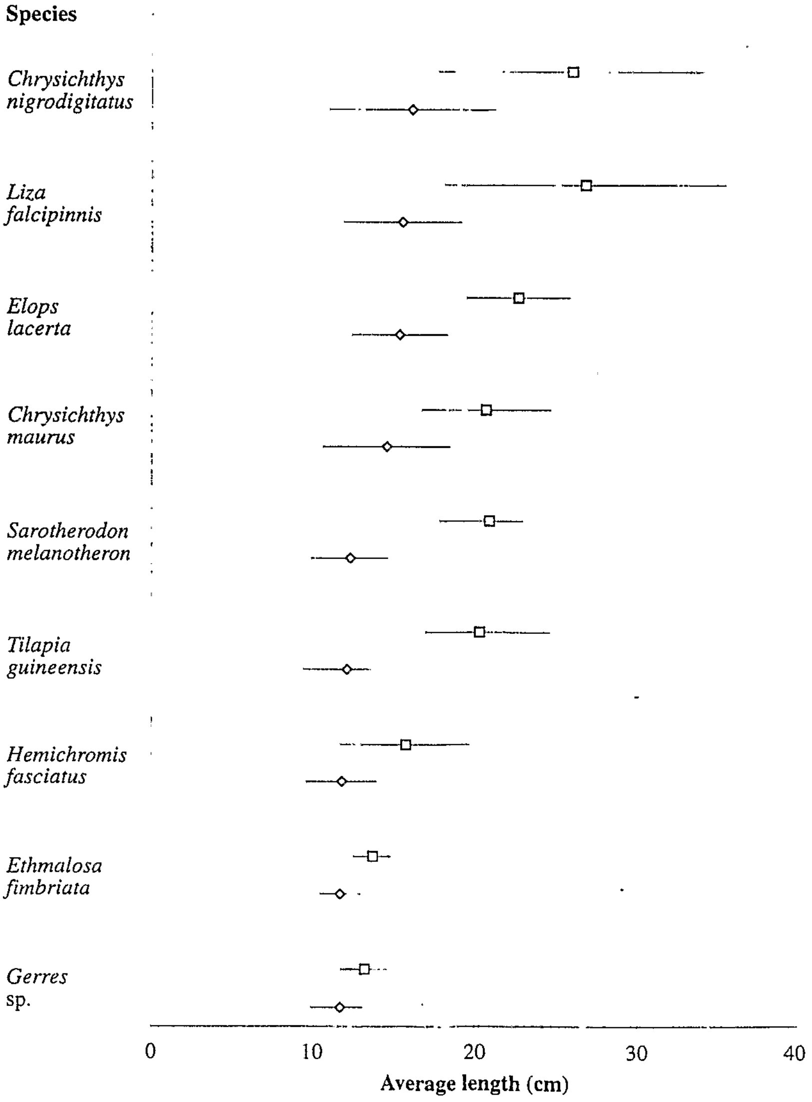

**Figure 4.** Average length at capture for the main species fished in lake Togo (◇) and Ebrie lagoon (□).

## Mortality

Using the growth equations derived from the Laë (1992a) data sets (Table 2), the instantaneous coefficient of total mortality ($Z$) for the four main species in Togo (Table 2) was estimated according to Ricker (1975). The exploitation rates (*[fishing mortality/total mortality]* × 100) were 38% for *Chrysichthys maurus*, 81% for *Chrysichthys nigrodigitatus* (Lacépède), 61% for *Tilapia guineensis* (Bleeker) and 76% for *Sarotherodon melanotheron*. The fishing mortality rates were very high relative to natural mortality (Table 2), especially for *Chrysichthys nigrodigitatus* and *Sarotherodon melanotheron* for which fishing mortality was more than three times higher than natural mortality. The high abundance of *Sarotherodon melanotheron* in catches was marked by a high mortality rate ($Z = 4.56$).

## Impacts of fishing pressure on yields

In spite of intensive fishing effort, observed yields in Togo (150 kg ha$^{-1}$) were greater than the average yields (113 kg ha$^{-1}$) calculated by Kapetsky (1984) from 128 lagoons. This is why a relationship between fishing effort and yield was sought using only available data from fisheries close to the study area (Table 3). The best relationship (Fig. 5) was:

$$\text{Log}_e\,(Y + 1) = \text{Log}_e\,(Y_{max}) \times (1 - \exp{-af})$$

where $Y$ is yield: kg ha$^{-1}$ year$^{-1}$, $f$ the number of fishermen km$^{-2}$, $\text{Log}_e(Y_{max}) = 5.134$ ($\sigma = 0.17$), $a = 0.3294$, $r^2 = 0.88$.

This relationship, which reaches an asymptote, is acceptable given the uncertainties in the

**Table 2.** Biological parameters for the main species fished in lake Togo

| Species | Von Bertalanffy $L_\infty$ | $K$ | $t_0$ | Natural mortality | Total mortality | Fishing mortality |
|---|---|---|---|---|---|---|
| *Sarotherodon melanotheron* | 326 | 0.44 | −0.21 | 1.08 | 4.56 ± 0.42 | 3.48 |
| *Tilapia guineensis* | 326 | 0.44 | −0.21 | 1.08 | 2.75 ± 1.09 | 1.67 |
| *Chrysichthys nigrodigitatus* | 849 | 0.117 | −0.87 | 0.34 | 1.82 ± 0.49 | 1.48 |
| *Chrysichthys maurus* | 325 | 0.50 | −0.01 | 1.16 | 1.88 ± 0.9 | 0.72 |

**Table 3.** African coastal lagoon data (the number of fishermen in Nigeria has been divided by two to take into account the low relative efficiency of fishermen in 1965)

| Country | Lagoon | Surface (ha) | Fishermen (number km$^{-2}$) | Yield t year$^{-1}$ | Source |
|---|---|---|---|---|---|
| Ivory Coast | Ebrie | 56 600 | 9.4 | 151 (78–82) | Laë (1992a) |
| | | | 5.5 | 61 (83–84) | Ecoutin *et al.* (1994) |
| | Aby | 42 400 | 8.4 | 153 (86) | Charles-Dominique (1994) |
| Ghana | Sakumo | 100 | 20 | 150 (71) | Pauly (1976) |
| Nigeria | Lagos & Lekki | 96 500 | 4.75 | 85 (65) | FAO (1969) |
| Togo | Lake Togo | 6400 | 28 | 150 (84) | Laë (1992a) |
| Madagascar | Pangalanes | 18 000 | 3.3 | 22 (72–78) | Lasserre (1979) |

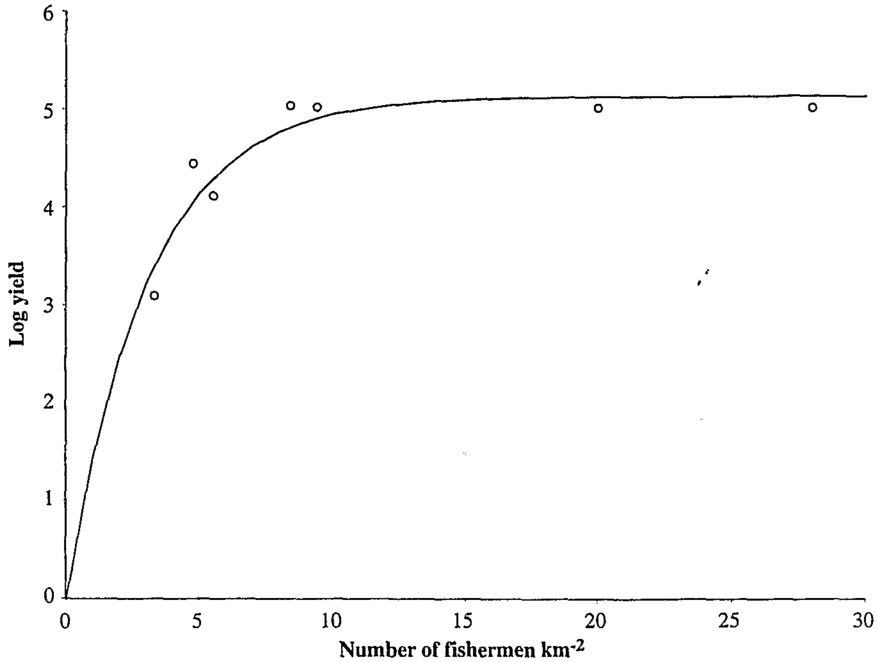

**Figure 5.** Relationship between fishing pressures and yields in several lagoons of Africa (Table 4)

definition of fishing effort and in the calculation of total catches. For intense fishing activity, there was no decrease in catches but a stabilization of yields: maximum yield would be reached at a number of 8–9 fishermen km$^{-2}$ and would remain stable at this level until at least 30 fishermen km$^{-2}$. The exponential model was used to define the fishing effort responsible for a collapse in the catches although a decrease in catches was not tested for.

## *Functioning of the food chain*

The lagoon fishes can be divided into six groups according to the following trophic levels: phytomicrophagous; zooplanktophagous; malacophagous; mixed predators; macrocrustacean predators; and ichthyophagous. In Ebrie lagoon 80% of species were classified as predators (ichthyophagous, malacophagous, large crustacean eaters and insectivorous) and about 20% as microphagous (Table 4; Albaret 1994). Among the latter, Mugilidae, *Ethmalosa* and tilapias are fish species at the lowest level of the food chain. The percentages of predator (73%) and microphagous species (27%) were similar in Togo. However, the combined abundance of species showed that the herbivorous or detritivorous group in Ebrie represented 55.5% of total catches in 1984 and 57.5% in 1978 (Table 5). This percentage in Togo was about 70.4% in 1984 because tilapias constituted more than 60% of the total catches. Similarly, the piscivorous group was 32.5% of the fish catch in the Ebrie lagoon in 1984, 26.3% in 1978 and 8.6% in lake Togo in 1984.

## *Characteristics of fish reproduction*

The life cycle of the main fish species in the Ebrie Lagoon was described by Albaret (1994). There was a peak of reproductive activity during the dry season (January, February, March) for *Pomadasys*, *Gerres*, *Ethmalosa*, *Trachinotus* and during the rainy season for *Tylochromis*, *Chrysichthys*. The same observations were made for *Chrysichthys* by Laë (1992a) in Togo and by Laleye (1995) in Benin.

Other species in the lagoon were not associated with seasonal reproduction. For example, in Togo in April 1984, females of *Sarotherodon melanotheron* were ready to spawn (27% in maturation phase and 49% in advanced maturation phase) (Laë 1992a). In July, spawning had occurred for some of the females (30% in post laying phase) but 27% were still in the maturation phase. Numerous authors describe the reproduction of *Sarotherodon melanotheron* and *Tilapia guineensis* as continuous (e.g. Fagade 1973; Pauly 1976; Legendre & Ecoutin 1989) and this appears to be the case for these two species in the Togolese lagoons. Furthermore, comparison of the smallest length at sexual maturity among species common to Lake Togo and Ebrie lagoon shows that they were the same for all species, except tilapias which were much smaller (Table 6) in Togo. It seems that the minimum length and age of sexual maturity for these two species in Togo were lower than in other west African lagoons.

**Table 4.** Main biological characteristics of fishes in the Ebrie lagoon (from Albaret, 1994): Plank = Plankton, Mben = Macrobenthos, Mol = Mollusc, Cru = Crustacean. L50 = length 50% mature

| Species | Site of reproduction | Season | Smallest maturity length (mm) (M & F) | L50 (mm) (M & F) | Feeding |
|---|---|---|---|---|---|
| *E. fimbriata* | Lagoon | Dry | 82–92 | 120–130 | Plank-Mben |
| *El. lacerta* | Sea | | | | Fish-Mol-Cru |
| *S. melanotherton* | Lagoon | all year | 148–146 | ?–180 | Plank-debris |
| *T. guineenis* | Lagoon | all year | 120–120 | 180–160 | Plank-debris |
| *C. maurus* | Lagoon | Rainy | 100–110 | 120–140 | Fish-Mol-Cru |
| *C. nigrodigitatus* | Lagoon | Rainy | 140–200 | | Mol-Cru-Zo |
| *T. jentinki* | Lagoon | Rainy | 143–147 | 158–158 | Fish-Mol-Cru |
| *G. nigri* | Lagoon | Dry | 62–70 | 72–82 | Fish-Mol-Cru |
| *Liza* sp. | Lagoon | | 188–214 | 230–230 | Plank-debris |
| *Polynemus* | | | | | Fish-Cru |
| *T. teraia* | Lagoon | Dry | 275–225 | | Fish-Mol-Cru |
| *Clarias* sp. | River | | | | |
| *Hemichromis* sp. | Lagoon | | 80–? | | Fish-Cru |
| *Heterotis* | River | | | | |

**Table 5.** Percentage distribution of fish catches by main trophic level

| | Ebrie 1984 | Ebrie 1978 | Togo 1984 |
|---|---|---|---|
| Herbivorous or detritivorous | 55.5 | 57.5 | 70.4 |
| Invertebrate | 12.0 | 16.2 | 21.1 |
| Piscivorous | 32.5 | 26.3 | 8.6 |
| Fishing effort (fishermen km$^{-2}$) | 5.5 | 9.8 | 28.6 |

**Table 6.** Length at sexual maturity (mm): smallest female in advanced maturation

| Species | Lake Togo | Ebrie Lagoon |
|---|---|---|
| *Sarotherodon* | 85 | 146 |
| *Tilapia* | 70 | 120 |
| *Hemichromis* | 86 | 80 |
| *Pellonula* | 74 | |
| *Ethmalosa* | 95 | 92 |
| *C. maurus* | 105 | 100–110 |

## Discussion

In Togo, intensive fishing activities would not result in a decrease in total catch, as usually proposed, and fish landings would remain relatively constant even when fishing pressure was increased three-fold beyond the point where the asymptote was reached. In floodplain-river ecosystems the existence of a levelling off, or plateau phase has already been observed (Ryder 1965; Welcomme 1989; Laë 1992b) and simulated (Welcomme & Hagborg 1977; Bousquet 1994; Morand & Bousquet 1994). The maintenance of high fish yields is consistent with several explanations and a proposed model for Ebrie and Togo lagoons is summarized in Figure 6. First, whilst fish landings are constant, fish biomass declines and CPUE decreases when the number of fishermen km$^{-2}$ increases (from 1710 to 530 kg fisherman$^{-1}$ yr$^{-1}$). Second, the persistence of high yields can partly be explained by the rejuvenation of fish stocks whose average length reduced from 19.6–12.7 cm. At the same time, the number of species representing 83% of total catches decreased from 11 to 6. The latter suggests the trophic-level response to overfishing by selection for phytophagous or detritivorous species. In Togo, this process was essentially based on the presence of tilapias and the high abundance of these species was probably not due to chance. Tilapias are considered as the world's most productive fish (Lowe-McConnell 1975) and are able to feed as detritivores and herbivores at the base of the aquatic food chain (Odum 1970; Fagade 1971; Bowen 1979, 1980, 1987; Pauly, Moreau & Prein 1988a). The strong abundance of *Sarotherodon melanotheron* (90% of the catch) in Ghana on the Sakumo lagoon was explained by its feeding on the fine fraction of the sediment (Pauly 1976).

In terms of life history strategies, the species selection in Togo was for those that were obliged to reproduce in lagoon water since the exchanges with the ocean were interrupted for 4 years. Then, the continuous reproduction observed for tilapias was an important factor in enabling these species to remain resilient, all of the other species becoming less abundant when subjected to intensive fishing pressure. Also the protection *Sarotherodon* gives to its eggs from predators seems to give it an advantage over *Tilapia*. Furthermore, the reduction of the length at first sexual maturity for tilapias has already been mentioned in the polluted bay of Bietri in the Ebrie lagoon for *Ethmalosa fimbriata* (Albaret & Charles-Dominique 1982) and in the Sakumo lagoon for *Sarotherodon* (Pauly 1976). The conclusion of the last author was that *Sarotherodon* was either a stunted species or, as seemed more likely, the stock was so heavily exploited that it consisted only of relatively young fishes. In Togo, studies on

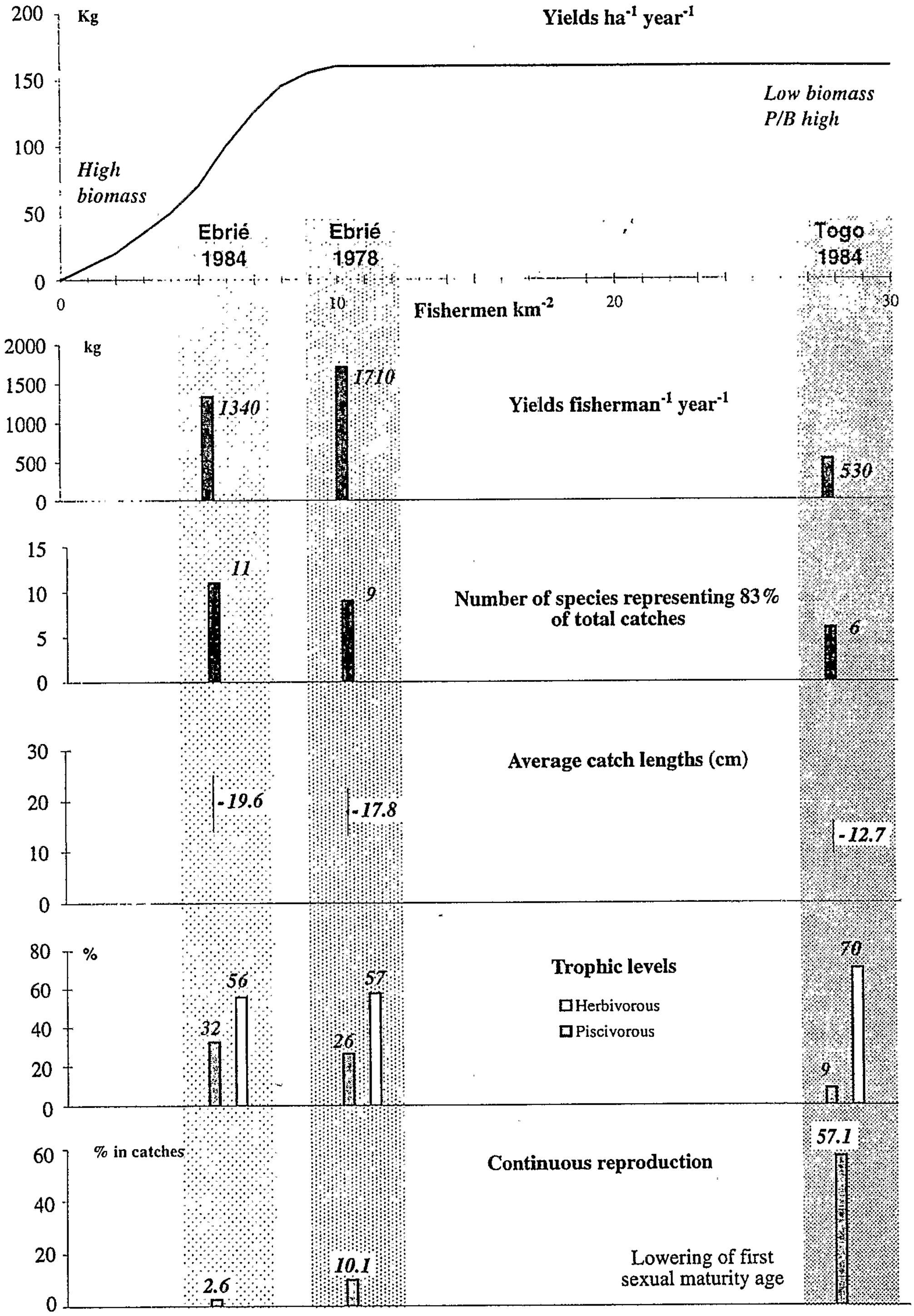

**Figure 6.** Evolution of fish communities with increasing fishing effort.

*Sarotherodon* growth showed that this species was not stunted. In addition, Legendre & Ecoutin (1989) observed species variation in individual fecundity, size of the ovocytes and laying frequency under natural and captivity conditions. Such adaptations appear to be very important for the species to remain resilient with respect to recruitment overfishing.

Finally, the continuous reproduction of tilapias and the lowering of the age at first sexual maturity leads to an increase in the number of reproductive cycles each year. These changes result in a rapid renewal of tilapia biomass and the mortality coefficient (4.56) of *Sarotherodon* can be interpreted as a large reduction of the residual biomass for equivalent fishing yields. Similar observations were made in the Sakumo lagoon by Pauly, Moreau, Lourdes & Palomares (1988b).

Some physiological qualities of tilapias can also help to explain the resilience of this species in the face of a changing environment. They show a great tolerance to low oxygen concentration (Philippart & Ruwet 1982) and are able to use the upper water layer with higher oxygen concentration (Dussart 1963). They can resist very high $CO_2$ concentrations, high turbidities and organic or inorganic pollution (Magid & Babiker 1975). They are euryhaline (Albaret 1994) and eurythermal (Welcomme 1972).

It is suggested that, except when negative non-anthropomorphic environmental changes occur, high yields may remain stable even when fishing pressure increases greatly. The response of fish communities to high fishing pressure is to reduce the number of species, especially planktophagous or detritivorous species (*Tilapia* and *Sarotherodon*) and predators (*Chrysichthys*) and to favour species with high reproductive capacities, especially those which have several short-lived annual cohorts. The major adjustment is obtained by shortening trophic chains and this particular point tends to emphasise the shifts in P/B relationships of the fish assemblage. In Lake Togo the response was mainly a result of the flexibility of stocks of tilapia species, particularly *Sarotherodon melanotheron*. Although a plateau can occur when the majority of the catch is drawn from one species, caution should be observed in generalizing because many Tilapia fisheries in African lakes have collapsed in the face of exploitation. In the same way, Caddy (1993), studying enclosed and semi enclosed seas, suggested that under nutrient enrichment and heavy fishing, both top-down and bottom-up trophic mechanisms acted in synchrony to change the trophic chain, leading initially to increase fishery productivity. The result was a decline in diversity, an initial increase in productivity of benthic/demersal and pelagic food webs, and then the progressive dominance of the production system by short-lived, especially pelagic species. Caddy (1993) observed that this phase was followed by negative changes as nutrient input increased.

This concept is distant from the current theory on fished stocks which typically aims to keep below the estimated maximum sustained yield of fish from a water body. Nevertheless, the reported observations, on the pretext of constant catches under increasing exploitation, does not signify that there is no need for fisheries management because even if yields are similar at the beginning and the end of the plateau, as predicted in the model, the situation changes for fish communities and fishermen.

The aim of managers in tropical inland fisheries is to ensure sustainability (Bayley 1995) and this can be achieved at different states of the plateau phase. However, high fishing effort towards the end of the plateau should be avoided because it could lead to a collapse in catches or to a deterioration of the economics of fishermen. Nevertheless, in developing countries, because different fishing efforts can provide equivalent total catches it can help managers to take account of social parameters and to divide the resource to maximize employment and to maintain populations so they do not exacerbate urban overcrowding. The choices can be different from developed countries and can favour the sharing of the resource without maximizing profit, with the provisos that: (i) the stocks do have a limit and therefore some level of prudence is necessary until that limit can be predicted; (ii) the catches by a fishing unit must release sufficient subsistence for fishermen's families.

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## References

Albaret J.J. (1994) Les poissons, biologie et peuplements. In: J.R. Durand, P. Dufour, D. Guiral & S.G.F. Zabi (eds) *Environnement et ressources aquatiques de Côte d'Ivoire. Les milieux lagunaires.* Paris: ORSTOM edns, pp. 239–279.

Albaret J.J. & Charles-Dominique E. (1982) Observation d'un phénomène de maturation sexuelle précoce chez l'Ethmalose, *Ethmalosa fimbriata* Bowdich, dans une baie polluée de la lagune Ebrié (Côte d'Ivoire). *Document Scientifique Centre Recherche Océanographique Abidjan* **13,** 23–31.

Andersen K.P. & Ursin E. (1977) A multispecies extension to the Beverton and Holt theory of fishing, with accounts of phosphorus circulation and primary production. *Meddelelser fra Danmarks. Fiskeri og Havundersogelser* **7,** 319–435.

Bayley P.B. (1988) Accounting for effort when comparing tropical fisheries in lakes, river-floodplains, and lagoons. *Limnology and Oceanography* **33,** 963–972.

Bayley P.B. (1995) Sustainability in tropical inland fisheries: the manager's dilemma and a proposed solution. In: M. Munasinghe & W. Shearer (eds) *Defining and Measuring Sustainability: the Biogeophysical Foundations.* Washington DC: The World Bank, pp. 321–327.

Bernacsek G.M. & Lopes S. (1984) Mozambique. Investigations into the fisheries and limnology of Cahora Bassa Reservoir seven years after dam closure. *FAO-Mozambique field Document* **9,** 145 pp. Ministry of Agriculture, Fisheries and Food GB.

Beverton R.J.H. & Holt S.J. (1957) On the dynamics of exploited fish populations. HMSO *Fishery Investigations,* Ministry of Agriculture, Fisheries and Food G.B. (2 Sea Fish), **19,** 533 pp.

Bousquet F. (1994) Des milieux, des poissons, des hommes: Etude par simulation multi-agents. Le cas de la pêche dans le Delta Central du Niger. Thesis, Lyon University, 199 pp.

Bowen S.H. (1979) A nutritional constraint in detritivory by fishes: the stunted population of *Sarotherodon mossambicus* in Lake Sibaya, South Africa. *Ecological Monographs* **49,** 17–31.

Bowen S.H. (1980) Detrital nonprotein amino acids are the keys to rapid growth of *Tilapia* in Lake Valencia, Venezuela. *Science* **207,** 1216–1218.

Bowen S.H. (1987) Composition and nutritional value of detritus. In: D.J.W. Moriarty & R.S.V. Pullin (eds) *Detrital and Microbial Ecology in Aquaculture. ICLARM Conference Proceedings* **14,** 192–216.

Caddy J.F. (1993) Toward a comparative evaluation of human impacts on fishery ecosystems of enclosed and semi-enclosed seas. *Reviews in Fisheries Science* **1,** 57–95.

Charles-Dominique E. (1994) L'exploitation de la lagune Aby (Cote d'Ivoire) par la pûche artisanale. Dynamique des ressources, de l'exploitation et des pûcheries. Paris: ORSTOM, T.D.M., 407 pp.

Crul R.C.M. (1992) Models for estimating potential fish yields of African inland waters. *CIFA Occasional Paper* **16,** 22 pp.

Durand J.R. & Skubich M. (1982) Les lagunes ivoiriennes. *Aquaculture* **27,** 211–250.

Dussart J. (1963) Contribution à l'étude de l'adaptation des Tilapias (Pisces Cichlidae), à la vie en milieu mal oxygéné. *Hydrobiologia* **21,** 328–341.

Ecoutin J.M. (1992) Dynamique des flottilles en pêche artisanale. L'exemple des sennes tournantes de Côte d'Ivoire. Paris: ORSTOM edns. 208 pp.

Ecoutin J.M., Durand J.R., Laë R. & Hié Daré J.P. (1994) Exploitation des stocks. In: J.R. Durand, P.

Dufour, D. Guiral and S.G.F. Zabi (eds).) *Environnement et ressources aquatiques de Côte d'Ivoire. Les milieux lagunaires.* Paris: ORSTOM edns, pp. 399–444.

Fagade S.O. (1971) The food and feedings habits of *Tilapia* species in the Lagos Lagoon. *Journal of Fish Biology* **3,** 151–156.

Fagade S.O. (1973) Age determination in *Tilapia melanotheron* (Ruppell) in the Lagos lagoon, Lagos, Nigeria. In: T.B. Bagenal (ed.) *Ageing of fishes.* Old Woking, England: Unwin Brothers Ltd, pp. 71–77.

F.A.O. (1969) Fisheries survey in the western and mid-western regions. Nigeria. Final Report. Rome, FAO/SF: 74/NIK/6: 142 pp.

Hanson J.M. & Legget W.C. (1982) Empirical prediction of fish biomass and yield. *Canadian Journal of Fisheries and Aquatic Sciences* **39,** 257–263.

Henderson H.F. & Welcomme R.L. (1974) The relationship of yield to morpho-edaphic index and numbers of fishermen in African inland fisheries. *CIFA Occaional Papers* **1,** 19 pp.

Kapetsky J.M. (1984) Coastal lagoon fisheries around the world: some perspectives on fishery yields, and other comparative fishery characteristics. In: *Management of coastal lagoon fisheries, FAO Studies and Reviews* **61,** 98–119.

Laë R. (1992a) Les pêcheries artisanales lagunaires ouest africaines: échantillonnage et dynamique de la ressource et de l'exploitation. Paris: ORSTOM edns. 201 pp.

Laë R. (1992b) Influence de l'hydrologie sur les pêcheries du Delta Central du Niger de 1966 à 1989. *Aquatic Living Resources* **5,** 115–126.

Laë R. (1994) Evolution des peuplements (poissons et crustacés) dans une lagune tropicale, le lac Togo, soumise à un régime alternatif de fermeture et d'ouverture du cordon lagunaire. *Aquatic Living Resources* **7,** 165–179.

Laleye P.A. (1995) Ecologie comparée de deux espèces de *Chrysichthys*, poissons siluriformes (Claroteidae) du complexe lagunaire lac Nokoué-lagune de Porto-Novo au Bénin. Thesis, Liège University, 195 pp.

Lasserre G. (1979) Bilan de la situation des pêches: aux Pangalanes (Est Zone Tamatave-Andevoranto) au Lac Anony (région Fort-Dauphin). Perspective et aménagement, PNUD-FAO-MAG/76/002, Tananarive, Ministère du développement rural et de la réforme agraire FAO, 38 pp.

LeCren E.D. & Lowe-McConnell R.H (eds) (1980) The functioning of freshwater ecosystems. *International Biological Programme no. 22.* Cambridge: Cambridge University Press, 588 pp.

Legendre M. & Ecoutin J.M. (1989) Suitability of brackish water Tilapia species from the Ivory Coast for lagoon aquaculture. I Reproduction. *Aquatic Living Resources* **2,** 71–79.

Lévêque C. (1995) Role and consequences of fish diversity in the functioning of African freshwater ecosystems: a review. *Aquatic Living Resources* **8,** 59–78.

Lowe-McConnell R.H. (1975) *Fish communities in tropical freshwaters.* London: Longman, 337 pp.

Magid A. & Babiker M.M. (1975) Oxygen consumption and respiratory behaviour of three Nile fishes. *Hydrobiologia* **46,** 359–367.

Marshall B.E. (1984) Towards predicting ecology and fish yields in African reservoirs from pre-impoundment physico-chemical data. *CIFA Technical Papers* **12,** 36 pp.

Melack J.M. (1976) Primary productivity and fish yields in tropical lakes. *Transactions of the American Fisheries Society* **105,** 575–580.

Millet B. (1984) Hydrologie et hydrochimie d'un milieu lagunaire tropical: le lac Togo. Thesis, Paris Orsay University, 236 pp.

Morand P. & Bousquet F. (1994) Modélisation de la ressource: relations entre l'effort de pêche, la dynamique du peuplement ichtyologique et le niveau des captures dans un système fleuve-plaine. In: J. Quensière (ed.) *La pêche dans le Delta Central du Niger.* Paris: IER-ORSTOM-KARTHALA. pp. 267–281.

Northcote T.G. (1988) Fish in the structure and function of freshwater ecosystems: a 'top-down' view. *Canadian Journal of Fisheries and Aquatic Sciences* **45,** 361–379.

Odum W.E. (1970) Utilization of the direct grazing and plant detritus food chains by the striped mullet *Mugil cephalus.* In: J.H. Steele (ed.) *Marine Food Chains.* Edinburgh: Oliver and Boyd, 552 pp.

Pauly D. (1976) The biology, fishery and potential for aquaculture of *Tilapia melanotheron* in a small west African lagoon. *Aquaculture* **7,** 33–49.

Pauly D., Moreau J. & Prein N. (1988a) A comparison of overall growth performance of *Tilapia* in open waters and aquaculture. In: R.S.V Pullin, T. Bhukaswan, K. Tonguthai & J.L. Maclean (eds), *The Second International Symposium on Tilapia in Aquaculture ICLARM Conference Proceedings* **15,** 469–479.

Pauly D., Moreau J., Lourdes M. & Palomares D. (1988b) Detritus and energy consumption and conversion efficiency of *Sarotherodon melanotheron* (Cichlidae) in a West African lagoon. *Journal of Applied Ichthyology* **4,** 190–193.

Payne A.I. & Harvey M.J. (1989) An assessment of the *Prochilodus platensis* Holmberg population in the Pilcomayo river fishery, Bolivia using scale-based and computer-assisted methods. *Aquaculture and Fisheries Management* **20,** 233–248.

Payne A.I., Crombie J., Halls A.S. & Temple S.A. (1993) Synthesis of simple predictive models for tropical river fisheries. London: MRAG Ltd. 85 pp.

Philippart J. & Ruwet J.C. (1982) Ecology and distribution of Tilapias. In R.S.V. Pullin & R.H. Lowe-McConnell (eds) *The Biology and Culture of Tilapias. ICLARM Conference Proceedings* **7,** 16–60.

Ricker W.E. (1954) Stock and recruitment. *Journal of the Fisheries Research Board of Canada* **11,** 559–653.

Ricker W.E. (1975) Computations and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada* **119,** 1–300.

Ryder R.A. (1965) A model for estimating the potential fish production of north temperate lakes. *Transactions of the American Fisheries Society* **94,** 214–218.

Ryder R.A. (1982) The morphoedaphic index: use, abuse and fundamental concepts. *Transactions of the American fisheries Society* **111,** 154–164.

Ryder R.A, Kerr S.R., Loftus K.H. & Regier H.A. (1974) The morphoedaphic index, a fish yield estimator. Review and evaluation. *Journal of the Fisheries Research Board of Canada* **31,** 663–688.

Schaefer M.B. (1967) Fishery dynamics and present status of the yellowfin tuna population of the eastern Pacific Ocean. *Inter-American Tuna Commission Bulletin* **12,** 89–136.

Schlesinger D.A. & Regier H.A. (1982) Climatic and morphoedaphic indices of fish yields from natural waters. *Transactions of the American Fisheries Society* **111,** 141–150.

Welcomme R.L. (1972) An evaluation of the Acadja method of fishing as practised in the coastal lagoons of Dahomey (West Africa). *Journal of Fish Biology* **4,** 39–55.

Welcomme R.L. (1985) River fisheries. *FAO Fishery Technical Papers* **262,** 330 pp.

Welcomme R.L. (1986) The effects of the sahelian drought on the fishery of the central delta of the Niger river. *Aquaculture and Fisheries Management* **17,** 147–154.

Welcomme R.L. (1989) Review of the present state of knowledge of fish stocks and fisheries of African Rivers. In: D.P. Dodge (ed.) *Canadian Special Publication Fisheries and Aquatic Sciences* **106,** 515–532.

Welcomme R.L. & Hagborg D. (1977) Towards a model of a floodplain fish population and its fishery. *Environmental Biology of Fishes* **2,** 7–24.

Werner E.E. (1986) Species interactions in freshwater fish communities. In: J. Diamond & T. Case (eds) *Community Ecology*. New York: Harper and Row, pp. 344–358.

Youngs W.D. & Heimbuch D.G. (1982) Another consideration of the morphoedaphic index. *Transactions of the American Fisheries Society* **111,** 151–153.