Improving productivity in tropical lakes and reservoirs

Review prepared for the

CGIAR Challenge Program on
Water and Food

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REFERENCE:

Kolding, J. and Zwieten, P.A.M. van, 2006. Improving productivity in tropical lakes and reservoirs. Challenge Program on Water and Food - *Aquatic Ecosystems and Fisheries Review Series 1*. Theme 3 of CPWF, C/o WorldFish Center, Cairo, Egypt. 139 pp. ISBN: 977-17-3087-8

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1. Introduction

Freshwater resources comprise a mere 2.5% of the earth's water, of which more than 99% is frozen in glaciers or stored in ground water. Lakes hold only about 0.4% of the global freshwater (Wetzel 1983, Table 1), but cover, together with wetlands, around 8% of the land area and contain about 40% of all fish species (Moss 1988)[1]. In contrast to their diminutive volume, the relative productivity of lakes, reservoirs, rivers, and wetlands is enormous, contributing about 15% of the world fisheries production (Table 1).

Table 1. Relative distribution of water resources and production figures between Marine and Inland fisheries. Figures in brackets exclude production figures from China. Sources (Wetzel 1983, SOFIA 2004).

	Marine			Inland		Relative	
	Water	Fisheries		Water	Fisheries		
	km^3*10^3	ton*10^6		km^3*10^3	ton*10^6	% of inland	% of total
Oceans	1 370 000						97.63
			frozen	29 000		87.06	0.02
			Ground	4 000		12.01	0.00
			Lakes	125		0.38	0.00
			Saline	104		0.31	0.00
			soil moisture	67		0.20	0.00
			Rivers	1		0.00	0.00
			Atmosphere	14		0.04	0.00
Capture		81.3 (67)	Capture		9 (6.5)	57.52	8.56
Aquaculture		16.7 (5.5)	Aquaculture		25.5 (7.5)	42.48	6.32
Sum	1 370 000	87.5		33 311	15.3		
% of total	97.6	85.1		2.4	14.9		

The immense relative productivity of freshwaters becomes even more suggestive when looking closer into the global distribution pattern (Fig. 1). Of the 1500 largest lakes in the world that account for most of the surface area, approximately 90% are located in the temperate and northern regions. They are predominantly of glacial (60 %) or permafrost (20%) origin (Wetzel 1983, Lewis 1996). The remaining 10 % are tropical lakes, most of which are of riverine (40%) or coastal (20%) origin. The majority of temperate lakes is from a capture fishery perspective unutilised, but has important recreational angling value[2]. More than 90% of the inland captures and nearly 100 % of the global freshwater aquaculture, totalling about 14 million ton (excluding China with its reported production of 2.2 mton), are from tropical developing countries (SOFIA 2004). Thus, nearly 15% of the world's reported fisheries production comes from the tiny percentage (approximately 0.2 %) of the global aquatic surface area made up by tropical freshwater aquatic ecosystems. The relative contribution from may be even higher taking into account that perhaps only as much as 30% - 50% of the inland capture production is officially reported: many countries do not consider their inland capture fisheries important enough to collect data, or it is often very difficult to collect them, due to the small scale, highly complex environments in which freshwater fisheries are done (Welcomme 1997, FAO 2003a, see also footnote 3).

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[1] Data on surface area can differ quite substantially between authors: Kapetsky (1998) mentions 1.7 million km^2 of lakes and 4 million km^2 of swamps, marshes and other wetlands, covering respectively 1.4% and 3.8% of the global surface.

[2] Recreational fisheries are very important in most of the affluent industrialised countries, and part of South America. They may produce a significant amount for domestic consumption and catch rates of 30-94 kg/ha are reported from Europe (Welcomme 1997).

These significant quantities of caught and cultured fish and other aquatic products are produced by a large variety of water bodies (Table 2). To get an insight in the potential for increased production from the world's freshwaters a reliable estimate of the total area of the different types of freshwaters would be necessary. In particular the small systems, highly variable in size, pose a problem when attempting to make reliable estimates of fish production, fishery or aquaculture potential and assess threats to sustainability of production. For instance, estimates of total global wetland areas vary between 704 000 km^2 to 9.5 million km^2 (Darras et al. 1998). However, good estimates on larger systems are lacking as well. Perennial lakes are estimated to account for 1.7 million km^2 (Kapestky 1997), but it is difficult to obtain a good estimate of the total area of reservoirs and lakes. Large reservoirs numbered at 36,235 in 1986 with 948 under construction in 1994, but with no information on size. In 2000 the World Commission on Dams reported 'more than 45,000' large reservoirs but estimated that there may be up to 48,000 large reservoirs. On average their size is 23 km^2 in size with an average capacity of 269 million m^3 (World Commission on Dams 2000; table 4). Next to that "uncounted small multiple purpose reservoirs" (Kapetsky 1998) exist.

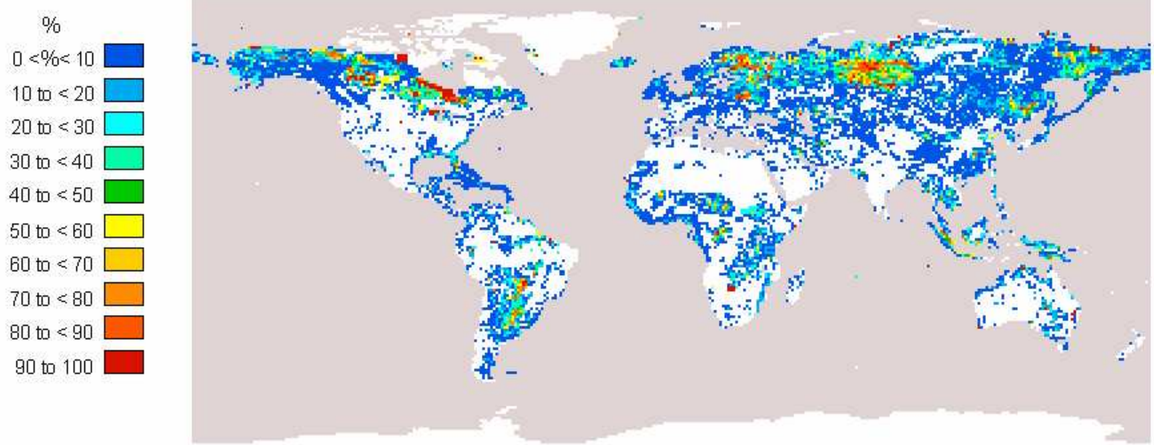

Figure 1. Distribution of lakes and wetlands over the world. The colour code is the percentage coverage by a pixel height of 1 degree, i.e. 1 nm^2 or 3.43 km^2. The map is generated by the fusion of a number of available data sources. The total wetland area computed from this map is 9.542.124 km^2 . It must be underlined that, as a result of the present analysis, this map may still underestimate the global wetland extent, especially the extent of seasonal wetlands (Darras et al. 1998. http://ceos.cnes.fr:8100/cdrom-00b2/ceos1/casestud/igbp/image62.htm).

Bearing in mind that the majority of marine fish resources is considered fully exploited or overfished it is difficult to imagine that there is still room for increased production within tropical lakes and reservoirs. For instance the reported inland fish production of Africa is 2.1 million ton, which is close to the maximum potential production estimated by Welcomme, (1976) and Henderson and Welcomme (1974). Freshwater fisheries and aquaculture invariably take place in multiple use environments and often are considered secondary activities, particularly in reservoirs meant for irrigation, hydropower, flood-control or water supply. Sometimes - especially in China - reservoirs are built with provisions for fisheries and fish culture activities already taken into account during the planning stage. This includes the preparation of the reservoir bottom for effective harvesting and setting up structures to minimise escapes of stocked fish.

Freshwaters are heavily fragmented by dams and through other human interventions; the average residence time of water in regulated basins has tripled to over one month worldwide (Vörösmarty et al. 1997). Dams, inter basin transfers, and water withdrawals for irrigation have fragmented 60% of the world's rivers and it is estimated that half the worlds' wetlands were lost during the 20th century (Revenga et al. 2000). However, despite the apparent production ceiling, multiple demands on water and the large scale habitat changes, overall trends in production are still quite positive. Over the past 15 year yields were stable or increased for 57% of the countries that do report freshwater fish production and who shared 81% of the total production (FAO 2003a). Furthermore there may still be large opportunities for improved production in freshwaters, particular in reservoirs, both from fisheries or through enhancements and culture based systems (Petr 1994 1998). The growth of inland water aquaculture production has been particularly strong in China, where it averaged 11.5 percent per year between 1970 and 2000 compared with 7.0 percent per year in the rest of the world (SOFIA 2002). This is much higher than the 1.6 % increase in production over the same period in freshwater capture fisheries. It is the widening gap between the increased demand for fish and the apparent limited growth potential for natural production from capture fisheries that various forms of culture based systems are invoked as panacea. This includes enhancements of natural production in larger water bodies as natural lakes and man-made reservoirs.

Table 2. Classification of fished water bodies.

Perennial waters	lakes, rivers, streams, ponds
Semi-perennial	intermittent waters: swamps, freshwater marshes, seasonally inundated waters including floodplains and floodplain lakes, flooded forest, ephemeral streams, large intermittent lakes
Brackish water	channels among mangroves, salt marshes, coastal lagoons, estuaries
Artificial waters	reservoirs, borrow pits, flooded quarries, surface mine pits, rice fields, village and household water supply ponds, stock watering ponds, irrigation channels and ditches

Despite the uncertainties in actual fish production and in the area from which it is or may potentially be taken, it is often invoked that an increased production from both natural and man made systems can be expected (SOFIA 2004) and should be realised (e.g. Lorentzen et al. 2001). A range of enhancement technologies are potentially available to achieve this goal including:

- *fisheries development* (from optimising the utilisation of the whole ecosystem to selectively fishing-down the food webs by elimination of predators/competitors),
- *manipulating stocks and species* (from increasing the stock to broadening the catch structure through culture based fisheries),
- *manipulating the environment* (offering favourable habitats through habitat modification to enriching the water nutrients through artificial eutrophication), to
- *closed enhancements* (various types of more or less closed cultures with or without artificial feeding but including water exchange with the natural environment).

Outline and objectives

In this review we will discuss the potential for increasing production within natural lakes or man-made reservoirs based on the various enhancement concepts. Enhancements are interventions in natural aquatic resources, and combine attributes of aquaculture - intervention in the life cycle of aquatic organisms - and capture fisheries - exploitation of natural resources. Enhancements are estimated to yield about two million metric ton per year, mostly from culture-based fisheries in fresh waters where they account for some 20 percent of capture, or 10 percent of combined capture and culture production (Lorentzen et al. 2001). The effectiveness of culture-based fisheries varies widely between locations, but reasons for this are not well known. The potential production of culture-based fisheries is strongly linked to ecosystem productivity. The assessment of stocking and harvesting regimes therefore requires quantitative insights in the biological basis for production and associated population processes (Peterman 1991, Lorenzen 1995). Our discussion of enhancement technologies therefore will be framed in a review of the biological basis for fish production following a set of fundamental ecological principles. The idea is that productivity limits for natural systems including large man made reservoirs exits and are based on physical (morphometric, climatic, edaphic, hydrologic) and biological (food-web, community, evolutionary constraints) factors, resulting in limits set by the carrying capacity of a system or by the scale in variability in carrying capacity induced by climatic variations (environmental forcing). These factors present natural limits to the potential increase of production through enhancement techniques in aquatic systems. Additional inputs to systems through eutrophication, direct feeding of fish or changes in habitat structure and hydrology, may change the natural carrying capacity, but always at some cost in potentially undesired trade-offs. A push in a direction of desired production through enhancement, for example, through manipulations of the population structure by decoupling recruitment and natural spawning in ways that are unattainable in self-recruiting stocks, also means a diversion of production from elsewhere in the ecosystem. This may only be deemed acceptable if the practice does not affect the general ecosystem functioning. There is a paucity of studies on the dynamics of the various types of enhancements and their rationale in a theoretical ecological perspective. As a result of the emphasis on the "aquaculture" attributes only rarely population interactions and other ecosystem effects are studied (De Silva 2003, Costa-Pierce and Soemarwoto 1990). Even though valuable insights can be gleaned from them (e.g. Hasan, et al. 1999, Haque et al. 1999), impacts of enhancements on ecological interactions are mostly studied on a trial-and-error basis. Learning will proceed from the experimental management stage only by linking culture based practices to ecological and population dynamics theory and through a meta-analysis of experimental data (Lorentzen et al. 2001). In this review the dynamic aspect of natural productivity of lakes and reservoirs will be emphasized as this is important in riverine lake systems and in particular in African systems. Concepts developed for floodplain and riverine systems, will be useful in thinking about the limits and dynamics of natural productivity in lakes and reservoirs and with that about the potentials to enhance production.

We will start with a short description of developments in freshwater fish production in the world, and make some initial generalisations on production in relation to size of systems and fisheries activities. In a vast literature, size or area is mentioned as one of the static morphometric features of a system to which production often is related. Next we will discuss some of the ecological principles of natural production, on the basis of physical and biological characteristics of freshwaters and their fish communities and use this discussion to generalise on the basis of freshwater fish productivity. From there we will move into a discussion on how productivity is regulated in constant and fluctuating environments, and how different types of mortality influence fish community structure. These principles are fundamental to address ways to optimize capture fisheries in different multi-species environment, without causing internal structural changes. The theoretical characterisations subsequently will be used to discuss potentials to manipulate productivity through the various enhancement technologies mentioned. Lastly we will make some remarks on management and consequences in changes of management of freshwater systems from a biological perspective and give research recommendations.

2. Production, size and area: extent of coverage for fisheries activities and yields

Freshwater fish production in lakes and reservoirs

Most of the countries with important inland capture fisheries are in Asia and Africa producing respectively 5.8 and 2.1 million ton[3]. The top 20 countries in inland capture fisheries production

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[3] The data used in this section are taken from FAO reports (FAO 2003, SOFIA 2002, 2004) and have their basis in the statistical reporting by the various countries to the FAO. SOFIA (2004) says the following about these data: "It should be noted (…) that reporting of global inland fisheries production continues to present problems owing to the lack of reliable information on catch quantities and species composition. In many countries, catches by rural communities, who are often the main users of the resource, are not reported in national statistics. Accordingly, the figures on total catch provided (…) should be considered indicative." Calculations based on human consumption and estimates from incidental surveys invariably confirm this statement. Some examples taken from the literature (see also

account for 84% of the global production: of these 10 are in Asia and 7 in Africa[4]. But on a per capita basis the importance of inland captures shifts from Asia to Africa. The top 20 then contains 13 African countries and only 4 from Asia, although Cambodia has the highest per capita of inland capture fisheries with 28.2 kg exceeding Chad, second in place, by a factor of more than three. Inland capture fisheries are particularly important in African land locked countries (Chad, Uganda, Mali, Zambia, Central African Republic, Malawi) with a range from 3.3 to 9.7 kg per capita (FAO 2003a). Inland capture data are not separated by type of water body, but refer to all rivers, lakes and reservoirs. Tropical lake fisheries are mainly important in Africa, though the continent has its share of large river systems as the Nile, Niger, and Congo etc. Actual figures are very difficult to obtain, and many lakes and reservoirs are part of large river systems (e.g. Lakes Bangweulu and Mweru are part of the Luapula river system which is the easternmost part of the Congo river basin; Lakes Kariba and Cahora Basa are part of the Zambezi river system). Of the total catch estimates of Zambia, Tanzania, Zimbabwe and Malawi, all countries with large lake fisheries, between 60-80% of the reported catch comes from their lakes (Jul-Larsen et al. 2003). A rough estimate for the continent would be that around 50% of the reported catch could come from lakes and reservoirs. Asian and South American inland fisheries used to be almost exclusively river fisheries, but both continents have a growing number of reservoirs that are important to capture fisheries. Coates (2002) has reviewed the problems with obtaining catch estimates from riverine systems (see footnote 3) and in general catch estimates are more easily obtained from lakes and reservoirs. Again a rough estimate could be that in Asia around half of the reported catches to FAO are from reservoirs. This in all probability and overestimate as actual catches from riverine fisheries are in far in excess of what is currently reported[5].

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http://www.oceansatlas.org/world_fisheries_and_aquaculture/html/resources/capture/swir/capture_statistics.htm) and own experience are:

- Brazil reported an inland capture of about 193,000 tonnes from all of its waters for 1991, but an independent estimate for the same year based on human population and fish consumption rates suggests about 319,000 tonnes for the Amazon Basin portion of Brazil alone (Bayley, 1998);
- Ghana's inland waters are dominated by Lake Volta (8,000 km^2). Ghana reported a capture from all of its inland waters of from 55,000 to 74,000 tonnes in recent years, but based on a partial frame survey, total production of Lake Volta alone is more likely to be around 150,000 to 200,000 tonnes per year (De Graaf and Ofori-Danson, 1997);
- Zambia reports a long term average total catch of 8,350 ton for its part of Lake Mweru but omits in its surveys an important light fishery on the clupeid *Microthrissa moeruensis* that is estimated to produce between 25,000 to 40,000 ton alone (van Zwieten et al. 2003);
- Cambodia has reported inland capture ranging from about 50,000 tonnes to 75,000 tonnes for the years 1984-1997; however, the actual range for the years 1994 to 1997 has been estimated based on human consumption at from 290,000 to 430,000 tonnes (van Zalinge et al. 1998);
- Inland capture fisheries are clearly seriously under-reported in Indonesia, Malaysia, Myanmar, Philippines, Cambodia, Lao PDR and Viet Nam according to a review by Coates (2002). The discrepancy between officially reported catches (where available) and estimates based upon independent scientifically based surveys (i.e. collection of actual data) varies by a factor of between 4.2 and 21.4. Overall, for all the countries combined, the total reported production from inland waters appears to be under-estimated by a factor of between at least 2.5 and 3.6

As these examples suggest, and on the basis of anecdotal information from other sources actual catches in inland fisheries will be at least between two (Coates 1995, Welcomme 1997) to four (Coates 2002) times as high as the data submitted to FAO by inland fishing countries suggest, and sometimes even higher.

[4] South America and Europe are good for 0.3 million ton each, while the remainder of the world produces 0.52 m ton (FAO 2003a) (but see note 3!)

[5] The difficulty of estimating the relative contribution of rivers and reservoirs can be shown as follows: considering a very moderate fishery production of 50 kg/ha/year for an average 45 km^2 Asian large reservoir and a total estimated Asian large reservoir area of around 1.38 million km^2 then would already yield an annual production of 6.9 million ton. This estimate is almost 20% higher than the reported catch to FAO and excludes all production from rivers and small reservoirs (see also figure 5 and table 3 for a justification of the production and area estimates).

Inland aquaculture production is dominated by finfish and currently provides 73.7% of total global landings of freshwater finfish species, with a growth rate of 9.9% over the period 1970 -2000. Cultured freshwater fish production is dominated by Asia. Africa is often considered a sleeping giant when it comes to aquaculture potential but has at present only a limited total production (FAO 2003b). The potential for further increase in production from various culture based systems is sometimes said to be high. Townsley (1992) estimated the potential production for small water bodies in Sub-Saharan Africa alone at around 1 million ton per year. And in Asia are an estimated 66 million ha of small water bodies suitable for culture-based fisheries (FAO 1999). De Silva (2003) estimated that with a 5% usage of this acreage for culture-based fisheries development at production levels comparable to those obtained in China a yield of 2.5 million ton over the next ten years should be possible. However, this optimistic estimate is based on very high production estimates from Chinese cage and pen cultures that may not always be attainable elsewhere. Furthermore, the particular approach to culture based fishery enhancements in China rely on constructing communities of selected species - usually indigenous carp species -, eutrophication by application of (in)organic fertilisers and other strong modifications of natural environments, interventions that may not be feasible or even acceptable in many places over the world. However, the example does show that already in Asia alone a significant boost to inland fish production could be expected from judicious use of available enhancement techniques.

Reservoirs: area, impacts and trade-offs

The total global reservoir area is unknown, but in 2000 the World Commission on Dams counted approximately 48000 large dams, 46% of which are in China and 19% in the rest of Asia; 3% in Africa (60% of which in South-Africa and Zimbabwe) and 2% in South-America (Table 3). The average size of a reservoir is almost the same in Africa compared to Asia. The total reservoir area in front of large dams in Africa was around 54600 km^2 which is about the 1.7 times the size of Lake Tanganyika and 80% the size of Lake Victoria. Compare this to the 1.4 million km^2 in Asia which is a bit more than half the size of the Mediterranean or almost 2.5 times the size of the North Sea. Globally the trend is to build fewer and smaller reservoirs (Kapetsky 1998, WCD 2000)[6].

Impacts of reservoirs on ecosystems are classified as first, second and third order impacts respectively involving (1) physical, chemical, geomorphological alterations including alterations of the streamflow; (2) changes in primary biological productivity of ecosystems including effects on riverine, riparian and downstream wetland habitats and (3) alterations on fauna (e.g. fish) caused by first or second order effects. The World Commission on Dams has summarised these impacts in their report (World Commission on Dams, 2000) and in a series of thematic reviews among others on ecosystem functions and environmental restoration (Bergkamp at al. 2000)[7]. Downstream and upstream impacts on riverine, estuarine and marine fisheries as a result of blockage of migratory routes, reduced sediment and nutrient flow and altered flood regimes are generally negative. Substantial losses in production have been reported from around the world both in upstream reaches where fisheries are dependent on migrations - e.g. the Port Primavera dam in the Rio Paraná, Brazil diminished upstream fish catches based on migratory species by 80% (WCD 2000) - and downstream. In particular, where altered hydrology limits or removes normal, historical downstream flooding, overall fisheries productivity throughout the system can be impacted negatively (Holcik and Bastl 1977, Welcomme 1976, 1985, 1986, Junk et al. 1989, Sagua 1997). Cumulative effects of dams can significantly block nutrient flow through the ecosystem, affecting fisheries in downstream reservoirs, river channels and estuaries. Water quality parameters recover only slowly when water is released from a dam. Oxygen levels may recover within a kilometre or two, while temperature changes may still exist 100 km downstream. Where the distance between dams does not allow recovery to natural levels, the biology of many hundreds of kilometres of river may be affected by a series of dams. On the Columbia River, the cumulative impact of an additional dam on salmon migrations is significant. It is estimated that 5–14% of the adult salmon are killed at each of the eight

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[6] See also: http://www.worldbank.org/html/extdr/pb/dams/factsheet.htm
[7] See also: http://www.dams.org/kbase/thematic/

large dams they pass while swimming up the river (WCD 2000, op.cit.). Eley and Watkins (1991) also found that 90% of young salmon are lost on the downstream run, mainly, because the ladders of the hydroelectric dam were designed to let adult salmon move upstream and did not allow for the return journey. Instead of being carried downstream by the natural current, the juvenile salmon more often get mutilated in unscreened generating equipment, get trapped inadequately designed screens, or languish in reservoirs until they die from predation, heat, or disease.

Table 3. The number and distribution of the world's reservoirs.

Continent	**World Estimate of Large Dams**[a]			**Number of large reservoirs**[c]	**Storage capacity of large reservoirs (km^3)**
	Number[b]	**Average area (km^2)**	**Avg. capacity (km^3)**		
Africa	1 269	43	883	176	1 000
Asia	31 340	44	268	815	1 980
Oceania	577	17	205	89[d]	95 [d]
Europe	5 480	7	70	576	645
North and Central America	8 010[e]	13	998	915	1 692
South America	979	30	1 011	265	972
Total world	25 420 ~ 48 000	23	269		
Total registered by ICOLD	25 420			2 836	6 385

Sources: WCD 2000, ICOLD 1998, Avakyan and Iakovleva 1998.

a According to the International Commission on Large Dams (ICOLD 1998), a large dam is 15 m or more high (from the foundation). If dams are between 5-15 metres and have a reservoir volume of more than 3 million cubic metres they are also classified as large dams.

b Based on World Commission on Dams (2000). Their primary source is ICOLD (1998) that lists the much lower figure mentioned. Reporting depends on member countries, but the ICOLD list is partial as member countries reported 41413 dams in 1996. WCD discusses the discrepancies. The main issue is the underreporting of dams in China. A reservoir may have more than one dam!

c Those with a volume of 0.1 km^3 or more, according to ICOLD 1998

d Includes only Australia and New Zealand

e 80% of which are in the USA

On the other hand productive reservoir fisheries may follow dam construction (examples can be found in Bergkamp et al. 2000). Few predictive or *post-hoc* studies have been made on the trade-offs between down- and upstream riverine and reservoir fisheries production. Oftentimes this is not at all possible as baseline data are either absent or unreliable. However, the overall direction of impacts seems negative. Compensation for loss in yield from river fisheries can be difficult to achieve through development of reservoir fisheries (G. Marmulla in: FAO 2003a). Some generalisations on the impacts of the position of a reservoir in a river system with respect to floodplain and delta fisheries can be made on the degree to which the reservoir replaces or exceeds the natural river fishery (Jackson and Marmulla 2000). These authors claim that (1) lowland dams have more impact on fisheries than highland dams; (2) beneficial reservoir fisheries exist in drier regions where they are constructed for agricultural purposes; and (3) benefits seem more pronounced for smaller, shallower reservoirs that have reasonably high concentrations of dissolved solids and that are located in the upper reaches of a river ecosystem. Thus, the larger the river and the more downstream the location of the dam the less potential there is to compensate in terms of yield for losses sustained by river fisheries. Compensation potentials apparently are higher in shallower reservoirs in tropical regions than they are in deeper reservoirs in more northern latitudes.

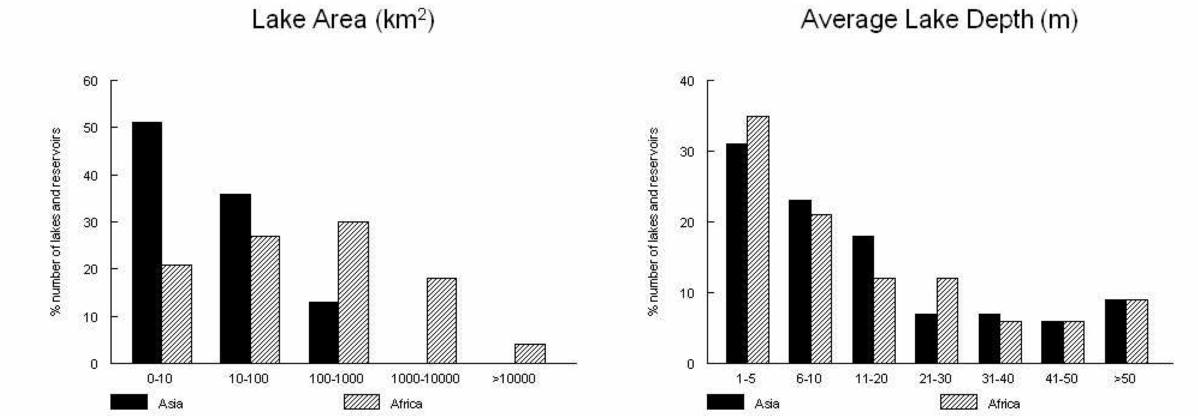

Figure 2. A comparison of size and depth distributions of Asian and African lakes supporting inland fisheries. Data from Asia are from the Thailand, Laos, Cambodia, Vietnam, Malaysia, Singapore, Indonesia, Philippines and Sri Lanka and represent a data set of 93 lakes and 149 reservoirs. From 163 of these the average depth was known; the data from Africa represent71 lakes and reservoirs (39 with average depth). Data from Asia are from Verdegem (1999) supplemented by data from Bernacsek (1995); data for Africa are from Crul (1992).The data from Sri Lanka do not include the 15,000 or so non-perennial reservoirs of <60 ha (De Silva 2003).

Productivity of lakes and reservoirs in Africa, Asia and South America

Natural lakes in the tropics are rare except for Africa where they are mainly found in the Rift Valley and in the vast basin of the Congo river (Payne 1986, Fernando and Holčik 1991) In contrast Asia and South America possess few natural lakes. The list of 242 lakes and reservoirs from nine ASEAN countries on which figure 2 is based contains 59 natural lakes in the Philippines and 14 in Indonesia, while a compilation for Africa of 71waterbodies only had 18 reservoirs. Based on total water surface alone Africa seems to have large potential for enhancements. However, the dominant productivity characteristic for African fisheries and hence their potential for enhancements is annual variability. Systems with large seasonal and inter-annual fluctuations in surface area – swamps, floodplains, shallow lakes and reservoirs – account for 57% of the total water surface area (Kapetsky 1998), but also in larger more stable systems climate driven fluctuations in productivity are dominant (Jul-Larsen et al. 2003, van Zwieten et al. 2002, Verburg et al. 2003).

The size and size range of African lakes and reservoirs are both markedly larger compared to the Asian waterbodies (Figure 2, left panel). According to Duncan (1999) this could account for the reported “underfishing” from many African lakes compared to the sometimes extremely high fishing intensities and “overfishing” from Asian lakes. The fished waterbodies in the eight Asian countries are similar in size range and all are rather small. Thus, a more complete coverage of the fishable biomass with artisanal methods is more likely in smaller than in larger lakes: the fairly recent development of fisheries on small pelagics in many African lakes attests to this phenomenon. Mean depths of the fished lakes and reservoirs have a wide range for both the Asian and African water bodies (Figure 2, right panel). Deep water is more difficult to fish efficiently with small scale artisanal methods: low levels of yields per fishermen in Thailand could be partially explained by its higher proportion of deep waterbodies and absence of lakes of less than 5 m depth, which is the most frequent depth class in African lakes, in the Philippines and in Sri Lanka (Duncan 1999 and Figure 3).

Annual yields per fishermen related to fishing intensity expressed as the density of fishermen are markedly different between Asian and African countries. On average African artisanal fishermen produce between 2000 and 3000 kg per year (Fig. 4), but Crul (1992) gives a very wide range from 525 to 12,975 kg per fishermen per year, with only 10% of the fisheries having densities of more then 5 fishermen per km^2. The Asian freshwater fisheries in the ASEAN list show an even wider range of production of between 296 and ~11,000 kg per fishermen. More than 61% of these fisheries have more than 5 fishermen per km^2 and attain a much lower annual average catch per fisherman: in

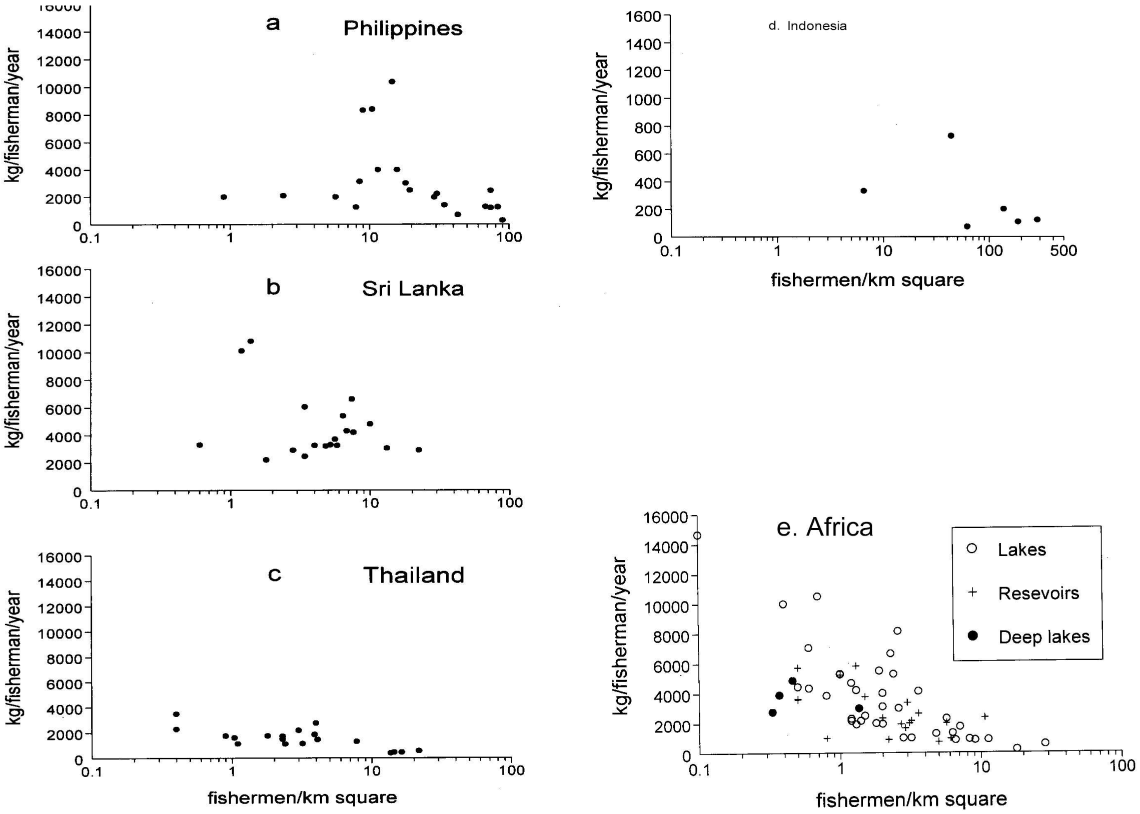

Figure 3. Relationship between annual yield per fisherman and fishing intensity in A: Philippine inland fisheries. B: Sri Lankan inland fisheries. C: Thai Inland fisheries. D: Indonesian inland fisheries and E: African inland fisheries. Data from Moreau and De Silva (1991), Balayut (1993) and Crul (1992). Figures taken from Duncan 1999.

Indonesia < 731 kg/fisherman and in the Philippines 296 – 2461 kg/fisherman). Thai reservoirs equally have a low production per fishermen most likely because of the low productivity of the reservoirs as well as the low fishing technology (Costa-Pierce and Soemarwoto 1990). Low fishing technology, however, is not a particular feature for reservoirs but is a more general trait of small-scale fisheries in throughout the world[8]. Maintaining the production in many of the Asian reservoirs is done through stocking, in particular with the highly successful exotic *Oreochromis* species. Thus the Asian inland fisheries are fished more intensively and produce a lower annual yield per fisherman than inland fisheries of Africa. The same applies to the Asian pelagic fisheries of lakes and reservoirs (Duncan 1999).

Generalisations of capture fish production per water surface area are difficult to make because of the paucity of data on water surface area in many countries that are neither comprehensively nor comparably available! An indication of the variety in production from a range of waterbodies is available from selected studies (see also: Jackson and Marmulla 2000). Productive reservoir fisheries have developed in small reservoirs in Africa with yields of up to 329 kg $ha^{-1}year^{-1}$, in Latin America and the Caribbean with yields up to 125 kg $ha^{-1}year^{-1}$ and in Asia with yields up to 650 kg. $ha^{-1}year^{-1}$ (SOFIA 2002). These data are difficult to compare as yield generally appears not to be proportionally related to the size of a lake. However, a direct comparison between the productivity of the various lakes and reservoirs in Asian, African and South America is possible when calculating annual yields for a hypothetical 1000 ha lake based on log-log regressions of yield and lake area (Fig. 5). This

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[8] It is possible that this is the only way in which these fisheries can survive given the high diversity in species and habitats and general large variability in annual outcome of these fisheries. In Africa investments in more developed and efficient technologies generally have failed for a number of reasons including the biological characteristics just mentioned (Jul-Larsen et al., 2003; SOFIA, 2004)

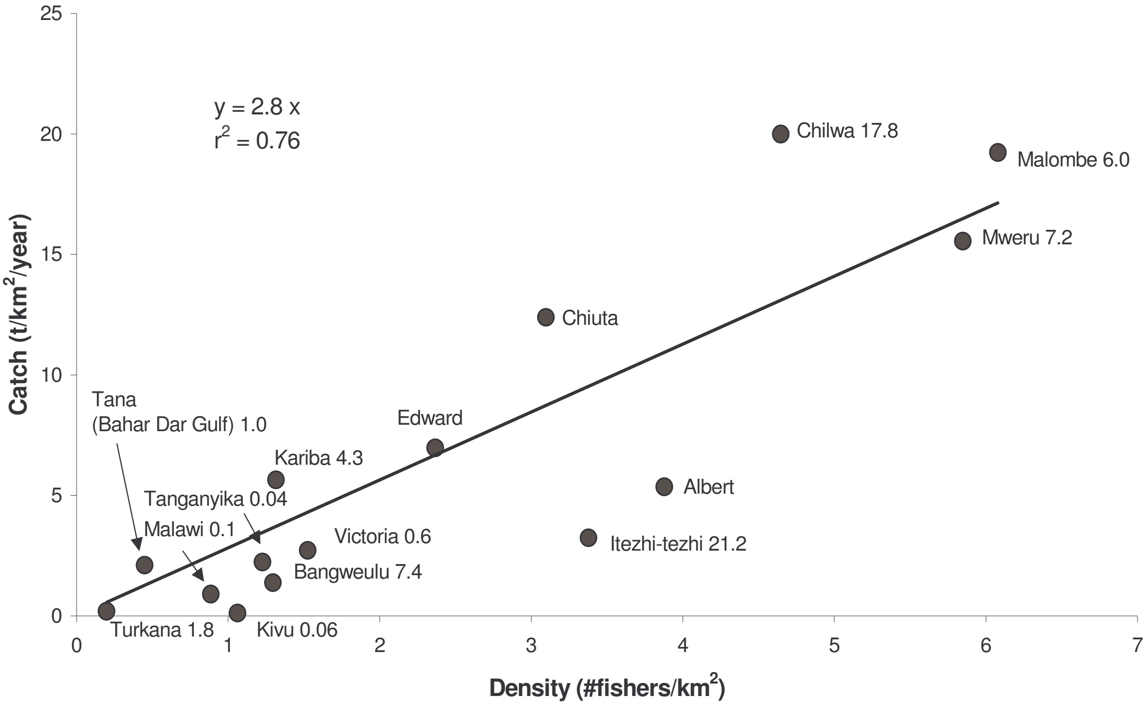


*Figure 4. Catch rates plotted versus effort density in 15 African lakes (data from the period 1989-92). The trend line indicates an average yield of about 3 tons per fisher per year irrespective of water body and country. The number behind 12 of the lakes is the system 'stability' index in terms of relative lake level fluctuations (RLLF= mean annual lake level amplitude/mean depth*100). Excluding Itezhi-tezhi, and Tana the explained variation between annual catch rates (t/fisher) and RLLF is 45%. (Modified from Jul-Larsen et al. 2003, SOFIA 2004)*

analysis of a selection of water bodies in ASEAN countries for which information was available gave estimates of annual yields of 365 kg ha^{-1} for Philippine lakes, 239 kg.ha^{-1} for Sri Lankan reservoirs, 79 kg.ha^{-1} for Chinese reservoirs, 74 kg.ha^{-1} for Thai reservoirs and 65 kg.ha^{-1} for Indonesian reservoirs (Densen et al. 1999). Similar regressions for South American reservoirs gave annual yields for a 1000 ha reservoir of 144 kg ha^{-1} and for Mexico of 234 kg.ha^{-1}. By comparison a hypothetical African lake of 1000 ha would, according to the log-log regression over 14 lakes with yield data from the late 1980-ies, produce 316 kg.ha^{-1}. This confirms Duncan's (1999) conjecture that the often mentioned "underfishing" in the African lake fisheries production is merely a function of their large size (Fig. 2). Only in Philippines the catch increased proportionally with size of water body, whereas in China, Thailand and Cuba and in the African lakes the Catch per Unit Area decreased significantly with an increase in lake area. In contrast, a set of small reservoirs in various South American countries encompassing very small ponds and reservoirs with high stocking densities, showed a significant increase in yield per unit area with water body size (Fig. 5, Quirós 1998).

In the previous analysis the Chinese average may not be representative while during the period 1980 – 1988 the Catch per Unit Area from all reservoirs increased from 85 to 215 kg.ha^{-1}: an annual increase of 12% unaccounted for by changes in effort for which no data are available! In 1995 yields were reported of 45 – 750 kg.ha^{-1} in medium sized (60 – 670 ha) reservoirs (Li and Xu 1995), while small reservoirs of less than 70 ha could produce up to 3000 kg.ha^{-1}. Despite these high growth rates and despite that all reservoirs are stocked, many medium sized Chinese reservoirs do not seem to be very productive as our analysis of a hypothetical 1000 ha lake shows.

In contrast medium sized Sri-Lankan reservoirs are highly productive, with catches sometimes well above 200 kg.ha^{-1}yr^{-1}. The catch is dominated by the introduced tilapia which is produced without

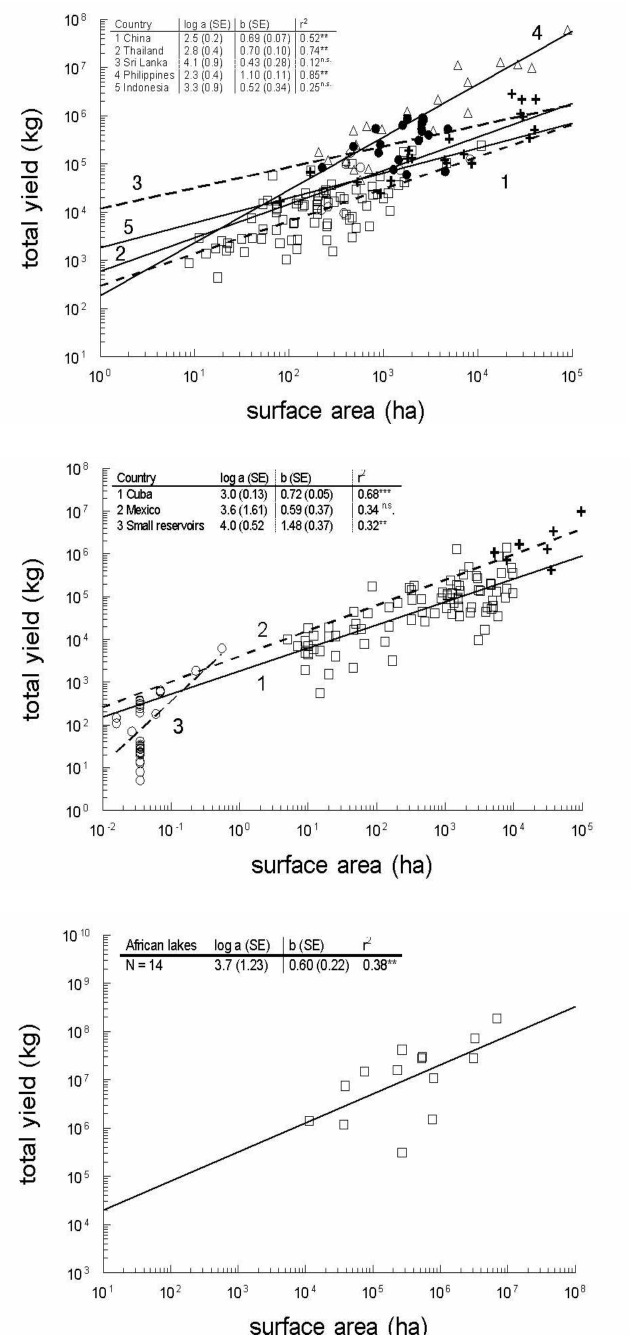


Figure 5. Top: Plot of total catch (C) on surface area (A) for 1. (open squares) 83 reservoirs in China of 9 – 10,824 ha (De Silva et al. 1992); 2. (crosses) 20 reservoirs in Thailand (1,280 – 41,000 ha); 3. (dots) 19 reservoirs in Sri Lanka (225 – 7,825 ha); (triangles) 17 Philippine lakes (206 – 90000 ha including Laguna de Bay) (Moreau and De Silva 1991) and 5. (open circles) 9 reservoirs in Indonesia (Hardjamulia and Suwignyo 1988). Plot redrawn from van Densen et al. 1999. Middle: Plot of total yield on surface area for 1. (open squares) 86 reservoirs in Cuba (5 – 7,945 ha) 2. (crosses) 7 reservoirs in Mexico (5,200 – 96,000 ha) 3. 31 small reservoirs in Brazil, 1 in Peru, 1 in Costa Rica, 4 in Others (0.016 - 0.07 ha). Data from Quirós 1998. Bottom: Plot of total catch on surface area for 14 African lakes and reservoirs (11, 300 - 6, 880, 000 ha). Data from van den Bossche and Bernacsek (1990) and Bayley (1988). All regressions are according to:
$^{10}\log Y_{ij} = {}^{10}\log a + b.{}^{10}\log S_i + \varepsilon_{ij}$ *, where* Y_{ij} *= total yield (kg),* S_j*= area (ha), log a = intercept and b = slope. SE = the standard error,* r^2 *= proportion of explained variation, n.s.= not significant = p>0.05, ** = p<0.01, ***=p<0.001.*

supplementary stocking. In India reservoirs yield an average of 20 kg.ha^{-1} which seems to be far below the potential. Even a moderate increase of 100 kg.ha^{-1} for small and 50 kg.ha^{-1} for medium and large reservoirs could provide an additional 170,000 t of fish in the sub-continent (Sugunan 1995). Mexican medium sized and large reservoirs, though classified as 'extensively used' by Quirós (1998), appear as productive as the smaller Sri-Lankan reservoirs. This may be explained as supplemental stocking with native and introduced fish species is a usual practice to manage large water bodies and medium-sized and small reservoirs in Mexico, though this needs to be confirmed.

In general many – smaller - reservoirs are thought to have substantial potential for fishery enhancements using a range of technologies. For example in China the use of "cove culture" in the water inlets to reservoirs is reported to bring productivity up to the level of pond aquaculture with its astonishing range in productivity of approximately 4500-7500 kg.ha^{-1} (Li 1994), which is in the range of intensive culture systems. Cage culture may also be used to increase production. First developed in China cage cultures are now operated in an increasing number of countries and a large variety of habitats. It is often viewed as a means of increasing aquaculture potential without using scarce land resources, as well as a way of compensating for loss of agricultural land under reservoirs. The full range of enhancement technologies, including cages- has been estimated to potentially increase freshwater yields by up to 20 percent (Lorentzen *et al*. 2001).

Fundamentally, the productivity of natural lakes and of artificial reservoirs follows the same basic ecological principles and limnological processes that will be outlined below. There are however, both some physical (Table 4) and perhaps societal differences in terms of management. While the physical differences will have some impact on the natural productivity, particularly the generally higher hydrodynamic variability in reservoirs (discussed below), the societal differences have normative cultural and political overtones. It is an open question whether we, man, can alter and modify to our own desire an ecosystem we ourselves have originally created. In other words, since reservoirs all are man-made and artificial, should we then apply the same aesthetic and conservation principles to their ecological management, as we would do for a natural lake? We will not answer this question here, as there are no general answers and it often is a matter of choice. But it is obvious that any individual political decision can have profound effects on the potential productivity of a dam in terms of appropriate enhancement methods.

Table 3. Comparison of the characteristics of dam reservoirs and stratified lakes. Modified from Straškraba 1996.

Characteristics	**Lakes**	**Reservoirs**
Qualitative (absolute) difference		
Nature	natural	man-made
Geological age	old	young
Aging	slow	rapid (first few years)
Formed by	depressions	river valleys
Shape	regular	dendritic
Shore development ratio	low	high
Maximum depth	near centre	extreme (at the dam)
Bottom sediments	autochthonous	allochthonous
Gradients	wind-driven	flow-driven
Outlet	surface/none	deep
Quantitative (relative) difference		
Ratio watershed/lake area	low	high
Retention time	high	Low
Coupling with watershed	less	great
Morphometry	U-shaped	V-shaped
Level fluctuations	Less	great
Hydrodynamics	more regular	highly variable
Cause of pulses	Natural	man-made drawdowns

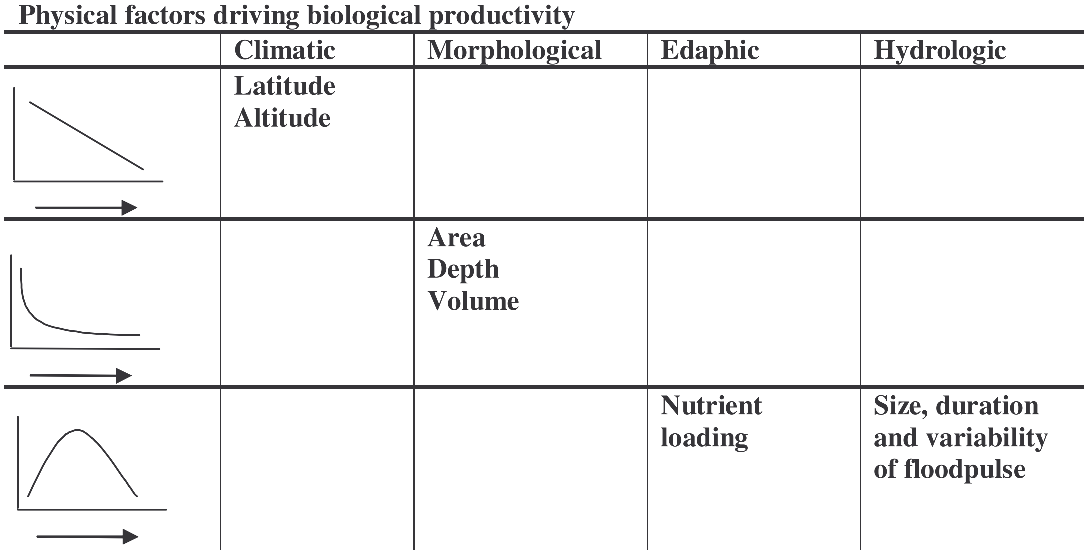
Before discussing the various possibilities for enhancement we will now discuss the physical and biological basis for lake and reservoir productivity.

3. The physical base for productivity

Understanding the basis for the observed high productivity in tropical freshwaters is fundamental for evaluating the potential for increase in production through enhancements. All biological production is fundamentally based on the rate of photosynthesis, with three main limiting constraints: temperature, light, and nutrients. Availability of, and interaction between energy and nutrients, are the primary constraints on a fish production system (Ryder 1978). As temperature and light regimes, everything else being equal, are relatively constant function of latitude and altitude, the most dynamic variable is the generation, addition or cycling of primary nutrients. For these processes the most important parameters are the climatic and edaphic (i.e. soil and substratum) features of the environment.

Climatic factors

Latitude is perhaps the most important physical parameter for classifying a freshwater system and to determine its potential productivity (Lewis 1987, 1996). Latitude determines the climatic conditions, which again controls variables such as temperature, light, wind and precipitation[9]. All these play a major role in the nutrient cycles and hence the regeneration of biomass. Firstly, the combination of high annual insolation and low seasonal variation at low latitudes, creates aquatic systems with corresponding high temperatures with low seasonal variability, i.e. the difference between annual minimum and maximum temperatures are small (Straškraba 1980, Lewis 1987, 1996). This again creates relatively warm and homogenous water column temperatures, which reduces the formation of density layers and thus potential stratification. As a result, tropical lakes are characterised by much higher instability and susceptibility to wind-induced mixing. Most tropical lakes and reservoirs are polymictic or monomictic with a relatively short stratification period. Some, even the deep Lake Turkana, rarely stratify. Shallow tropical lakes, due to the high daily heat uptake, will have a strong



Physical factors driving biological productivity

	Climatic	**Morphological**	**Edaphic**	**Hydrologic**
	Latitude **Altitude**			
		Area **Depth** **Volume**		
			Nutrient loading	**Size, duration and variability of floodpulse**

Figure 6. Generalised effects of climatic, morphological, edaphic, and hydrological factors (X-axis) on productivity (Y-axis). See text for further explanation

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[9] In the present context latitude and altitude are considered synonymous representing more or less the same climatic conditions, except daylight. High altitude alpine lakes within the tropics, such as Lake Titicaca (3800 m.a.s.l.) or Asian cold water lakes (Petr 1999, Petr and Swar 2002), has therefore not been included in this review.

tendency to develop diurnal stratification and mixing, which may be extremely important to their metabolism (Lewis 1987). The high temperatures combined with recurrent mixing and re-circulation of nutrients result in elevated primary production rates in tropical aquatic environments.

Upwelling phenomena are found in all of the deep rift valley lakes Turkana, Tanganyika and Malawi (Kolding 1989, Coulter 1991, Menz 1995,Verburg et al. 2003). Seasonal trade winds along the length axis cause large scale oscillations of the thermocline. With that nutrient rich colder waters mix with the epilimnion. The result is a seasonal change in productivity that is translated into fish biomass. Increase in water temperature and a decrease in wind velocity as a result of climate change contributed to a reduced primary productivity in Lake Tanganyika resulting in a decrease of pelagic yields of up to 30% (Verburg et al. 2003).

Edaphic factors

The edaphic conditions determine the chemical composition of the soil in the surrounding watershed, and thus the supply of nutrients and trace elements for organic synthesis (Ryder 1978). Highly fertile zones are usually associated with fluvial deposits or previously submerged land, whereas relatively infertile zones are mainly associated with old pre-Cambrian bedrock formation. Lateritic substrates (the typical tropical red soil containing alumina and iron oxides, but little silica) are relatively rich, but subject to rapid leaching and nutrient losses (Payne 1986). Lakes and reservoirs are supplied with nutrients largely through their inflowing rivers, and partly from rainwater. Typically, the nutrients tend to accumulate in the water basins due to evaporation, biological activities, and sediment interaction. The average conductivity in lake Kariba, for example, is nearly twice as high as the inflowing Zambezi which contributes about 80% of its water (Karenge and Kolding 1995a). In tropical rivers, the most frequent major ions are sodium (Na^+) and bicarbonate ($HCO3^-$) mainly due to flow through alkaline volcanic areas, although Calcium (Ca^+) can be the dominant cation when sedimentary rock is present within the catchment area (Payne 1986). In arid area lakes with closed basins, where evaporation exceeds inflow and precipitation over the long term, saline conditions are created. Lake Turkana, for example, the fourth biggest African lake, with its present content of 2.44 g/l dissolved solids (Kolding 1989) lies close to the definition by Williams (1981) of truly saline lakes, containing an excess of 3 g/l of total dissolved solids.

Nitrogen (NO_3^- -N) and Phosphorus (PO_4^- -P) are the two most important limiting plant nutrients, with a theoretical basic N:P ratio in phytoplankton of 7:1 (the Redfield ratio). In general for tropical lakes, however, phosphorous concentrations are usually high (when volcanic rock is present) and nitrogen concentrations are low, less than 30 µg/l due to the very high biological turnover in the warm and sunny climate (Talling and Talling 1965, Payne 1986, Wood and Talling 1988, Talling 1992). The often high abundance of nitrogen fixers (heterocystous blue-green algae) in many tropical waters also suggests nitrogen deficiency, and, in general, due to rapid oxygen deficiencies and ensuing denitrification, tropical lakes appear more inclined to nitrogen limitation rather than phosphorous limitation (Talling and Talling 1965, Payne 1986, Lewis 1996, 2002) in contrast to temperate waters. Still, although inorganic nitrogen and phosphorous usually are present in negligible, often undetectable quantities, high-sustained production, in the presence of such nutrient depletion, is also a typical feature for tropical freshwaters (Payne 1986, Lewis 1996). This indicates very efficient recycling pathways, with rapid overturn, and tropical waters are generally considered more efficient in primary productivity, on a given nutrient base, than temperate lakes (Lewis 1996).

Morphological factors

The morphology of a lake or reservoir, particularly area, volume, depth, and shoreline development or gradient, is of major importance to the productivity (Ryder 1978). The mean depth, as a single morphometric parameter, encapsulates several of these morphological attributes and has been considered as the most important (Rawson 1952, Ryder et al. 1974, Henderson and Welcomme 1974). The mean depth, or the volume to area ratio, determines the energy needed for vertical mixing, and hence the rates of recycling nutrients into the trophogenic production zone. These effects become more extreme in meromictic lakes, such as Lake Tanganyika and Lake Malawi, where the concentrated dissolved solids below the chemocline provide additional resistance to overturn. Such habitats, with permanent pycnoclines (density layers) and anoxic hypolimnion can even function as nutrient sinks. In terms of fish productivity, an anoxic hypolimnion, may cause additional problems than the inhabitability of the bottom itself., It can serve as a refuge for the phantom midge *Chaoborus* which therefore, instead of being prey, can become a major competitor (see section below on the biological base for productivity).

A high shoreline development (the ratio of shore length to the circumference of a circle enclosing the same area as the lake) and/or a low land gradient represent a large littoral zone and a long riparian ecotone (the land-water interface). The ecotone is the most productive part of an aquatic ecosystem because it combines both terrestrial and aquatic processes (Moss 1988, Junk 1996, Zalewski et al. 2001). The changing interlinked set of inorganic chemical and bacterially mediated reactions (solution, oxidization, nitrification, denitrification, etc) as a function of the fluctuating redox potential creates a particular efficient nutrient transfer.

Morphological parameters are conceptually static, as they are difficult to define in fluctuating aquatic environments. In contrast to most temperate lakes with relatively small lake level fluctuations, many tropical flat-land lakes, and particularly the widespread highly productive endorheic, often saline, lakes undergo large variations in their size, depth, and shorelines as a function of water level changes (Nilssen 1984, Moss 1988, Talling 1992, Junk 1996). This feature they share with man-made reservoirs built for hydroelectricity or irrigation, where the annual drawdown often exceeds the mean depth. In such cases, the morphological characteristics used to evaluate potential productivity may be better represented by dynamic indices like the amplitude of water level changes.

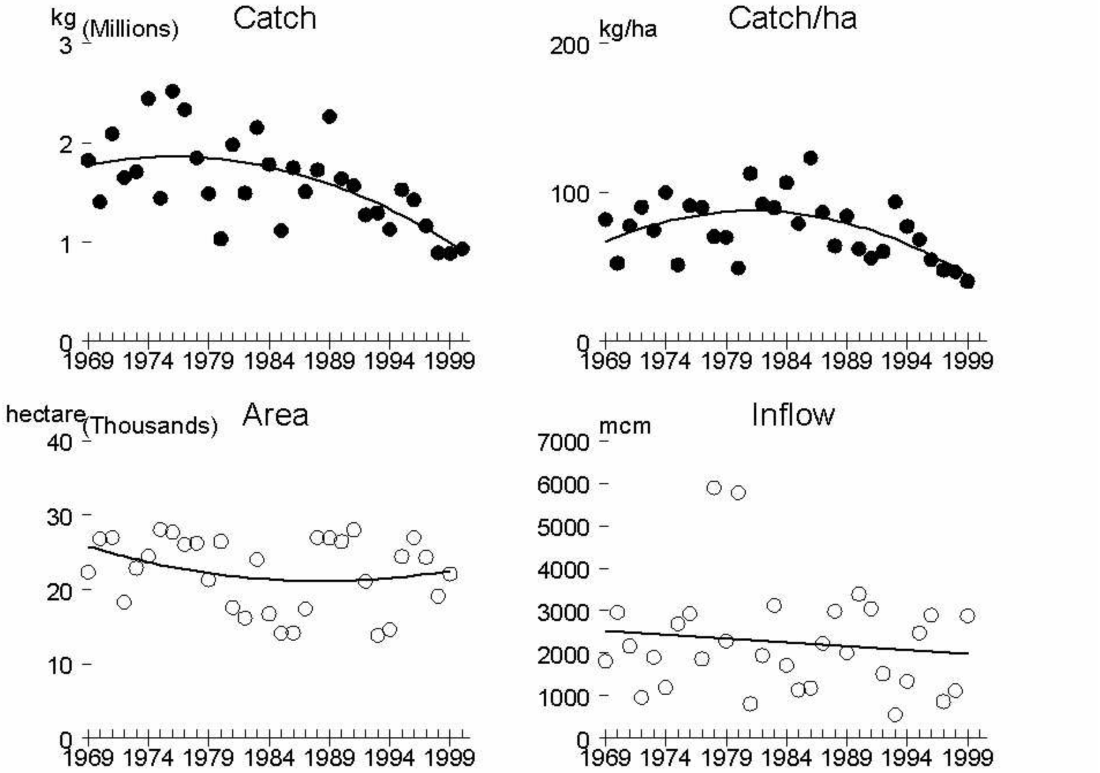

Figure 7. Development of production (catch), productivity (catch/ha) in relation to annual change in area and inflow in Ubolratana reservoir (Thailand) between 1969 and 1999. The graphs show that while area and inflow vary over the years but are stable on a long-term, total catch and productivity, with high inter-annual variability, gradually decline with the age of the reservoir. Though no strong inferences can be made, it is possible that the reservoir is now entering a less productive phase compared to the initial years after inundation (data kindly made available by B. Sricharoendham).

Seasonality and dynamics

Besides latitudinal position, there is no easy single classification of tropical freshwaters. In fact, standing inland waters and reservoirs are perhaps the most diverse of aquatic systems and the variety and extremes of tropical lakes exceed those from temperate climates (Payne 1986). Classification of tropical lakes is traditionally attempted on basis of the water chemistry and conductivity (e.g. Talling and Talling 1965, Rai and Hill 1980), which mostly have a close relationship with productivity (e.g. Ryder et al. 1974, Henderson and Welcomme 1974). Freshwater systems are, however, rarely closed entities and their chemical composition is therefore a function of the hydrological regime and the geological nature of the surrounding catchment area. Schindler (1978) found that external nutrient loading explained most of the variance in phytoplankton production in a global lake review, irrespective of miction pattern and/or latitude (i.e. climatic seasonality). Similarly in tropical waters, with high temperatures and small seasonal variations, temporal biological variability is often prominent and caused mainly by seasonal injections of nutrients (Lowe-McConnell 1979). Nearly all reservoirs and manmade lakes become less fertile some years after inundation as the initial supply of nutrients are washed out or fixed in sediments (Lowe-McConnell 1973, Balon 1974, Petr 1975, 1978, Kolding et al. 2003a, Fig. 7 and 8). This is a major piece of evidence that lakes and reservoirs do not maintain their fertility unless an external loading of nutrients is continually applied (Schindler 1978, Moss 1988, Karenge and Kolding 1995a).

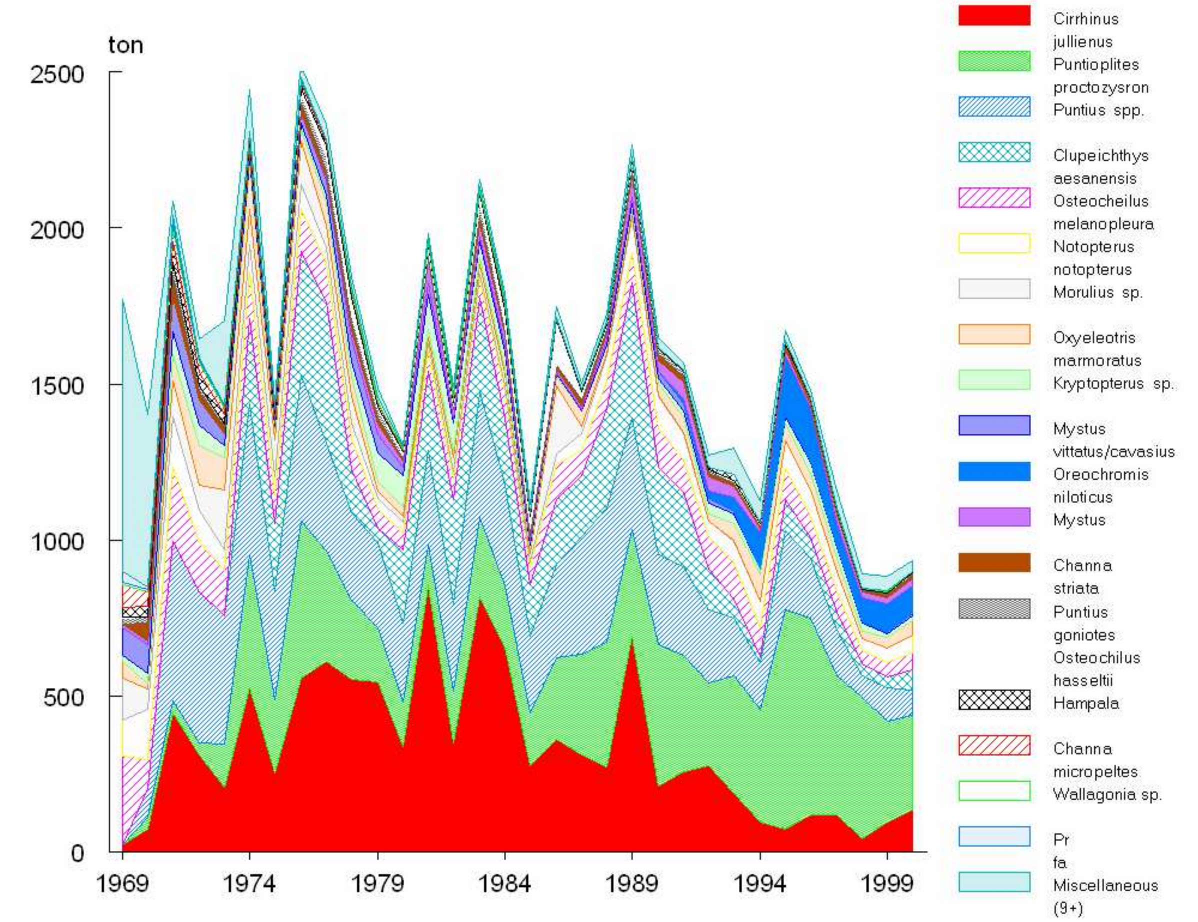

Figure 8. Species change in the catch of Ubolratana reservoir (Thailand). As the reservoir gets older a shift in species composition appears to take place. Similar changes have been observed in other reservoirs (e.g. in Kariba, Karenge and Kolding 1995a, Lowe-McConnell 1999). Note the limited effect of the introduction of Oreochromis niloticus (darkblue) in the late 1980-ies (data kindly made available by B. Sricharoendham).

Hydrological changes – the flood pulse concept:

It has been suggested (Melack 1979) that there are three patterns of periodic changes in the production of tropical lakes; those with pronounced seasonal fluctuations, those with a lower degree of fluctuations and finally those with irregular but abrupt changes. The first category constitutes the majority, although the range of variation in seasonal production is mostly smaller than that observed in temperate waters. In these systems it is the recurrent vertical mixing of the water masses (the miction pattern) driven by the wind regimes and the resulting periodic establishment and destruction of thermoclines that governs the recycling of nutrients and hence the production rates. Lake Victoria, Tanganyika and Malawi are examples of such lakes in East Africa. There are, however, waters in which production is dominated by changes in the hydrological regimes and among these are lakes and reservoirs intimately associated with rivers (Payne 1986, Talling 1986). Although stratification may also play a part in the annual cycle, the enhanced nutrient conditions are predominantly dependent on the inflowing, 'allochthonous', material and subsequently the phytoplankton blooms are closely connected with the annual floods. Under such conditions the whole biology of the fishes is geared to the flood cycle (Lowe-McConnell 1987). Rai (1978) has suggested the term 'allotrophic' for systems where the oscillations between the extremes of production are controlled by the hydrological regime. Even large lakes in Africa such as endorheic Lake Turkana, exorheic Lake Mweru and man-made Lake Kariba are examples of such systems (Kolding 1994).

This strongly suggests that nutrient inputs from rivers and the flooded marginal areas are very important in stimulating fish production in lakes and reservoirs. When lake level rises terrestrial vegetation is submerged and nutrients leaching from decomposing organic matter (dung, terrestrial grass, shrubs and trees) and directly from rivers, result in increased plankton and fish production (McLachlan 1970, 1974, Marshall 1982, Talling 1992, Allanson et al. 1990, Kolding 1993b, Karenge and Kolding 1995b). Flooding of the marginal areas and increased river flow result in better spawning conditions, especially for potamodromous species, and excellent conditions for growth and survival of juveniles of inshore fish species. For most tropical freshwater fish species the dominant breeding peak coincides with the local rains, monsoons, or floods (Lowe-McConnell 1979, 1987, Payne 1986).

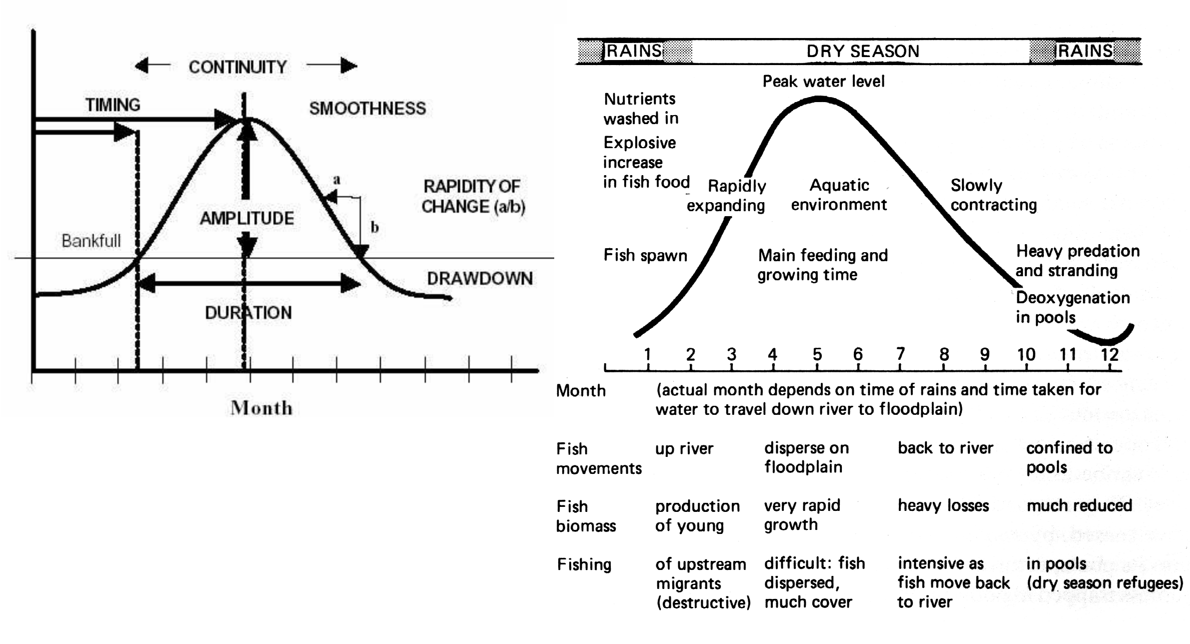

Figure 9. Left: various parameters of a flood curve having biological significance. (from Welcomme and Halls 2001); Right: the seasonal cycles of events in a floodplain river (from Lowe McConnell 1987)

Floodplain fisheries are considered among the most productive in the tropics (Welcomme 1979, Junk et al. 1989), with an average potential fish production rate 2.5-4 times that of tropical lakes and reservoirs on an annual mean water surface area basis (Bayley 1991). They appear to take advantage of most of the above-described principles for high productivity. They are fluvial, shallow and unstable, continuously oscillating, generally but not always with a high predictability between a terrestrial and an aquatic phase, and with a high external nutrient loading. These regular fluctuations, generated by the hydrodynamics, provide a great mixer and acts as a nutrient pump. This is the so-called flood-pulse concept initiated by Junk et al. (1989), that keeps the environment in a stage of early succession, which means that it is dominated by biota with r-selected10 traits (Bayley 1991). Combined with the high insolation and temperatures the basis for primary- and higher order productivity is optimal. Unlike stagnant water, however, the constantly changing water levels move the ecotone, which not only facilitates the nutrient recycling (by fluctuating redox potentials), but also prevents sedimentation and the formation of permanent oxygen deficiencies, although periodic hypoxia may be prominent.

The typical flood regime contains several characteristics (Fig. 9) that may influence the recruitment, growth and survival and growth of the individual fish species. An understanding of these characteristics will help determine flow criteria for the maintenance of floodplain fish faunas and design appropriate flood curves that maximize benefits from the water available. Strong year-classes of fish tend to result from gradually increasing water levels combined with high amplitude. Conversely, a constant high water level may decrease production because of development of stagnant water conditions, with associated stratification and oxygen constraints (Junk et al. 1989). Bayley (1991) has labelled the difference in relative production between fluctuating hydrological environments and systems with constant water level the ’flood pulse advantage’, which could account for a doubling in productivity rates. Apart from climatic variations in the rainfall, a slow increase in water level, with a long inundation period, will depend on the gradient of the shorelines of the adjacent land (morphometric attributes). Lakes and reservoirs may share many of the properties of riverine and floodplain systems, and are in fact in many instances part of a river system. The potential impact of changing water levels in lakes and reservoirs thus is relative to the scale and size of the system and the time scale of the fluctuations:

- from long-term trends and fluctuations and complete resetting of systems acting on the composition of whole fish communities,
- via short-term trends and interannual fluctuations operating on fish species within communities on a short term with impacts depending on lifespan and response of species to changes in externally driven lake productivity,
- to variations in seasonal pulses acting on the recruitment of species with short lifespans, triggering fish migrations and, being the starting point of the annual productivity pulse, the year-class strength of longer-lived fish.

By examining different scales of variability, we can thus position a system within a general classification of lakes in terms of system stability. Based on this a general classification of lakes from pulsed systems to constant systems can be made (Jul-Larsen et al. 2003).

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[10] *r*-selected species are good colonizers, reach sexual maturity rapidly, are short-lived, with high fecundity, have low investment in care for the young, and are generalist feeders and poor competitors.

4. The biological base for productivity

Predator-prey interactions and top-down versus bottom up control

While the primary productivity in lakes and reservoirs mainly is governed by the nutrient concentrations and loading from physical and climatic attributes of the environment, including the seasonal oscillations (Schindler 1987), there is no simple uniform relationship with the fish production at higher trophic levels. The energy flux and pathways through the system depends on complex interactions between bottom up and top down control, and cascading effects among these. The tropic cascade hypothesis state that while the potential productivity of lakes is set by the nutrients (bottom up control), then deviations from the potential are due to top-down food-web effects (Carpenter et al. 1985, Carpenter and Kitchell 1993). In endorheic Lake Turkana, for example, where there is a strong linear correlation between nutrient input (river inflow) and production (Kolding 1992), the ecotrophic community structure in the unfished pelagic zone changed dramatically over a decade (Kolding 1993a). In the 1970s the system appeared limited by zooplankton production and energy accumulated in the stocks of small pelagic fish. Later the slower growing predator stocks of Nile perch (*Lates* spp) proliferated and in the 1980s energy was accumulating at the top predator level. This resulted in a strong increase (250%) in predation mortality on small pelagic species, which would explain the five-fold decrease in their biomass. This was much more than was expected, from the relative decrease in secondary and primary productivity between the two periods. Thus the regulatory mechanisms in the open lake ecosystem appeared to have shifted from bottom-up to top-down control between the two periods. It is a general tenet in system ecology that predator-prey interactions tend to generate coupled time-lagged oscillations due to shifting phases of abiotic (bottom up) and biotic (top down) cascading effects, particularly in fluctuating environments (Fig. 10).

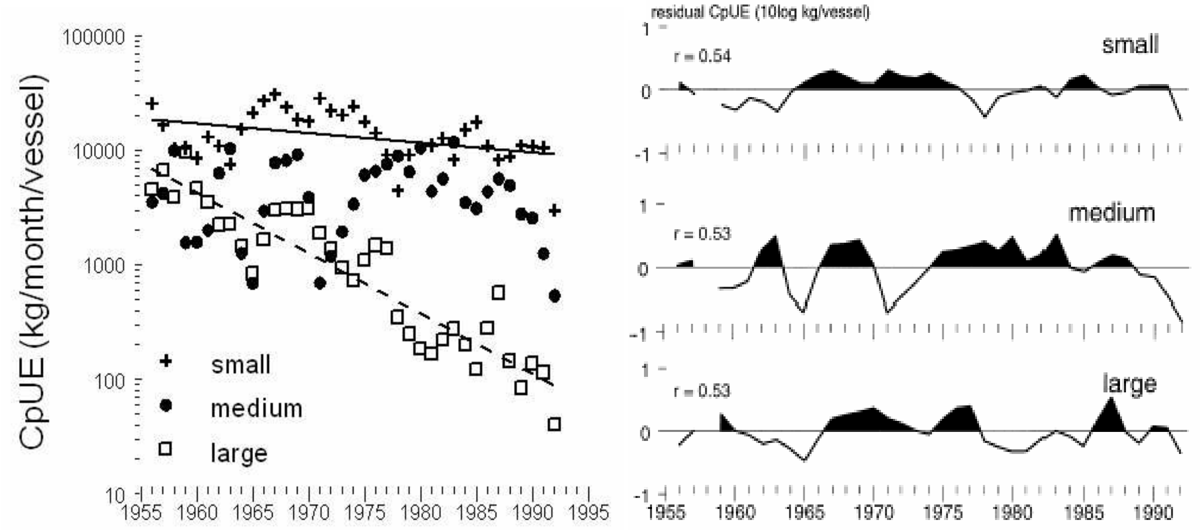

Figure 10. Left: development in catch per unit of effort of the industrial fishery of Burundi, northern Lake Tanganyika by commercial group. Small (<20cm) = Stolothrissa tanganicae, Limnothrissa miodon *and juvenile* Lates stappersii*; medium (20-40cm) =* Lates stappersii*; large (>40cm) = three* Lates *spp. The elevated catches of the category small during the period between 1964-1976 is caused by a long term change in wind patterns resulting in changed upwelling patterns and hence productivity of this part of the lake (Spigel and Coulter,1996, Verburg et al. 2003). Right: long term persistence in de-trended catch rates of the three commercial groups. The black areas highlight periods of catch rates elevated relative to the long term trend. At this temporal scale, where stock dynamics act on abundance levels, alternating abundances of predator and prey are observed, indicating time-lagged oscillations in availability to the fishery. r= auto-correlation coefficient at lag = 1 year (adapted from van Zwieten et al. 2002).*

Also competition among various predators may have profound effects on the harvestable part of the potential production. For example the phantom midge (*Chaoborus* sp.) may, due to its intense predation on the entire spectrum of the zooplankton herbivores, sometimes be a major top-down controlling factor in the food-chain (Lewis 1977). This suppression occurs primarily during the stratification periods, where the anoxic hypolimnion provides a refuge from fish predation, and *Chaoborus* instead becomes a very effective competitor. In some meromictic lakes, such a Lake Malawi, and recently also Lake Victoria, the permanent anoxic bottom layer has provided conditions for large standing populations of phantom midges that most likely will decrease fish production. In Lake Tanganyika, *Chaoborus* is absent and efficient planktivorous fish present and this lake is relatively more productive than Malawi and Victoria (Hecky 1984, Coulter 1991). For the pelagic zone of Lake Malawi it is estimated that 98% of the primary production is consumed by *Chaoborus*, while only 8% of the *Chaoborus* production is consumed by fish (Degnbol 1993). He concluded that the pelagic part of Lake Malawi produces midges, not fish. However, the implication by introducing a competing zooplanktivorous species, as suggested by Turner (1982) was seen as opening the box of Pandora. Later model outcomes strongly disagreed with the suggestion that the introduction of a more efficient zoo-plankton feeder would be justified (see Menz 1995 and references therein).

Food webs – detrivory and herbivory

An important general difference between tropical and temperate lakes is that herbivore and detrivore fish are relatively more frequent in the tropics (Nilssen 1984, Lowe-McConnell 1987, Fig. 11).

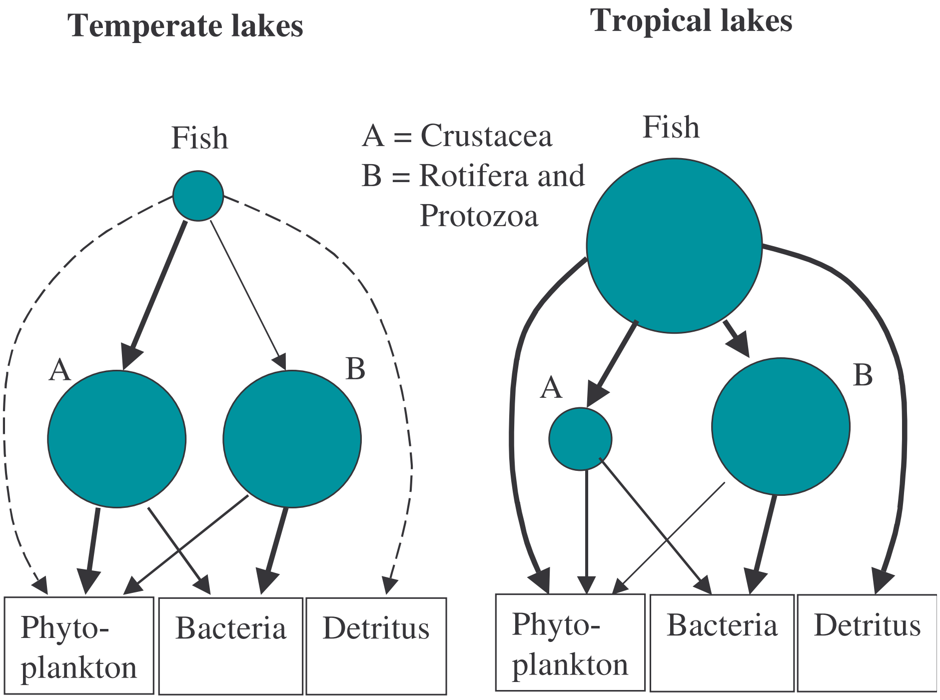

Figure 11. A simplified food-web structure in tropical and temperate lakes. The relative sizes of the circles represent hypothetical biomasses and the arrows the direction of consumption and its magnitude. Modified from Nilssen (1984).

Although, the number of primary consuming fish species in the tropics are relatively low compared to the total number of species (less than 10%), their wide distribution and high abundance makes them disproportionately well represented in individual aquatic ecosystems, often comprising more than half of the total ichthyomass (Bowen 1988). Tilapiine species (particularly Tilapia sp. and Oreochromis sp.) are the mainstay of most African small-scale freshwater fisheries (FAO 2003a), and high yields in tropical lakes and reservoirs outside Africa are generally only found when these cichlids have been successfully introduced (Fernando and Holčik 1991). Actually, the most important introduced and stocked fish in lakes and reservoirs, and which constitute the bulk of inland aquaculture production in developing countries, are detrivorous/herbivorous or filter-feeding species such as tilapias and carps (SOFIA 2002). The main reason for the success of tilapias is their direct connection to the base of the food web, which makes them 5-10 times more efficient than secondary consumers (Bowen 1988), but in addition they appear particularly well adapted to fluctuating environments (Kolding 1993b, Weliange and Amarasinghe 2003)

Lacustrine versus riverine fish

Africa is the only continent with large natural tropical lakes, and outside Africa the lacustrine fish fauna is remarkably poor (Fernando and Holčik 1982, Lowe-McConnell 1999). Riverine fish faunas, on the other hand, are generally very rich, and several basins consist of more than 1000 species, in Mekong for example there are between 1200-1700 species (Coates et al. 2003). As most riverine fish are adapted to changing environmental fluctuations from hydrological oscillations (Welcomme 1999, Welcomme and Halls 2001), their feeding and breeding habits differ from lacustrine species. Breeding is typically seasonally defined in tune with the floods (Fig. 9), and the feeding habits are mainly omnivorous or piscivorous. Specialised herbivorous or planktivorous species are generally rare (Fernando and Holčik 1982 1991). As a result, the pelagic zone in many reservoirs built in environments with no indigenous lacustrine fish fauna remains uninhabited and under-utilised from a fishery perspective. This may represent a major loss in potential productivity. Several of the larger reservoirs in Africa, such as Lake Kariba, Cahora Bassa, Lake Kainji, and Lake Volta all have introduced or self-established pelagic clupeids, which contribute the bulk of the fish yields. In Lake Kariba, for example the introduced pelagic clupeid *Limnothrissa miodon*, originating from Lake Tanganyika, has increased the productivity of the lake by a factor of five. This fishery, which has had no adverse effects on the indigenous fish fauna (Karenge and Kolding 1995a, Kolding *et al.* 2003a) has now developed into a million dollar industry, with between 20-30000 t landed annually[11], economically vastly outstripping the inshore fishery, and with theoretical potential for further expansions (Machena *et al.* 1993, Marshall 1992, 1993, Kolding 1994).

Man-made Lake Nasser, in contrast, has a typical riverine fish fauna, with a relatively low yield, and lacks a pelagic planktivore. On the other hand it has a relatively high standing biomass of medium-sized copepods and cladocera, which suggests that the introduction of a pelagic zooplanktivorous fish should be assessed (Marshall 2000, El-Shabrawy and Dumont 2003).

According to Fernando and Holčik (1991) the development of indigenous species pre-adapted for lacustrine conditions, or introduced pelagic species substantially increases the ichthyomass and potential yields of reservoirs. In tropical reservoirs, the clupeids, have proved exceptionally suitable for doing this without apparent negative effects (Marshall 1995). Even small or medium sized reservoirs may benefit from such introductions as has been shown in Itezhi-tezhi (Zambia). *Limnothrisa miodon* was introduced into the rather small reservoir (area 370 km^2, mean depth 15.4 m) in 1992 and has established itself successfully without negative effect on the indigenous fish fauna (Mbewe 2000).

The high productivity of some tropical lakes and reservoirs, can in general be attributed to the short food chains from primary sources (phytoplankton and detritus), to harvestable biomass. Indigenous or introduced tilapiine cichlids are the mainstay of capture fisheries in the majority of tropical lakes and reservoirs. Small planktivore fish in the tropics are particularly high yielding due to their extremely high biological turn-over (The P/B-ratio of *Limnothrissa miodon* in Lake Kariba for example is around 6 per year, Machena et al. 1993; of *Microthrissa moeruensis* in Lake Mweru is around 5 per year, van Zwieten et al. 2003), which means that sustainable landings are higher than the standing biomass. Where pelagic fisheries exist, they often vastly outstrip the productivity of the inshore resources.

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[11] Equivalent to 40-60 kg ha^{-1}. In comparison the herring and anchovy fishery in the North Sea, considered among the most productive in the world, is yielding around 10 kg ha^{-1}.

5. The functioning of tropical aquatic ecosystems

Diversity and stability

Conventional wisdom states that stability should increase with system complexity (e.g. Margalef 1968, Odum 1969) and that diversity is an expression of complexity. Consequently, the high species diversity associated with many tropical communities have traditionally been related to environmental stability (e.g. Sugihara et al. 1984) and the interrelationship between the two terms have been almost axiomatic (Margalef 1969). Although the cause-effect seems somewhat tautological and obscure (Pianka 1966, Orians 1975), the 'diversity-stability' hypothesis has found extensive acceptance in ecology and has often led to the suggestion that highly diverse communities are particularly fragile to exploitation (May 1975, Sainsbury 1982). Similarly, there has been a widespread related preconception (e.g. Larkin 1982, Caddy and Sharp 1986) that tropical communities are usually equilibrial and competitively structured and that they remain constant through time. For example Pauly (1980, p. 41) wrote "biological processes in the tropics often occur in the 'pure form', unmediated by strong fluctuations of the abiotic environment". Most of the limnological and freshwater fisheries work in the tropics has been focused on the large, old tertiary lakes, such as Victoria, Tanganyika and Malawi (e.g. Beadle 1974). Consequently many of the generalisations of tropical lakes originate from these studies, and this has created the *a priori* assumption that tropical lakes were more complex and vulnerable than temperate ones (Nilssen 1984).

Gradually these notions are being replaced by a much more dynamic view of tropical systems already formulated a few decades ago since they neither seem to have general applicability or be supported by evidence (Huston 1979). On the contrary, reviews (e.g. Connell and Sousa 1983, Pimm 1984) reveal that (1) there is a continuum of temporal variability in the dynamics of most observed natural populations and communities, (2) there appears to be no evidence of multiple stable states[12], and (3) the more numerous the species, and the more strongly they interact, the less chance there is of stability. Theoretical advancement in species diversity generation, notably the 'intermediate disturbance hypothesis' (Connell 1978), (with examples from the paragons of stability: tropical rain forests and coral reefs) and the 'dynamic equilibrium hypothesis' (Huston 1979), build on such non-equilibrium dynamic community assumptions. Both infer that frequent but irregular disruptions are a major agent in maintaining high diversity communities.

According to these recent hypotheses, also high diversity multi-species fisheries could be variable and subject to environmental changes. Lowe-McConnell (1969) concluded that high tropical diversity was found both in the stable environments of the Great Lakes of Africa and in the very unstable, fluctuating conditions in the rivers and that tropical communities in general are extremely dynamic, changing all the time. In extreme cases as in Lake Chad, substantial shifts in abundance patterns of species can take place in relation to the hydrological status of the lake. Rare species, in most natural communities only a few species are abundant whereas most are rare (Magurran and Henderson 2003), become abundant and vice versa under changing ecological conditions (Lévêque 1995). Larkin (1982) inferred that the variability in abundance, even in virgin or lightly fished tropical stocks, seemed to indicate that fluctuating environmental factors are important in shaping the community structure. Actually, evidence has been accumulating for synchronous changes in widely separated fish stocks, and it seems almost certain that global patterns of atmosphere-ocean interaction are somehow responsible (Mann 1993).

As these new uniform patterns begin to emerge, there seems no justification for treating tropical aquatic systems as separate entities in terms of theoretical distinctions. As stated by Larkin (1982 p. 314), "there is as yet no ecological evidence indicating that tropical systems are organized in a fundamentally different way than are temperate communities". For tropical lakes, this was sustained by Nilssen (1984). Thus, the overall applicability of the formerly established paradigms is now changing. Tropical systems are not always inherently stable, neither on land (e.g. Deshmukh 1986,

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[12] But see Scheffer 1998, and Scheffer and Carpenter 2003

Vetaas and Kolding 1991), nor in water (Lowe-McConnell 1969). Similarly, there are no reasons to expect diverse tropical communities to exhibit more or less biotic regulations than temperate ones, nor to anticipate they should be more or less fragile to exploitation than temperate (Sainsbury 1982).

The relationship between environment and productivity

In general fish productivity per unit area will tend to be (Ryder et al. 1974, Fig. 6):

- a domed-shaped function of nutrient concentrations, with the descending part being a result of increased eutrophication, which leads to bacterial decomposition and ensuing oxygen deficiencies.

- a negative exponential function of the habitat volume, area, and mean depth due to the corresponding decreased rates of nutrient recycling into the euphotic layer with these parameters.

Numerous empirical correlations have been produced between productivity and various abiotic and biotic variables in freshwater ecosystems (see reviews in Leach et al. 1987 and Downing et al. 1990). Of the more well known are the empirical yield equations of Henderson and Welcomme (1974) based on the morphoedaphic index (MEI) in 31 African lakes, and that of Melack (1976) based on the primary productivity in 8 African lakes. Predictive yield models have been developed based on limnological parameters and/or chlorophyll concentration (Melack 1976, Oglesby 1977, Liang et al. 1981, Downing et al. 1990), morphometric features as depth volume and area (Rawson 1952, Jenkins and Morais 1971, Bernascek 1995), combinations of morphometric and limnolgical parameters as the MEI (Ryder 1965, 1982, Rempel and Colby 1991 and others), and catchment landuse patterns (De Silva et al. 2001).

The empirical yield equations of Henderson and Welcomme (1974) and Melack (1976) are probably the most widely used, at least in African lakes and reservoirs. However, when matching the predictions with the observed yield, it is often observed that the MEI predictions produce considerably lower values (Kolding 1994). Usually such discrepancies are explained by inadequacies in the data and/or various ad hoc hypotheses[13]. According to Downing et al. (1990) fish production, in general, is actually uncorrelated with MEI but closely correlated with annual phytoplankton production, phosphorous concentration, and standing biomass. There are, however, several deficiencies in most of the empirical prediction models. Firstly, very few predict rates of biological production, but are mostly relating observed yield, irrespective of the fishing intensity level, to observed independent variables (Bayley 1988, Downing et al. 1990). The observed yields in the various African lakes at the time of the correlations (early 1970s) may have been at their sustainable maximum, but, judged upon later development in some systems they most likely were not (Vanden Bossche and Bernacsek 1990). Thus, the classic empirical equations only give an estimate of the observed mean yield in various systems in comparison with environmental parameters at the time of investigation (see also review by Marten and Polovina 1982). Theoretically, however, they say little about how far a fishery can expand in terms of long-term sustainable yields (Kolding 1994). Secondly, they are all based on either static independent variables, like morphometric features, or a few point-estimates of fluctuating variables such as water chemistry and primary production. As most of the systems they are applied to are highly variable, both in terms of biological production and the underlying factors regulating this (see above), the predictive power obviously becomes low. For predicting productivity it is therefore important that the dynamic aspects of the lakes and reservoirs are incorporated in the independent variables and particularly the hydrodynamic fluctuations which are driving the nutrient most of the observed variability.

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[13] A typical example of discrepancies is observed in Lake Tanganyika where the pelagic yields are many times the predicted value (see Coulter 1991).

System variability: water level as environmental driver

In river and floodplain fisheries of Africa, for example, the flooding regime (timing, pattern and duration) has long been considered of major importance to the fish yields (University of Michigan 1971, Welcomme 1975, 1976, 1978, 1979, 1986, Welcomme and Hagborg 1977, Welcomme and Merona 1988). This being generally accepted, the ensuing published discussions have mainly concentrated on which hydrological indices or how many previous years should be included to obtain the best empirical fit to the catches.

Table 5. The relative effect of hydrological changes and effort on catch rates in three African lakes. The complete statistical regression model used is: Annual mean catch rate$_{ijk}$ *= overall mean + effort*$_i$ *+ lag(hydrological variable*$_j$*) + effort*$_i$*·lag(hydrological variable*$_j$*) + residual variation*$_{ijk}$*. Only significant effects are retained in the model and shown here as positive (+) or negative (-) effects. In some instances the hydrological variables and effort were confounded meaning that both parameters were significant alone, but in the complete model one or the other became non-significant depending on the order in which they were entered into the model. In such situations it is not possible to quantify the relative effect of both parameters simultaneously. N= number of years, lag = in years, % = proportion of sum of squares explained by that variable in the model. Reproduced from Jul-Larsen et al. (2003).*

Dependent variable		***Independent variables***								
Annual mean catch rate (CpUE)		Water level				**Effort**			**Interaction**	
System Variable	N	Lag	Variable	Sign	%	Variable	Sign	%	Sign	%
Lake Kariba Zimbabwe										
Artisanal (kg/net)	27	1	Annual change (Δ)	+	29	# fishers	-	44		
Artisanal (kg/net)	27	1	Annual change (Δ)	+	19	# nets	-	26		
Experimental (kg/net)	29	0	Amplitude	+	39	# fishers				
Experimental (kg/net)	29	0	Amplitude	+	39	# nets				
Kapenta (ton/night)	26	0	Mean	Confounded		# boats/night	Confounded		-	56
Lake Kariba Zambia										
Artisanal (kg/net)	20	0	Mean	+	32	#f ishers				
Artisanal (kg/net)	20	0	Mean	+	32	# nets	-	9	-	8
Experimental (kg/net)	20	0	Mean	+	31	# fishers				
Experimental (kg/net)	20	0	Mean	+	34	# nets	-	23	-	11
Kapenta (ton/night)	18	0	Mean	Confounded		# boats/night	Confounded		-	60
Lake Malombe Malawi										
Kambuzi seine (kg/haul)	18	3	Minimum	+	47	# nets	-	32		
Gillnet (total kg/100m net)	18	0	Maximum	+	68	# 100m nets				
Gillnet (kg Oreochromis/100m)	18	3	Minimum	+	77	# 100m nets				
Lake Chilwa Malawi										
Gillnet (kg/100m net)	18	1	Mean			# 100m net	-	38	+	38
Gillnet (kg Oreochromis/100m)	18	0	Maximum	+	20	# 100m nets	-	26	+	30
Seine (kg/haul)	18	0	Maximum	+	16	# hauls	-	54		
Longline (kg/hook)	18	0	Maximum	+	9	# hooks	-	57	+	20
Trap (kg/trap)	18	0	Minimum	+	17	# traps	-	43	+	13

In lake and reservoir fisheries, direct associations between the hydrological regime and yields are more scarcely documented, although Lévêque and Quensière (1988) rank the hydrology among the most important factors on the community structure in shallow lakes. Likewise, Moreau (1980) used the model of Welcomme and Hagborg (1977) to describe the fish production in shallow Lake Alaotra on Madagascar. Stauch (1977) found a significant inverse correlation between falling lake levels and increased catches between 1969 and 1974 during the drought at Lake Chad. This, however, was due to the concentration of the fish stocks and the increasing ease of their capture, a phenomenon also deduced by van Zwieten et al. (2003) who attributed the relative increase in catch rates of species to concentration effects as a result of falling lake levels in Lake Chilwa (Malawi). In both cases during the following years the yields fell sharply. Furse et al. (1979) found that the yields and species composition in the shallow Lake Chilwa varied as a function of the lake level. Tweddle and Magasa (1989) demonstrated a significant correlation between the difference of actual and predicted catch and the changes in the lake level three years previously in a cichlid multispecies trawl fishery of Lake Malawi. This association they attributed to different recruitment success. Catches each year compared with lake-level changes for the same year showed no relationship. Kolding (1989, 1992) found a linear correlation ($r^2 = 0.88$) between commercial catch rates and the previous years mean lake level over a 16 years period in the endhoreic highly oscillating Lake Turkana, Kenya. Agaypi (2000) found a similar linear correlation ($r^2 = 0.61$) between catch rates of *Oreochromis niloticus* and lake levels two years previously over 25 years in man-made Lake Nasser. In a study from Australia, Davies and Sloane (1988) considered variations in water levels of a Tasmanian lake the principal factor dictating the dynamics of trout populations. In lake Kariba, Karenge and Kolding (1993b) analysed the relationship between the fisheries and the hydrology in Lake Kariba and found that experimental, artisanal and offshore kapenta catch per unit of effort were all highly significantly correlated with mean annual lake level fluctuations, but not with the absolute lake levels. Jul-Larsen et al. (2003) analysed the combined effect of fishing effort or water level on catch-rates in three African lakes and found that environmental variability in all cases explained as much of the variance as effort, and that these two factors often interacted (Table 5).

Lakes and reservoirs can vary from highly stable systems to highly pulsed, where most reservoirs will be in the pulsed end of the spectrum (see Table 3). In order to quantify this gradient we have suggested (in Jul-Larsen et al. 2003) to combine the flood-pulse concept with the important morphometric parameter mean depth, which is also used in the MEI-model (Henderson and Welcomme 1974). We proposed to use a ‘relative lake level fluctuation’ index (RLLF), defined as:

$$\mathrm{RLLF} = \frac{mean\ lake\ level\ amplitude}{mean\ depth} \cdot 100$$

where the hydrological changes are serving as a proxy for nutrient loading. By calculating this index both for the average inter-annual (change in annual mean = RLLF-a) water level and the average seasonal pulse (RLLF-s), the index can show both the average inter-annual stability of a system and the average strength of the seasonal pulse with which different systems can be scaled. So far this index has shown some promising results. Species diversity, for example, seems related to the variability and the size of the system (Fig. 12). Lake area and altitude were found to be the two major determinants with predictive power for fish species richness in a study by Amarasinghe and Welcomme (2002), and the relation with variability remains to be investigated further. The species area relationship in lakes, and the relationships between species and drainage basin area in rivers, indicates that also these relationships increase faster in tropical regions compared to temperate regions. This could be a function of the higher rates of change in habitat availability due to more pronounced climatic fluctuations in tropical regions, or simply a higher speciation rate due to a generally lower generation time.

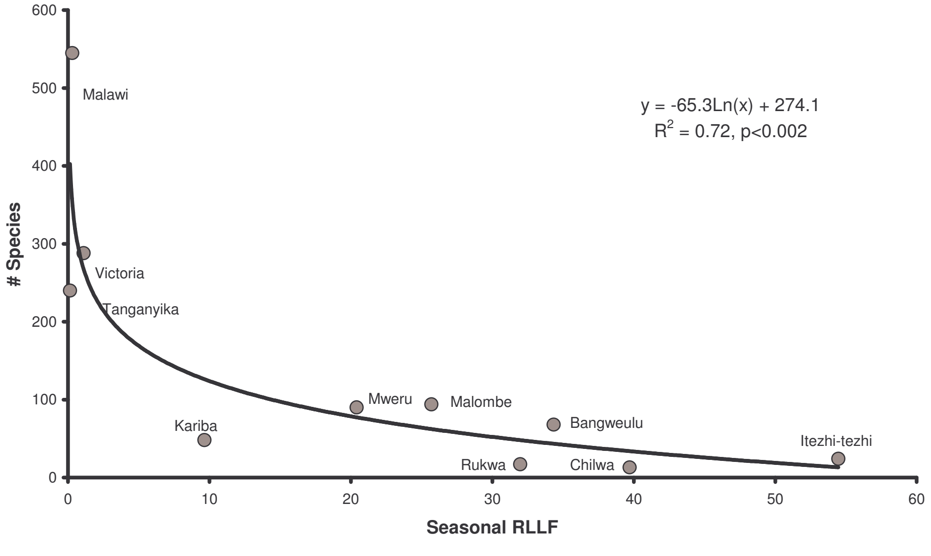

Figure 12. Number of fish species in ten SADC lakes related to the seasonal Relative Lake Level Fluctuations (RLLF-s). Reproduced from Jul-Larsen et al. (2003).

But also the system productivity has a high correlation with the RLLF (Figs. 4 and 13).

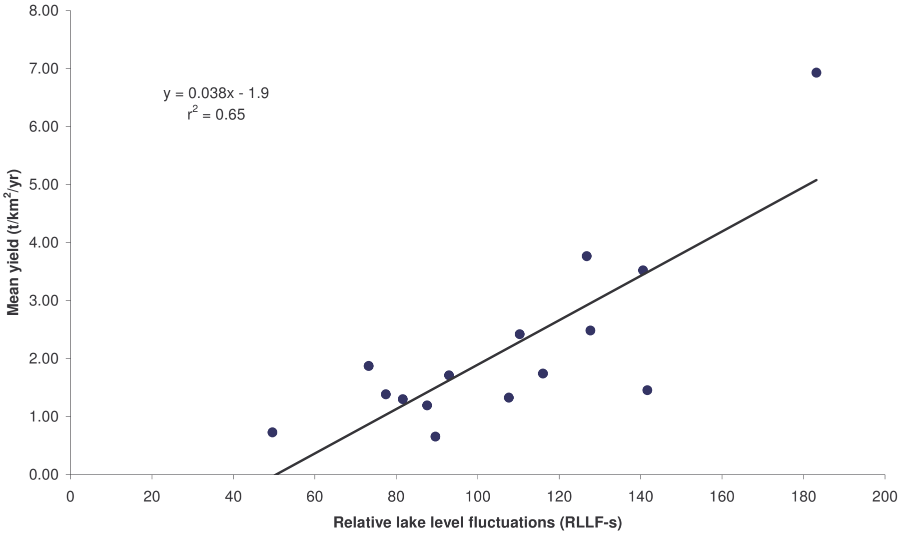

Figure 13. Relationship between mean annual yield (t/km^2) and relative seasonal lake level fluctuations (RLLF-s = %(annual drawdowns/mean depth)) in 15 reservoirs of the lower Mekong countries. Data from Bernascek (1995).

In general, system productivity seems to increase with increased instability. Some of the most productive African lakes, such as lake Chilwa (Fig. 4), which regularly dry out, are in fact behaving like floodplains. The regenerative rate of fish in these unstable systems is phenomenal. The Khasm el-Girba reservoir in Sudan, for example, is flushed and completely drained on an annual basis due to siltation problems, causing massive fish kills. Still, El-Thair and Kolding (1995) found that the recurrent flushing had little impact on either the species composition or the potential yield of the fish community.

6. Fish production and exploitation pattern in multi-species capture fisheries

Productivity, trophic level, density dependence, and P/B ratio

Biological production (P) is the total amount of tissue generated in a population in a particular space during a given period of time, regardless of its fate. It is of central interest in the exploitation of renewable resources, since the yield (C) is a fraction F (Fishing mortality) of the mean biomass and is a fraction (x) of biological production P

$$C = F \cdot \overline{B} = x \cdot P$$

Production thus includes both living organisms and organisms that died within the time period. Gains in biomass are a result of individual growth, new offspring, and immigration whereas death and emigration cause losses in biomass. 'Surplus' production, or the net production after natural density dependent mortality has been subtracted, is essential for any population in order to expand and/or withstand predation without declining. When biomass does not change (dB/dt = 0) then surplus is equal to output and a stock is said to be at an equilibrium. The *ecotrophic efficiency* (x in the above equation) is defined as the fraction of total production which is consumed by higher trophic levels. Production is thus a density dependent *quantity* expressed in kilograms or tons often scaled by area or volume. Productivity is the rate or *speed* at which production is generated and is a function of both the individual biological regenerative characteristics of a particular species (the per-capita rate of increase, r), and the density (B) of the stock. Productivity is the instantaneous rate of biomass production $r \cdot B$. At any constant population size the average total death rate (Z) is equal to the per-capita rate of increase, which implies that the total mortality rate that a population can sustain is closely related to the life history characteristic of the species, and in particular to the intrinsic rate of increase (r_m) (Kolding 1994, Kirkwood et al. 1994, Beddington et al. 1997).

Production processes are usually associated with the rates at which biological tissue moves between trophic levels, and are thus dynamic quantities, which can rarely be measured directly. The production/biomass ratio (*P/B*), however, is one way of envisioning the time scale, by indicating the turn-over rate and thus the speed of the biomass regeneration. The *P/B* ratio tends to decrease from one trophic level to another with distance from the primary production level, and also tends to have a general non-linear negative relationship with the sizes (or longevity) of organisms involved (e.g. Dickie 1972, Lévêque et al. 1977, Welcomme 1999). This means that changes in size-composition of a population from human exploitation or predation will be reflected in the P/B ratio. The P/B ratio is thus an extremely useful parameter to comparatively characterise different systems, species or trophic levels within a system (see e.g. Le Cren and Lowe-McConnell 1980). If the death rate is simple exponential, as mostly assumed for fish populations, then the instantaneous mortality rate (Z) is equal to the P/B ratio (Allen 1971). Thus, the gross production per unit time, $P = B \cdot Z$, is entirely a function of the mean biomass and average mortality rate.

Productivity is also used more loosely in as for example when “changes in lake productivity” are related to “changes in fish yield”. What is meant in these expressions is that through environmentally driven processes, such as changes in water inflow in lakes and resulting water levels, the productivity at different trophic levels changes resulting in changes in fish production and hence fish yields. Therefore, in a changing environment, the idea of a constant carrying capacity (which is the underlying assumption for surplus production modelling) is neither plausible nor necessary for conceiving density dependence or equilibrium situations.

Population size determined by the climate or the community?

Steady state means that the $dB/dt = 0$. In a growing population $dB/dt > 0$ and in a declining population $dB/dt < 0$. The frequency and amplitude of oscillations in biomass changes must then be mainly related to the variability of the environment (the extrinsic factors). In fish, the change in dB/dt is dependent both on abiotic factors, such as temperature and oxygen, and biotic factors such as food and predation. Climate or predators influence the fluctuations, and depending on the environment, one or the other has overwhelming importance. Thus we may generalise to two situations: one in which population size is largely determined by climate, and another where other animals largely determine it. In both cases mortality is still the most important common denominator as intrinsic natural rate of increase can be considered a species-specific constant (Kolding 1994, Jul-Larsen et al. 2003).

Diversity, stability, resilience and regenerative capacity

Fishing, predation, and environmental changes all causes stress, and the capacity to recover, persist, endure or ‘bounce back’ to a previous state, is theoretically associated with the two concepts: *stability* and *resilience*. According to one of the better known definitions (Holling 1973) stability is "The ability of a system to return to an equilibrium state after a temporary disturbance, the more rapidly it returns and the less it fluctuates, the more stable it would be". Resilience is according to Holling (1973) "A measure of persistence of systems and the ability to absorb change and disturbance and still maintain the same relationships and composition between populations or state variables (irrespective of relative abundance)". In Holling's view, instability in the sense of large fluctuations, produce a highly resilient system capable of repeating itself and persisting over time until a disturbance restarts the sequence. Thus systems can be very resilient and still fluctuate wildly. Holling (1973) states that these two distinct properties alone define the behaviour of ecological systems. However, any measure of stability requires a time-perspective that must be seen in relation to the life span of a species or community. The ambiguities in the literature between stability and resilience might thus, like the equilibrium and non-equilibrium models discussed later, simply be a matter of scale (Kolding 1997, Walker et al. 2004). The mortality rate or *P/B* ratio represents the speed of regeneration against which stability and resilience should be measured. As illustrated by the slopes of the biomass size distributions in figure 14 species from 'stable' environments have on average a low intrinsic growth rate (*r*) and total mortality (Z) with a corresponding longer life span, whereas 'resilient' species in pulsed environments have a high r and *Z* and shorter life-span. What determines resilience and stability depends on the combination of stress (continuous selective or discrete non-selective mortality), and the trade-off between the advantages of being big, or develop specialised behaviour, and the probability of dying with time.

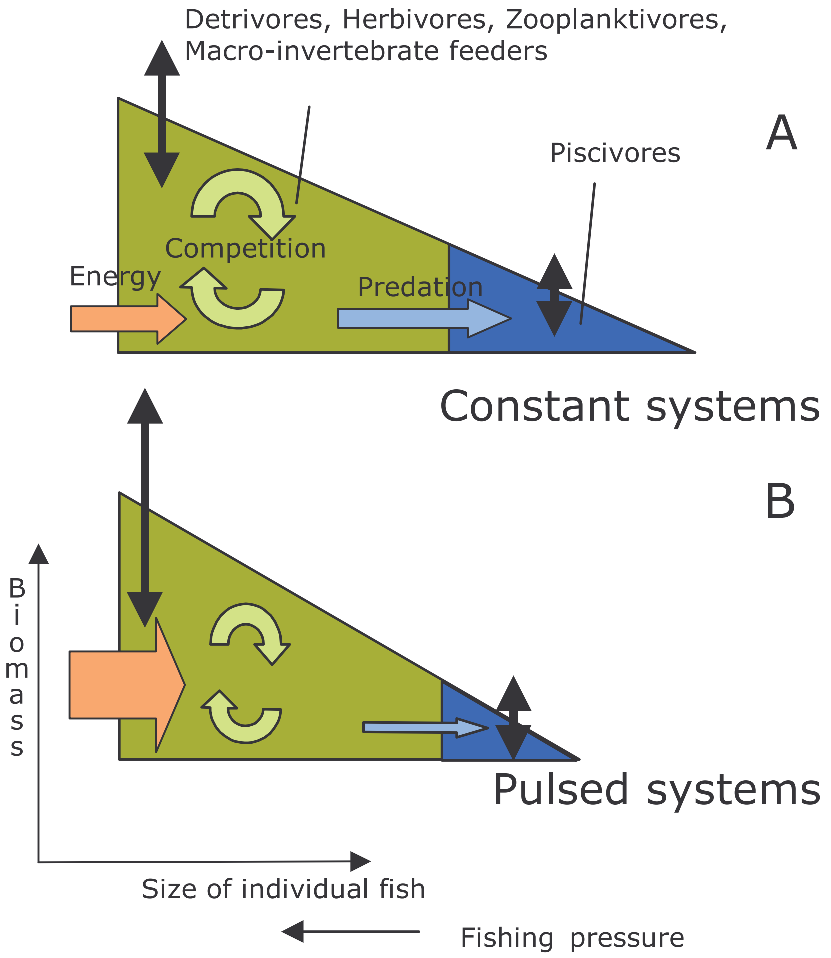

Figure 14. Biomass-size distributions, variability, and energy pathways in A) constant and B) pulsed systems. Triangles characterise fish communities by biomass and size while variability (vertical arrows) and energy flow (horizontal arrows) indicate dominant mortality patterns. The slope of the hypotenusa is proportional with the overall community mortality rate ≈ intrinsic growth rate ≈ P/B ratio. Biomass decreases with fish size and predatory fish (blue triangles) are generally larger than their prey. Energy flow through pathways start from seasonal input of nutrients resulting in seasonal changes in productivity (red arrows). Energy in a fish community is partitioned through competition and predation (green and blue arrows). Variation in biomass caused by changes in energy input is larger with smaller sized fish (black arrows). Increasing fishing pressure generally results in decrease in biomass of large fish and increased catches of smaller fish. Reproduced from Jul-Larsen et al. (2003)

The coexistence of several species in an ecosystem, so-called biodiversity, and particularly the natural regulation and maintenance of biodiversity is theoretically a challenge (Kolding 1997). The basic unit in biodiversity is the individual species and normally the focus is on the number of species and the relative abundance and distribution of individuals within an ecosystem (*alpha* diversity). The more species, the more diverse is the ecosystem, and the more we tend to value it. Consequently, fisheries are facing a dilemma against the drive of conserving biodiversity. For instance, FAO (1992, p. 5) wrote: "Continued high fishing intensity will contribute to a loss of biological diversity,(...) and this may lead to more unstable, and possibly lower, catches in the long term". In general, the various hypotheses for the regulation of diversity can be grouped into so-called equilibrium and non-equilibrium models (Tonn and Magnuson 1982, Petraitis et al. 1989, Begon et al. 1990). Selective -, density dependent -, predator induced mortality is belonging to the first category, whereas catastrophic -, non-predictive -, density independent – environment induced mass mortality belongs to the latter. However, common to all these hypotheses is that population reduction in the form of either selective (predation) or non-selective mortality (environmental disturbances) is the main mechanism for the regulation of diversity. The logic is that individual population densities must be kept lower than the carrying capacity to prevent the effects of strong mutual interactions, the so-called *competitive exclusion principle* (Hardin 1960). Both the selective mortality based hypotheses (equilibrium models), and the hypotheses based on non-selective population reductions (non-equilibrium models) predict the highest diversity to be at an intermediate level of predation, stress or disturbances, i.e. the various populations never gain enough dominance to competitively exclude others. Thus the difference between the two groups of models can simply be reduced to a situation where the population reductions are either continuous or discrete (Kolding 1997). In other words, the creation and maintenance of biodiversity can be considered regulated by the mortality pattern in the ecosystem. In lake Kariba, for instance, where overall fish diversity has steadily increased over the past 40 years, the inter-annual changes in Shannon’s diversity index were significantly negatively correlated to mean annual lake level changes and to the abundance of the main predator, the tigerfish (*Hydrocynus vittatus*). These two factors, one abiotic bottom-up and one biotic top-down, can be regarded as disturbing agents of the system that play a regulatory role (Songore 2002, Kolding and Songore 2003).

In summary we can generalise these ecological concepts and processes into two broad categories where the environment determines the prevailing mortality pattern:

- The unstable environment characterised by discrete, density independent, non-predictive, non-selective mortality induced by physical changes
- The stable environment characterised by continuous, density-dependent, predictive, and size-selective mortality induced by the biotic community.

The two broad categories represent extremes on a gradient, and (in)stability must be seen as a time function in relation to the mean generation time of populations. Thus, even for the ‘unstable’ environment there are two life-history strategies: either follow the fluctuations (boom-and -bust ephemeral species), or endure the disturbances (long-lived resistant species). For the latter, the environment may even no longer be unstable, only periodic (Kolding 1994).

Patterns in life-history diversification

The environmental variability experienced by a lake or reservoir is reflected in the biological responses of the various fish species in its community assemblage. The typical community assemblage of a system - its resource characteristic - is more or less determined by the ruling pattern of mortality that is determined by the community’s physical and biological environment. Depending on the variability of the abiotic drivers of a system at different temporal scales, dominant mortality patterns are either by abiotic or biotic causes (see previous section). Life history-traits of a species determine the population responses to environmental forcing and are based in fundamental demographic trade-offs. The essential features of these trade-offs can be captured by the relationships between three basic demographic parameters: survival, fecundity, and the onset and duration of reproductive life. Species can be classified along the three axes formed by these parameters into (Winnemiller and Rose 1992):

- opportunistic – small, rapidly maturing, short lived fish
- periodic – larger, highly fecund fish with long life spans

- equilibrium strategists – small and intermediate size fish that often exhibit parental care, and produce fewer but larger offspring

Table 6 Life history strategies and implications for management

	Life history strategy		
	Opportunistic	**Periodic**	**Equilibrium**
Environment	Temporally stochastic with small-scale patches	Seasonal with large-scale patches	Stable with fine-scaled spatial variation
Demographic trade-off			
1. age at maturity	low	high	high
2. fecundity	low	high	low
3. juvenile survivorship	low	low	high
Demographic character	Maximise (re)colonising capability of habitats over small spatial scales	Maximise age-specific fecundity, spreading of reproductive effort over many years and/or large areas	Maximise juvenile survivorship in resource limited, density-dependent environments
Life history traits			
- size	Small	Large	Small/medium
- age at maturity	Early	Delayed	Delayed
- size at maturity	Small	Medium/large	Medium
- clutch size	Small	Large	Small
- egg size	Small	Small	Large
- larval/YOY growth	Rapid	Rapid	Slow
- reproductive season	Long	Short	Long
- parental care	No	No	Yes
Primary management objectives	- Maintain critical minimum spawning biomass - Protection against large scale or chronic perturbations that eliminate key refugia in space and time	- Maintain appropriate age structure (including large specimen) - Spatial refuges directed at adult stock (including spawning habitats and migration routes)	- Maintenance of adult stock - Maintain integrity of adult habitat

Characteristics of the life-history traits associated with these strategies and the typical environment in which they appear are summarised in Table 6. The three strategies represent extremes over a range. To account for this, in particular for the large number of species found in between periodic and opportunistic strategists, later authors have added an ‘intermediate’ strategy (King and McFarlane 2003). Another useful category appeared to be a ‘salmonic’ strategy, very similar to the opportunistic strategists, but containing semelparous species with relatively high degrees of parental investment (McCann and Shuter 1997).

Freshwater fish appear to have a much more restricted range of strategies within the life-history space than marine fishes (Winemiller and Rose 1992). The opportunistic strategists differ from the classic *r*-strategists by having small rather than large clutches of eggs and yet have high reproductive effort. Equilibrium strategists differ from K-strategists by being generally small rather than large species. Among the periodic strategists are many migratory species, seeking for favourable habitats for spawning and reduce uncertainty by exploiting large scale temporal and spatial environmental variation. They have massive clutches of small eggs, spread over large areas. The life-history strategies thus are linked to population dynamics and responses to environmental drivers. For each life history strategy general management frameworks can be devised. For fisheries with limited information on catch history, no biomass information and limited biological data, information on life-history parameters such as maximum length, egg size, fecundity, size-at-maturity, growth-rate, generalised habitat and trophic characteristics of the adult populations will go at great lengths to provide basic insights in their reaction to fisheries potential (King and McFarlane 2003). In an ecosystem approach to enhancements, these basic characteristics could be more informative than trophic position alone, as they are informative on species reactions to environmental perturbations as well.

The regulation of populations and mortality as a key parameter

Fishing activity is but one of many stress factors to a population. If we can understand the adaptations and life history traits of a population to resist natural mortality factors (Table 6), we can also evaluate the effect of fishing on these stocks, their regenerative capacity and the potential for various fisheries based enhancements (stocking, introductions of new species). The diversity and abundance of natural populations is maintained and regulated through a series of interacting factors and associated fundamental concepts in population and community ecology such as: *density dependence*, *compensatory mechanisms*, *stability* and *resilience*. There is a distinction between internal processes that are regulated by the abundance of the population itself such as density dependence and external processes that are controlled by the surrounding environment and community of other species. Without compensatory properties, a population in a density controlled multi-species system exposed to long-term increased mortality from predation or fishing, would ultimately perish. Most theories on population and community ecology and life-histories can be reduced to show that the processes they aim to explain can be closely associated with the pattern and rate of mortality (Kolding 1994, 1997).

Probably few, if any, natural animal populations utilise or occupy their environment to carrying capacity (Andrewartha and Birch 1954, Slobodkin et al. 1967, Stearns 1977). Species will mostly either compete for the resources, or be predators. The influence that species have on each other is difficult to measure. On the other hand, if a competitor or predator is removed from the system and we then observe an expansion of other species, then competition or predation is demonstrated. Such multi-species interactions have been observed in many fresh water fisheries (Paloheimo and Regier 1982, Carpenter et al. 1985), where heavy fishing pressure on larger slower growing species lead to an expansion of smaller faster growing organisms. In a top down controlled system it is reasonable to presume that predation in the long term would 'maintain' prey populations close to their highest average surplus production rate (Slobodkin 1961, 1968, Mertz and Wade 1976, Pauly 1979, Caddy and Csirke 1983, Carpenter et al. 1985, Kolding 1994). The argument follows simply from the sigmoid curve where the highest sustainable surplus production of the prey population (dB/dt = max = MSY) is also the 'carrying capacity' (K) of the predator population. The predators can in theory grow to reach K (= $\mathrm{MSY}_{\mathrm{prey}}$), but if they overshoot they will reduce the net prey production and consequently decline themselves from food limitations. Any additional mortality at this stage (as in time lagged predator-prey oscillations), however, requires a change in the life history strategy if the prey is not to perish (Slobodkin 1974). In other words, when a population adapted to a relatively stable environment is submitted to more long-term changes in the external mortality forces, it must somehow respond by increasing the intrinsic growth rate (r) (Roff 1984). This requires stress response or compensatory mechanisms (intrinsic changes) which again are related to phenotypic plasticity, a trait that is particularly prominent in fish (Stearns 1977, Stearns and Crandall 1984).

r- K selection and size-specific mortality

In evolutionary terms, changes in the survival rate are less efficient in improving r than increasing the turn-over rate by decreasing the generation time. Empirical studies have shown that there is a strong inverse correlation between age at maturity and mortality, which can be considered as a trade-off between the advantages of being big and the probability of dying with time (Adams 1980, Gunderson 1980, Hoenig 1983, Roff 1984, Gunderson and Dygert 1988). Traditionally the explanation of this phenomenon was based on the well-known theory of *r*- and K selection (MacArthur and Wilson 1967, Pianka 1970, 1972, Southwood et al. 1974, Boyce 1984). This theory was associated with the environmental stability, or rather the degree of 'saturation' (density) a population can reach in relation to fluctuating and limited resources. However, considering the indefinable relationship between the carrying capacity (K) and life history traits (Stearns 1977, Kozlowski 1980, Reznick et al. 2002), the original interpretation of the *r*-K selection is in many ways an inadequate explanation. Other authors (Murphy 1968, Schaffer 1974, Wilbur et al. 1974, Stearns 1977, Horn 1978, Roff 1984) have therefore suggested that the different life-history styles should be considered a function of relative size-specific mortalities. In essence: abiotic mortality, caused by the physical instability of the environment, is generally considered to influence the whole age structure of the population of a species. Thus a low-somatic and high-reproductive allocation of energy indicates that continued existence of the individual beyond the first reproduction is not profitable due to the risk of dying from physical disturbances. On the other hand, biotic mortality (mainly predation) is considered foremost to affect the small/young individuals in a population (Cushing 1974, Ware 1975, Bailey and Houde 1989, Caddy 1991). Hence, if mortality is reduced with increasing size, it is advantageous to initially invest more in growth relative to reproduction. Empirically, this is corroborated by 'Copes rule' which states that in the evolution of relatively stable ecosystems there will be a tendency towards the development of larger sizes within the food-chains (Pianka 1970, Dickie 1972, Begon et al. 1990). In conclusion, the balance between reproduction and growth, in an optimal life history, seems determined from the relation between adult and juvenile survival (Charnov and Schaffer 1973, Horn 1978).

From this interpretation of the *r*-K selection principle, then theoretically, even for 'K-selected' species, a compensatory strategy against increased mortality on the adult stages would be to increase the turnover rate ($P/B = Z = r$, see Fig 14) by reducing the generation time. This has been corroborated by empirical studies (e.g. Power and Gregoire 1978, Kolding 1993b) that all showed a decreased age of maturity at increased adult mortality. Thus density, individual size, generation time, and changes in these attributes over time, are all seemingly close functions of death rates in a population. The product of density and size gives the biomass and the integration of biomass over time gives the production. A further condensation of biomass and production into the P/B ratio then directly reflects the mortality rate and vice versa.

The optimal exploitation rate and exploitation pattern

All the above principles can be used to outline a theoretical optimal exploitation. In a fish community with several trophic levels, the amount of production, the speed at which it is generated, and the way it is dispersed through the food-web, determines the production that can be harvested. For fisheries management, the most important implication of density-dependent limitations to growth is that a fishery must substitute one form of mortality for another, as the yield is simply the fished fraction of the total deaths. Consequently, in the traditional single-species production models, a reduction of stock size (from the theoretical $B\infty$ at the carrying capacity K) is the prerequisite for increasing the 'surplus', and calculations are aimed at estimating the point of highest net regeneration rate (MSY). However in a multi-species situation, if natural predation is already harvesting the resource close to this rate, then a fishery is an additional uncompensated source of mortality and the population is driven to collapse. Fortunately, predation mortality is in practice simultaneously alleviated, as few fisheries are focused on one single species and the predators are also being harvested. In fact, the top levels in an ecosystem often are the first to be exploited intensively (Regier 1977, Beddington 1984, Welcomme 1999). Management questions are then

1) how much of the production can be harvested (the exploitation *rate*), and
2) what is a rational harvesting strategy or exploitation *pattern* on the community; that is what rates should be applied to each stock.

These proportions (the optimal exploitation rate and pattern) are complicated in a multi-species situation (Dickie 1972, May et al. 1979, Beddington and May 1982, Caddy and Csirke 1983, Beddington et al. 1997). This is because the fishing mortality on one species not only will affect the target species, but also cascade through the system by either increase the lower trophic levels or decrease the higher trophic levels (Carpenter and Kitchell 1993). The proportion of the total generated production which can be considered as surplus, that is the part which is not used to maintain the population at a given level, is extremely difficult to define, and in fish stock assessments mostly depends on the mathematical model chosen.

In ecology, the *ecotrophic coefficient* (*E*) is defined as the proportion of the production (*P*) over a period of time by trophic level (*n*) available as 'yield' (consumption) to the next trophic level (*n+1*). Dickie (1972) deduced, based on theoretical considerations, that the ecotrophic coefficient in nature is unlikely to exceed a value of 0.5, from the relationship

$$\frac{P_{n+1}}{P_n} = E_n \cdot K_{n+1}$$

when the ratio of production between two trophic levels (transfer efficiency) takes the conventional value of 10% (e.g. Kozlovsky 1968, Christensen and Pauly 1993), and the gross growth efficiency (*K*) has a value of 20% (e.g. Kozlovsky 1968, Jones 1982). Similarly, Heal and MacLean (1974 p. 95) concluded "consumption [=ecotrophic] efficiency for vertebrates preying on vertebrates may exceptionally reach 1.0, but is probably below 0.5 in most cases". The upper operating limit of E of around 0.5 has been corroborated by quantitative analyses of trophic interrelationships in lake ecosystems (Machena et al. 1993, Kolding 1993a). In fisheries theory the *exploitation rate* (E) is defined as

$$E = \frac{C}{P} = \frac{F}{Z}$$

and in single species models, where man is the only predator, the exploitation rate also has a general recommended maximum value of 0.5. In a multispecies fishery situation, however, the ecotrophic coefficient is the fraction which should be *shared* between fishers and the fish predators, implying that the exploitation rate should be equal or less than the ecotrophic coefficient (Kolding 1993a).

The impact of fishing on a fish community can be illustrated by combining the fisheries and ecological concepts. In summary: The yield or catch is a fraction of the production and defined as $C = F \cdot \overline{B}$. From the *P/B* ratio production can be defined as *P* = *ZB*. The Maximum Sustainable Yield (*MSY*), which is the carrying capacity of the next trophic level, has a theoretical maximum value of around half the total production, thus:

$$MSY_{prey} = K_{predator} \approx \frac{P_{prey}}{2} \approx \frac{Z_{prey} \cdot \overline{B}_{prey}}{2}$$

The answer to the question how to share the MSY (or surplus production) depends on how one wants the fish community to be composed. In the absence of other information, a conservative exploitation rate of 0.5 on top-level predators and 0.25 on lower levels could be used which means that man becomes the new top predator and otherwise share the rest fifty-fifty (Kolding 1993a, 1994). Such a fishing pattern will in theory keep the relative abundance of fish in the community unaltered, but will lower the overall biomass. The principle, together with the impact of different fishing patterns, is illustrated in figure15, which for simplicity, assumes a steady state community where *MSY = 0.5P =0.5BZ*. Under logistic conditions the corresponding biomass would be at $B\infty/2$. The system is closed, the primary production finite, and we require that the original species composition (in this case 3 stocks at 3 trophic levels) should be conserved.

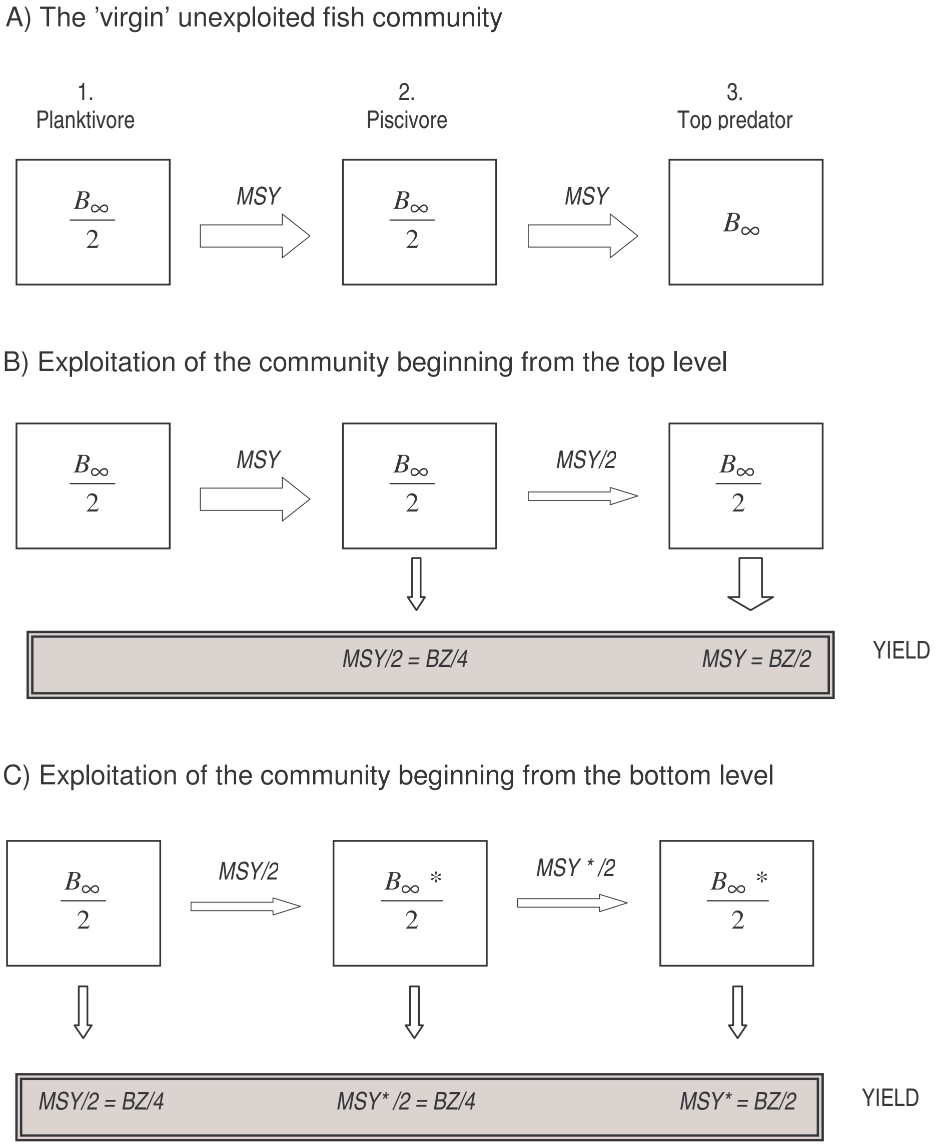

Figure 15. A simplified fish community of three trophic levels. Each box represents the biomass of each level (not to scale) relative to the 'virgin' biomass (B_∞) of each level, under logistic conditions. Arrows indicate the flow of energy (net production) through the system. See text for explanation.

Under unfished 'virgin' conditions (Fig. 15A) the energy source of each trophic level is defined by the maximum 'yield' from the level below. We then start exploiting the system from the top level (Fig. 15 B) by harvesting the MSY (i.e. reducing the 'virgin' biomass by half). This will decrease consumption by half and thus release half the 'yield' from the second level (MSY/2) for human exploitation, but in theory no 'surplus' is made available from the first level. In Figure 15C exploitation starts from the bottom level. Removing a proportion of the MSY from the first level will reduce the 'carrying capacity' of the next level and thus reduce its 'virgin' steady state biomass to a new value: B∞* (B∞*< B∞). This reduction will cascade up through the system and also affect the potential yields (MSYn*< MSYn), but in theory the system will find a new balance under the new carrying capacities. As the lower trophic levels are having the highest productivity (highest *P/B* ratio), the fishing pattern sketched in Figure 15C seems the most rational solution to exploiting the whole system (i.e. maximizing the output) without causing deep disturbances (Caddy and Sharp 1986, Kolding 1994). In theory, due to gear selectivity, such an exploitation pattern in a multi-species community can only be achieved by employing a multitude of fishing gears, which in combination can generate a size-specific fishing mortality that is proportional with the natural size-specific mortality pattern. Incidentally, in contrast with most fisheries theory based on single species considerations, effort in such a fishing pattern should in most systems be highest on the smaller sizes to match the prevailing natural mortality and at the same time conserving large specimen too (in particular of equilibrium and periodic strategists).

Fishing down the food webs and unselective fishing gear

Fishing almost invariably start with being highly selective, usually targeting the larger components of the community, which often are predators. Thus in virtually any fishery the first effect, that often also is perceived as sign of overfishing, is the decline of the larger species at the top of the food web (e.g. Fig. 10 and Turner 1977). This initial effect can in theory be considered as predator or competitor removal (see below), which releases surplus from lower trophic levels (Fig. 15B) though this may not have to be fish. For instance in Lake Malawi smaller, faster-maturing species have not become more abundant as the abundance of larger species has declined as a result of fishing (Turner et al. 1995). Normally the fishermen react by targeting the smaller individuals at lower trophic levels in the fish community (Welcomme 1999, Jul-Larsen et al. 2003). This, so called 'fishing-down-the-food-web' strategy has been suggested as highly questionable with regards to sustainability due to cascading implications for the stability of the ecosystems (Pauly et al. 1998). This conclusion was based on a general lack of increased landings with increased fishing on lower trophic levels in some selected marine areas. These areas, however, are largely managed by quotas and size-limit regulations, which could prevent the expected increase in reported catches. There are, to our knowledge, no data from freshwater fisheries that support the observation that fishing on lower trophic levels has resulted in stagnating or reduced overall catches. Furthermore, community metrics like trophic level, species diversity and composition in the catch, slope of the biomass size-spectrum (overall productivity) appear to be much more resilient properties of at least some ecosystems than size and relative abundance (Darwall 2001; Fig. 16 and 17).

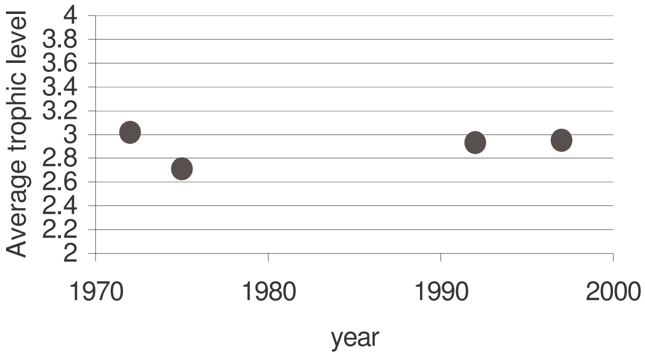

Figure 16. Development in trophic-level of the demersal cichlid community (114 species examined) in the experimental trawl catch of the heavily fished southernmost area of the South East Arm of Lake Malawi (based on Darwall 2001).

When the larger species decline the management authorities and the fishers usually react in opposite directions: the management by enforcing gear or mesh-size regulations, the fishermen by adopting other fishing techniques in order to compensate for the decreased catch rates by utilising the increased surplus at lower trophic levels. One such response is typically a decrease in the mesh sizes and increase in active methods such as seining (Jul-Larsen et al. 2003). Soon, a tug-of-war is established, and the fishermen are fulfilling the expectations as unruly members of the society that employ destructive, unselective fishing methods. In fact, it is this persistent tug-of-war that has initiated the recent massive implementation of various co-management programmes in small-scale fisheries (e.g. Norman et al. 1997).

The rooted perceptions of selectivity, however, are inherited from single-species theoretical models, and the feared destructive impact of the indiscriminate methods is rarely validated. In the few instances where the actual impact of non-selective (often illegal gear) used in small-scale fisheries has been studied, it is in reality an open question how "detrimental" these fishing methods are

(Misund et al. 2002). In the Bangweulu swamps, for example, the vast majority of fishing gears used are technically illegal, and consequently repeated fears of overfishing has been expressed. A closer investigation, however, revealed that while more than 85% of the catches were taken by illegal methods, there were no biological signs of overfishing, except on a few of the larger predators. Moreover, the overall fishing pattern (i.e. the combination and relative proportion of gears, methods, and mesh sizes) by the local communities appeared on an aggregated level finely tuned to match the composition of the fish community, and resulted in a maximised yield at a multi-species level (Kolding et al. 2003b). Similarly, the multi-gear, multi-species artisanal floodplain fisheries often seem to be producing an overall species-, abundance-, and size composition that closely match the ambient ecosystem structure (MRAG 1994, Claridge et al.1997, Hoggarth et al. 1999a,b). On the ecosystem level such an exploitation pattern may be considered unselective across the species diversity range, and floodplain fisheries, particularly in Asia, seem to have persisted unchanged (albeit with natural fluctuations) with a very high fishing effort for as long as our observations can tell.

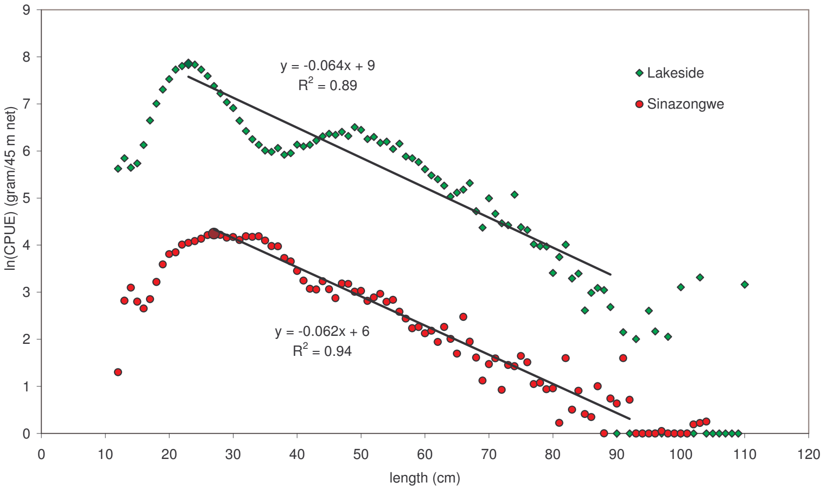

Figure 17. Comparison between a fished (circles, Zambia) and non-fished (squares, Zimbabwe) areas in inshore Lake Kariba. Mean biomass-size distribution with linear regression from experimental multi-mesh fishing during the period 1980-1994 for all fish caught in mesh sizes 50-152 mm. Linear regressions on ln-transformed standardised catch rates (gram/45 m net set) were made from length range 23-89 cm (Zimbabwe) and 27-92 cm (Zambia) (from the highest value to first 0-observation). The SE of the slopes are 0.0028 and 0.0020 for Zimbabwe and Zambia respectively which means that the slopes are not significantly different at 95% confidence level. The difference between the intercepts is the difference in the average standing biomass. Reproduced from Kolding et al. 2003a.

Many small-scale artisanal freshwater fisheries, particularly in freshwater environments, use a multitude of fishing techniques (some of which often are illegal such as small mesh sizes, barriers, weirs, and seines) in order to take advantage of all productive parts of the system they exploit (Turner 1996, Welcomme 1999, Misund et al. 2002). As a result of the multi-gear, multi-mesh situation they generate an overall fishing pattern which has a relatively uniform selectivity over a large range of the organisms and sizes. While such a fishing pattern generally is condemned and persecuted for being ‘harmful’, ‘unselective’ or ‘indiscriminate’, the actual result on the community could very well be a fishing pattern close to the theoretical optimal illustrated in Figure15C.

In lake Kariba, for example, the fish regulations on the Zambian side are virtually un-enforced, and with the increased fishing effort, the average mesh-sizes in the fishery have steadily decreased since the fishery was started. In addition, many fishermen are increasingly taking up illegal fishing methods such as beach-seining and ‘beat’-fishing. The average annual yield in the inshore Zambian fishery is presently around 20-30 kg/ha, which is 4 times higher than the highly regulated inshore fishery in Zimbabwe. However, when comparing the effects on the inshore fish communities, it appears that the relative community composition is the same both in terms of species and sizes (Kolding et al. 2003a). In other words, when comparing this practical example (Fig. 17) with the theoretical optimal fishing pattern (Fig. 15C), it appears that the unregulated inshore Zambian fishery, by intense competition leading to an unselective fishing pattern, is adopting an exploitation which optimise the yields while conserving the ecosystem structure. The relative abundance among the components (system structure) is relatively unchanged, only the standing biomass has been reduced proportionally over all sizes (Fig. 17).

7. Possibilities for increasing fish production in lakes and reservoirs

Increasing the aquatic production from lakes and reservoirs can be accomplished by better utilisation of the existing potential, either through fisheries management and better control of post-harvest losses, or through enhancements. Enhancements are interventions in the physical or ecological functioning of aquatic resources to increase food-production or production of high valued species for trade or for sport-fishing. They combine attributes of aquaculture - intervention in the life cycle of aquatic organisms - and capture fisheries - exploitation of natural resources Enhancement technologies include culture-based fisheries, habitat modifications, fertilisation, feeding, and elimination of predators/competitors. From the previous discussion we derive that increased production and enhancement technologies fall into three broad categories:

- increase the output from the available natural production
- modify the physical basis of production
- manipulate the biological basis for production

The first option is a better utilisation of the natural production through *fisheries development,* which includes ways of optimising the utilisation of the whole ecosystem through fishing or to increase relative surplus production by fishing down processes (Fig. 17). The second category ranges from *edaphic enhancements* by enriching or fertilising the water through artificial eutrophication, to *habitat enhancements* from improving favourable habitats, to offering specialised structures such as brush-parks, coves and cages that interact with the natural environment while containing the target species. Though not often seen as a potential for improving production, habitat enhancement should also include restoration of habitats by restoring the longitudinal and lateral connections between floodplains and rivers and between reservoirs and rivers; restoring the diversity of ecotones in reservoirs and/or by making use of the ‘flood-pulse advantage’, i.e. *hydrologic enhancements* by restoring timing, duration and amplitude of the food pulse in reservoirs in relation to life-history patterns of key-species. Combinations of habitat and edaphic enhancements (i.e. making use of the flood-pulse) exist where fish are concentrated and reared at falling water in depressions, ponds and lagoons in floodplains and flooded wetlands, sometimes with application of fertiliser and food, until they are harvested later in the dry season. The third option, changing the biological basis for production, includes enhancements by *manipulating stocks and species*. This option ranges from stocking of native species, to broadening the catch structure by introducing new species, constructing faunas of selected species, and eliminating competitors or predators that affect the mortality rates of the desired target species. All of these techniques have been utilised in natural systems and reservoirs, both in the context of enhancements to fisheries and in the context of rehabilitation to damaged lake and reservoir ecosystems. Most lakes and reservoirs are part of a river basin and approaches to management and options for restoration should be in an ecosystem/holistic context. Possible options to restore lake ecosystems depend on the spatial scale and the extent at which the perturbation has taken place (Fig. 18). For some practical advice and examples on rehabilitation of damaged lake ecosystems the reader is referred to Cowx (1994, 2002) and Cowx and Welcomme (1998). EIFAC is preparing a text on methodologies for rehabilitation of lakes and reservoirs. (FAO 2002).

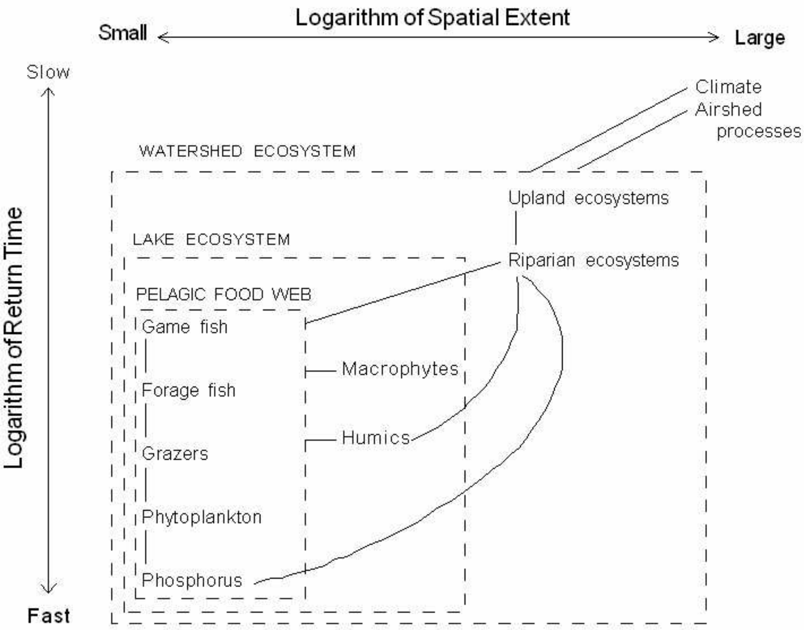

Figure 18. Major interactions in the normal dynamics of lakes as a function of spatial extent (x-axis) and return time (y-axis). Boxes enclose 3 commonly-recognized subsystems: the watershed (largest box), lake (medium-size box), and pelagic zone (smallest box) (Adapted from: Carpenter and Cottingham 1997)

The spatial scale of possibilities of control and impacts

The range of techniques that are used to enhance fish production in reservoirs and lakes can be ordered in rough orders of magnitude of production per unit area of water (Fig. 19). This ordering also follows a simultaneous axis of increased human control over the life-history parameters of the targeted species or the parameters controlling the fish community assemblages. All enhancement techniques are attempts at reducing temporal variability and optimising the biogenic capacity of natural systems. However, the productive area (spatial scale) over which control can be successfully exerted also decreases with increasing intensification.– where success is measured as an increase in predictability of outcome. In short, the size of the system can be said to be inversely related to the enhancement potential apart from the natural production (Kapetsky 1998).

While fishing takes place over the range of the coverage of resources from the space of an individual sports-fisherman to spaces as large as the Pacific-Ocean fished by fleets of long-liners and driftnetters, stocking and introductions have impacted lakes as large as Lake Victoria with the introduction of the top-predator Nile perch (*Lates niloticus*). For most of the larger inland lakes and reservoirs as a whole, it can be safely claimed that they are technically out of reach for any type of productive enhancement other than through fishery development and introduction or stocking of species. The outcomes of species introductions are extremely difficult to predict and great care should be taken, especially when dealing with large natural systems (see various contributions inPitcher and Hart 1995, and Hall and Mills 2000). In generally species introductions can be done with more confidence with species at lower trophic levels as pelagic zoo-planktivores (e.g. Coasta-Peirce and Sumarwoto 1990, Pitcher 1995) or detrivores and herbivores (Hickley et al. 2002), at smaller spatial scales and in more predictable and/or stable environments. Impacts of stocking and introductions of species at lower trophic levels in relatively confined and stable ecosystems at the scale of oxbow-lakes and small reservoirs can be predicted fairly accurately (e.g. Phan and De Silva 2000), and advise on the relative stocking rates of suites of species has been given based on some

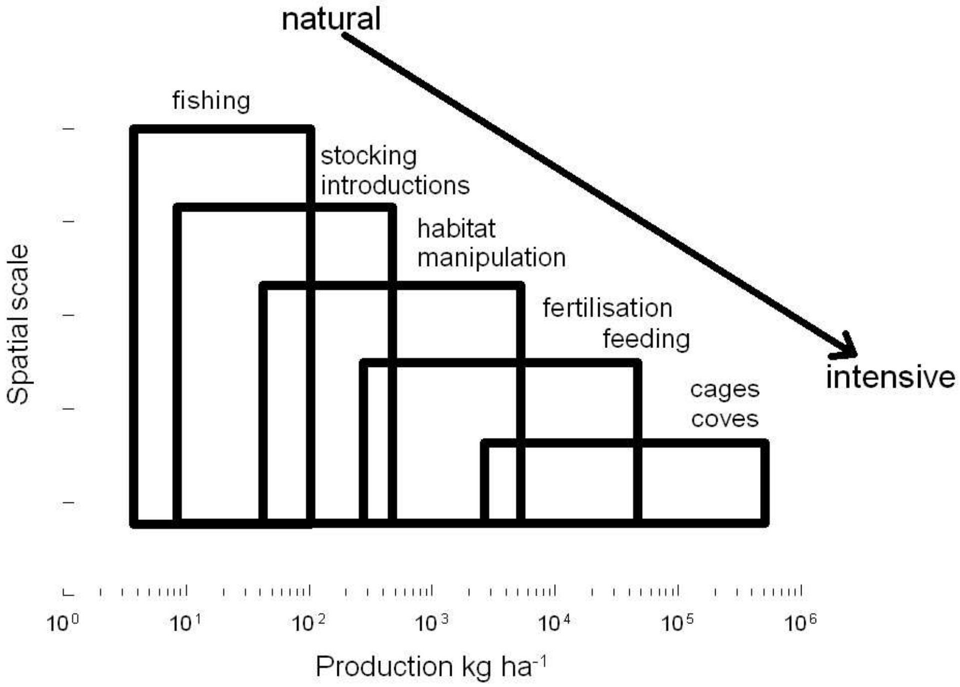

Figure 19. Production potential per unit area versus spatial scale of production units of the various methods used in lakes and reservoirs. Arrow indicates the perceived increased environmental impacts moving from natural harvest to intensive culture. (Ranges of production are tentative).

simple measures of the lake environment as transparency and macrophyte cover in relation to particular carp species (Hasan et al. 1999). Yet, even at these small scales of oxbow lakes unsuspected interactions with the existing communities can take place (Haque et al. 1999 see below). Cascading effects of impacts of species removal at lower trophic levels in relation to the trophic status of the ecosystem can be relatively well predicted in some cases. For example the removal of the detrivorous bream *Abramis brama* in temperate shallow lakes lead, in combination with reduction in phosphorous load, to a complete state-shift from turbid to clear water with different (fish) communities associated with each of the two states (Scheffer 1998). It remains, however, extremely difficult in large environments - for instance on the scale of a river - to advise on the scale of habitat change or protection necessary to achieve desired fish communities (Grift 2001). As is clear from the ongoing debate on the impact of marine parks on fisheries, this is true as well for other open environments (e.g. Russ et al. 2004). Habitat manipulations on smaller confined spaces could be more successful (Scheffer 1998), and elimination of species through removal of essential habitats seems easier than improving stock status by offering or constructing new habitats.

The role of the littoral zone for productivity along lakes and reservoirs is now well known. Therefore, improving stocks of species important for fisheries by regulating the flood pulse within reservoirs and below dams in concordance with the seasonal habitat requirements of these species, should give ample scope for enhancements with effects on relatively large scales. Habitat manipulations that aim at changing the trophic status of smaller lakes can be well predicted, for instance in attempts at reversing effects of acid rain. However increasing productivity through fertilisation and eutrophication usually has been limited to smaller inland waters. Nevertheless, some of the increased production in parts of the North Sea (Boddeke en Hagel 1994) or the Mediterranean (FAO 1995a) is believed to be caused by nutrient inflow from land-based activities, ranging from release of untreated municipal waste water on rivers to agricultural activities. The technological scales at which more intensive cultures – pens, cages, brush-parks - can be practised, including their operational requirements, makes them shore bound. This means that for these types of enhancement, shoreline length and development are much better indications for enhancement potential then lake surface area.

In the following section we will briefly discuss a number of options to enhance fisheries in lakes and reservoirs. We refer to Welcomme and Bartley (1998), Petr (1998), De Silva (2003) and Moehl and Davies (1993) and references mentioned in the various sections below that give more in depth information on the many possibilities that we can only briefly hint at here. Instead we will attempt to link the various possibilities for enhancements to the ecological principles outlined in earlier chapters, and to mentioning a few possibilities rarely encountered in the literature.

Increased yields through fisheries management

- Utilising maximum productivity of ecosystems over long ranges of effort
  - increase in production by exploiting small pelagics
  - ecosystem fishing according to productivity of each trophic level and adaptability to fluctuations
  - fishing down; by reducing predator biomasses

In natural resources management the only available methods are regulating the exploitation rate and/or the exploitation pattern. Consequently, the management options in most capture fisheries basically consist of either effort control[14], or gear regulations, where the latter is the predominant type in most small-scale freshwater fisheries. Due to the scarcity of available data, the impact of unlimited effort control is difficult to demonstrate in tropical freshwater fisheries, particularly in fluctuating environments where natural changes often play as big a role as effort (Table 5, Welcomme 1999). In Africa, where nearly all fisheries are of open access nature, there has been no clear indication that increases in nominal effort *per se* has led to declining yields in contrast to situations where increases in effort were caused by directed technological improvements (Jul-Larsen et al. 2003, SOFIA 2004). On the contrary, total yields in small-scale multi-species and multi-gear fisheries are surprisingly stable over a large range of effort, and a decrease in overall catches is mostly due to adverse environmental conditions. Furthermore, variations in nominal effort levels were found to a large extent to be a reflection of the variations in the productivity of the ecosystems (see Fig. 4), rather than vice versa as the classical stock assessment models assume. If productivity is driving the effort then the catch per unit effort would, in terms of an economic break-even, probably be a regulating factor by itself, or as Beverton (1990) puts it "[some].. fisheries cannot be driven to extinction because fishing will disappear before the fish".

Mesh size- and gear restrictions are among the most easily applied and widely used management regulations. Consequently most nations have imposed legislation, which bans certain gears and mesh-sizes with the aim of protecting the resource (Gulland 1982). Capture devices are intrinsically associated with selectivity, and selectivity, or the impact of fishing on an ecosystem, is an essential component of most management schemes. The importance of selectivity is therefore rooted in most researchers and managers, and any non-selective capture method automatically carries the connotation of being harmful, bad, or destructive (Misund et al. 2002). Although numerous authors have already pointed to the problems of defining the “right” mesh-size (e.g. Gulland 1982, Marten and Polovina 1982, Turner 1996, Murawski 2000, Hilborn *et al*. 2004) in a multi-species fishery, the notion of regulations on selectivity still persists. Small-scale freshwater fisheries often use a variety of gears, both traditional and modern such as synthetic gillnets. Many of these gears, and particularly the traditional, such as seines, small mesh-sizes, drive- or beat fishing, barriers, and weirs, are often classified as illegal under the pretext of being non-selective with assumed negative impacts on the fish populations.

On the other hand, the multi-gear (overall unselective) fishing pattern employed in many small-scale fisheries, combined with the ability of fishermen to change their target species within a single trip, is perhaps the closest example of the optimal exploitation pattern that exists. Therefore, the established fishing practises versus legal frameworks may easily become not only an infinite tug of war, as seen

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[14] Quotas and TAC’s are just another way of regulating the exploitation rate, but require generally more data to implement.

in most instances where small-scale fisheries have resisted the implementation of gear restrictive regulations, but also a completely futile tug-of-war as seen from the perspective of ecosystem conservation (Misund et al. 2002, Jul-Larsen et al. 2003, Fig. 15 and 17). From the point of view of productivity there is no doubt that the largest natural potential is from the lower trophic levels of the harvestable community with highest P/B ratios. It is therefore a paradox that management authorities, either through decree - or more recently through co-management approaches – persistently insist on minimum mesh-size regulations, and that "fishing down the food webs" has a conceived negative image. Small-scale fisheries in tropical freshwater systems that employ a high diversity of fishing gears, including many which are technically non-selective, are far more yielding than those under forced regulations, and few, if any, has resulted in negative ecological effects (see section 6.7). We believe that there is a great potential for improved productivity if the present paradigms are changed and more effort is dedicated in studying a multi-gear fishing pattern in multi-species fisheries.

Enhancements through manipulation of the physical base of production

Edaphic enhancements

- Nutrient loading

In general it can be said that stocking alone will not result in long term sustainable increase of production unless it goes together with some measures to increase the carrying capacity of the system stocked and/or reduce predation. One of the measures that can be taken – besides habitat modification or stocking of mixtures of species that in themselves will change the carrying capacity of the system by utilising resources more efficiently (discussed below) - is through nutrient enhancement or fertilisation. The practice is widespread in small water bodies in China and Russia (viz. citations in Welcomme and Bartley 1998) and fertilisations of North American lakes has been proposed varying according to climate regime, lake type and species (Moehl and Davies 1993). Regional specifications are necessary in order to predict the impact of eutrophication on larger natural or man-made ecosystems. In Europe, for example, Salmonidae, Percidae and Cyprinidae succeed each other along a trophic gradient as the dominant group from low to high productivity, and expectations can be formulated as to the effect of eutrophication on natural fish communities. No such generalisations can be made in South East Asian (and Asian in general) or African waters because of the high taxonomic differences and diversities between various bio-geographic areas of these regions. However, it may be possible to make a crude categorisation of the fish community on the basis of altered trophic relationships along the productivity gradient, but within different ecosystem types – as for instance deep branched reservoirs vs. shallow saucer-shaped lakes or stable and pulsed systems. This approach might be more feasible for the different bio-geographic regions as a whole. Not only the impact of a fishery, species introductions and/or the stocking of juveniles (Densen et al. 1999), but also the effect of nutrients through deliberate or inadvertent eutrophication may be more clearly shown.

Dams can enhance some riverine fisheries, particularly tailwater fisheries immediately below dams that benefit from discharge of nutrients from the upstream reservoir (WCD 2000 op.cit.).

- Temperature

Areas where heated cooling water is released in natural waters near power plants are often used to construct cages, pens or other structures to produce fish. If discharge is from the lower layer of water in the reservoir, lowered temperatures in the receiving tailwater can curtail or eliminate warmwater river fisheries and require stocking with exotic coldwater species such as salmonids (assuming that the water is sufficiently oxygenated). Productive tailwater fisheries targeting these coldwater fish can ? be achieved but generally they require supplemental hatchery programmes and the introduction of coldwater invertebrates to serve as food for these fish (Jackson and Marmulla 2000)

- Artificial upwelling

Though we have no information on any theoretical or empirical work that considers the possibility of artificial upwelling in freshwater systems, artificial upwelling is viewed as a potential to increase marine production in enclosed areas such as fjords (Y. Olsen, pers. comm.) as well as open oceans

(Kirke 2003). Productivity could be enhanced by pumping nutrient-rich deep ocean water to the surface to feed phytoplankton, the bottom end of a marine food chain, mimicking natural upwelling which sustains the most productive ocean fishing grounds in the world. Various pump types and power sources have been proposed for this purpose.

Hydrologic enhancements

- restoration or inducement of flood pulse
- adapt drawdown and inflow of reservoirs to life cycles of important species

Many medium-sized lakes and reservoirs are intimately related to the rivers that flow into them. The productivity of these waters is dominated by the change in hydrological regime through periodic influx of nutrients. Equally important for the fish production of these systems are the flooded marginal littoral areas – the ecotone. A continuous gradient from floodplains to lakes could be constructed based on the impact of the flood-pulse to such systems (Jul-Larsen et al. 2003). Water levels of reservoirs in particular, being dammed rivers, can be regulated to induce a flooding regime to the requirements of the various species that make use of the periodic inundations of the littoral zone. Welcomme and Halls (2001) present a series of generalised recommendations to regulated floodplains that can be adapted almost unchanged for reservoirs:

- Floods of marginal areas in reservoirs must be induced, preferably every year but if not every year then at least with sufficient frequency as to allow all species that make use of the littoral to reproduce within their life spans.
- Flood releases should be timed to arrive after the wetting of the marginal areas by local rainfall. This means that the water volume is used to maximum efficiency in flooding rather than in saturating the desiccated soils.
- Flood curves should be as smooth as possible to avoid repeated advances and withdrawals of the water that strand and desiccates eggs adhering to marginal vegetation and nests.
- Rises and falls in level should be relatively slow. This in order to avoid rapid submergence of nesting sites, and failure of vegetation to adapt and grow in the rising phase and stranding during the falling phase.
- High short floods should be alternated with lower but longer ones to favour all groups of species.

Habitat enhancements

- preparation of reservoirs for fishing and culture activities in planning stage
- destroying potential spawning or nursery habitats of unwanted species

Habitat enhancements are meant to improve on the specific requirements of fish species and communities for feeding, breeding, nursery and shelter. Preparations of reservoirs prior to filling may include the removal of trees and general preparation of the reservoir bed for effective harvesting, and grading of shores to offer specific habitats. Destruction of critical spawning or nursery habitats for unwanted species (in particular predators) is common practice in smaller reservoirs in China.

- habitat restoration: connectivity, rehabilitating soils, offering of specialised structures to enhance long range migrations and short range movements.

Where rivers have extended floodplains, fish production is elevated, and the same can be said of reservoirs with well functioning ecotones to enhance lateral processes (Junk et al. 1989, Karenge and Kolding 1995a,b). Suitable habitats, vegetated lakes or marshes along lake shores, are important for limnophilic species. Restoring connections of secondary channels and oxbow lakes in floodplains of rivers that are normalised and embanked is needed to rebuild populations of rheophilic species (Grift 2001) and to enhance upstream processes (Vannote et al. 1980). Construction of fishways (fauna passes) etc. to maintain or restore longitudinal migrations (upstream and downstream) in even the smallest weirs or dams is imperative. Fish pass technology can be adapted to the local context, including flow regimes and characteristics of the ichthyofauna (e.g. species composition; latitudinal gradients in anadromy/catadromy; size of migrants; species with drifting eggs; incentives to migration) and should be constructed to allow up- as well as downstream passes of fish.

- offering new habitats
  - Light attraction
  - Fish Aggregating Devices
  - Artificial reefs
  - Brushparks, vegetation parks

Enhancements of fisheries through offering specialised habitats that attract species have developed in many areas in the world. Light attraction, fish aggregating devices, artificial reefs and brush-park systems have been invented many times over in different places of the world. For instance light fisheries developed in many African medium sized lakes during the seventies and eighties, while Fish Aggregating Devices (FAD) used in medium sized lakes as Lake Mweru and Lake Malawi are a very recent development, in Lake Malawi as recent as this century (van Zwieten pers. obs.). Artificial reefs are now being proposed as one solution to the depleted fishery of Lake Malombe in Malawi (Bell and Jamu 2003). All techniques are combinations of local enhancements of habitat by offering shelter and/or enhanced food availability by which species are attracted, while brush parks and vegetation parks also may act as breeding grounds. Vegetation parks appear under a range of names in various parts of the world. Basically there are two main types (Azim 2001, Welcomme 2002): those constructed from dead branches of trees and shrubs (brush parks) and those constructed of floating vegetation (vegetation parks, FAD's) and may appear in rivers, lakes and reservoirs. Brush parks are usually confined to more shallow waters, while the use of floating vegetation, often anchored to the bottom, may be utilised in deeper lakes and reservoirs as well. Yields from brush parks and vegetation parks may be very high, when used as aquaculture systems, to the point of semi-intensive aquaculture systems (Welcomme 2002). How brush parks perform as enhancement technology, depends on the function it has for fish species attracted by them: shelter, as fish aggregating device (FAD) or as spawning/nursery area. Only in the latter case it can benefit other fisheries when fry distributes from the park into the lake/river system, but otherwise they compete with adjacent fisheries in space and resources. Studies to investigate the feasibility of brushparks for fish ranching are now carried out in various places in Asia (Azim 2001) and Africa, e.g. in Lake Chilwa, Malawi (Jamu et al. 2003).

Tugend et al. (2002) investigated the use of abiotic enhancements and divided habitat structures into four general categories: cover, spawning, shoreline stabilization, and substrate structures. The majority of habitat structures surveyed were used to attract fish to improve angler catch and harvest (71%), but other objectives included improved recruitment of juvenile fish (39%), increased fish production via creation of spawning habitat (34%), and creation of adult habitat or sanctuary (30%). The most widely used habitat enhancement structures were brush piles due to low cost and availability of materials. Although habitat enhancement structures were widely used, only 40% of respondents evaluated for fish-population responses. Evaluations usually comprised catch-per-effort of fish in structures but did not assess fish recruitment or survival responses to habitat enhancements.

Enhancements to improve the biological base for production

Enhancements through manipulation of the fish community

- species introduction
  - single species introductions
  - multispecies introductions
- stock enhancements
  - single species enhancements
  - multispecies enhancements
  - predator enhancement
  - predator control

Stock enhancement has two components: to add or subtract species or to alter the relative stock density. Apparently adding new species is viewed as a viable management option, judging from the high number of introductions that have taken place and are still taking place around the world. A few facts to illustrate the impact of introductions[15]

- It is estimated that approximately 17% of the world's fin-fish production is due to introduced species.
- The production of the introduced and cultured African tilapia is much higher in Asia (>700 000 metric tonnes in 1996) than in most areas of Africa (39 245 metric tonnes).
- Introduced salmonids in Chile support a thriving aquaculture industry that is responsible for approximately 20 percent of the world's farmed salmon and directly employs approximately 30 000 people.

The successful introductions of small lacustrine pelagic species in many African reservoirs were mentioned earlier.

Much attention is directed to constructing faunas of selected species, by introducing balanced mixtures of species exploiting various trophic levels and spatial niches. Usually these include mixtures of bottom feeders, higher vegetation feeders and pelagic zooplankton and phytoplankton feeders. Other mixtures occur but are not common (Welcomme and Bartley 1998). In China much experience has been gained in determining the relative composition of the mixtures of species in relation to system trophic status and other physical parameters in culture ponds. The remarkable success of culture-based fisheries in Chinese reservoirs that are reported to have raised average yields from 150 to 750 kg/ha/year (Huang et al. 2001), is based on the stocking of riverine major carps that are unable to reproduce successfully under the lacustrine conditions of reservoirs, but can make good use of the available food resources. Here, stocking of large fingerlings (50g = 5 months old!) is preferred as this is thought to reduce predation (up to 100 kg.ha^{-1} or 2000 individuals). Eradication of predators by netting adults also appears to be done, again mainly in smaller reservoirs. Long term removal of predators, particularly in larger reservoirs, is virtually impossible to achieve. In Bangladesh the development of culture based fisheries has been attempted through stocking oxbow lakes (successful) and floodplains (unsuccessful). In floodplains the exception was common carp that did very well as it profited from the debris of the marophyte canopy. Similar experience was obtained in Papua New Guinea when common carp was inadvertently introduced in the Sepik river (Ulaiwi 1990).

This highlights that the eventual success of introductions varies with local level conditions as for example the difference between phytoplankton and macrophyte dominated systems. The successful stocking of oxbow lakes with mixtures of carp species has been optimised by relating the relative composition and the stocking densities to light attenuation in the lakes. Apparently the culture-based fishery also impacted the production of naturally recruited indigenous species, when the catches of the latter exceeded the catches in non-stocked oxbow lakes (Haque et al. 1999). This shows that unexpected interactions with native species through a release of otherwise unavailable resources for fish production can occur even with relatively stable systems as oxbow-lakes. Non-predator introductions in natural or artificial lacustrine communities have often become established to a greater or lesser extent, which could be related to the plasticity in feeding niches and other life-history requirements of many of the detrivorous or herbivorous species used. This then would allow greater degree of “niche-packing” and restricts effects on long term stability of the existing fish communities. Resilience of species to introductions and “niche-plasticity” may also be a function of the adaptation of the species communities present in the highly predictable but variable conditions of the pulsed systems of floodplains.

In general, the successful and sustainable introduction of new species depends on the identification of open niches in the food web, such as margins (tilapia foraging on algae, plant material and insects), open waters (small, pelagic planktivorous) of newly built reservoirs (Fernando 1994, Fernando and Holčik 1991), or in natural systems with depauparate fish communities (Coates 1987, 1993). A similar understanding of trophic relationships, as for instance predation pressure of piscivores on

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[15] http://www.oceansatlas.com/; DIAS - Database on Introductions of Aquatic Species http://www.fao.org/figis/

small fish, and life-history requirements is also needed when stocking programmes for culture based species are planned (Manni 1992). The numerous attempts at polycultures in pond aquaculture of mixed predator-prey species have never been successful, which is an indication of the problems in understanding, let alone exploiting, predator-prey relationships in culture based systems.

Introductions of predatory fish can be done for various reasons: to improve angling possibilities for piscivorous game; to make greater use of fish production which otherwise might be lost, because prey fish are not caught or consumed; and as a tool in biomanipulation for the purpose of water quality management (Densen 1994). Predator enhancement is easier to apply in the controlled environment of a fish pond than in lakes or reservoirs. From a fishery point of view, the introduction of predators has been successful in some cases (*Glossogobius giurus* in Lake Lanao in the Philippines; *Cichla ocellaris* in Gatun lake in Panama, *Lates niloticus* in Lake Victoria, *Oncorhynchus mykiss* in Lake Titicaca in Peru/Bolivia), but all predator introductions resulted in long term perturbation, destabilisation and simplification of the natural community (Hall and Mills 2000). Often it is the endemic species that face greatest reductions to the point of extinction. From a productivity point of view, the introduction of predators, may not be the best solution. As shown in the previous sections predators play a major role in regulating fish communities in the tropics, through predator induced mortality of prey stocks. An interesting example of the long term effects of predator introductions comes from NE Brazil, a dry region with a sparse natural fish fauna, where lakes were stocked with predators in 1933. Here a significant relation between number of predator species and catch rates is reported: highest catch rates were produced with 2 predator species. With higher numbers of predators or only one predator lower yields were recorded (Paiva et al. 1994).

The opposite management option is to decrease predators in order to release fish production from desirable fish species at lower trophic levels. In culture based fisheries for Chinese and common carp in Chinese reservoirs, much higher catches are gained by predator control, such as the selective removal of the up to 2m long *Elopichthys bambusa* (Cyprinidae) (Ganscheng et al. 1992, Jiankang et al. 1992), and the smaller predatory cyprinids *Erythroculter dabryi* and *Culter erythropterus* (Jiankang et al. 1992). Similar fishery enhancements have been attempted in small Thai reservoirs with limited success due to the low survival rate of the too small fish used for stocking (Manni 1992).

Introduced *Puntius goniotus*, *Oreochromis niloticus* and *Labeo rohita* seldom gain dominant positions in the catches on larger reservoirs in Thailand, Malaysia as well as Indonesia (Densen et al. 1999; Fig. 8). These authors conclude that most inland fisheries in Malaysia, Thailand and Indonesia rely on endemic species with (sometimes) large shares of piscivorous snakeheads and catfish, whereas in the Philippines this position is taken by the goby *Glossogobius giurus*. Only in the Philippines do introduced/stocked species (common carp, tilapia) contribute significantly to the total catch of inland waters. Sri Lankan fisheries in small reservoirs depend almost totally on the introduced tilapia *Oreochromis mossambicus*, with a reduced importance of predatory fish because of intensive gillnet fishing (Pet 1995). In China the culture based fisheries in smaller reservoirs (mainly Chinese carps) benefit from predator control, even from small piscivores, while the opposite strategy - crop small trash fish in freshwaters by stocking the piscivorous sea bass *Lates calcariferous*, that only spawns in brackish water, is an option considered for Sri Lanka (Senanayake and Fernando 1985 cited in Densen et al. 1999).

Enhancements through culture based systems: from open to closed aquaculture

- Offering habitats in natural conditions: the link between aquaculture and enhancement
    - Collecting and reseeding (e.g. mussel cultures and many other shellfish culture systems) on settling and growing substrates
    - Drain-in ponds, fingerponds and control of floodplain lagoons
    - Coves
    - Cage culture

Enhancement practices range from making use of natural production in fisheries to almost complete control of environmental and life-history parameters in semi-closed systems. Many of the current enhancement practices find their origin in ancient practices of trapping fish and improving their growth under more or less controlled conditions. These practices are well known from floodplains where fish are trapped in natural and artificially constructed holes, lagoons and traps and pens during receding floods and reared with or without application of fertiliser and food until harvest[16]. In Uganda and Kenya so called "fingerponds" are extensions of such historic practices: they are dug at the swamp edge in the dry season, the excavated soil is spread around their perimeters and used for gardens. The ponds are stocked naturally during the seasonal floods with fish migrations into the littoral zone: they become cut-off as the waters recede. Trapped stocks of small fish are dominated by cichlids, mainly tilapias that constitute 80% - 90% of the total biomass, but with a high variability in 2000-3000g up to 10,000g per pond (corresponding to 100-150 kg and up to 500 kg ha^{-1}). Chicken or cow manure, from village compounds, is used to fertilise ponds. Fish harvests in various ponds ranged 85-1150 kg ha^{-1} after 7 or 8 months. Water and nutrient balances, food webs isolated in the ponds and fish yields are currently studied for optimisation possibilities (Denny et al. 2004).

Collecting from the wild and reseeding on more productive grounds are practised in various shellfish cultures in estuarine areas, and dammed brackish water areas. To our knowledge such practices are not done as extensively in freshwater systems. But, for example, in the fingerponds just described simple methods for transporting fish trapped in ponds with high densities to ponds where fish were needed for stocking are tried out.

Intensive culture practices are often done in areas of reservoirs or lakes that are cut of from the main body. This ranges from seasonal pen cultures, as practised in the Tonle Sap in Cambodia or Laguna de Bay in the Philippines, where species are trapped and reared in large structures set-up when the lake is flooded. The dendritic form of many reservoirs gives good possibilities for isolation of bays through various means, where the isolated area can then be utilised as an intensively managed fish pond. Very small reservoirs may be used as large fishponds: in small 16 ha ponds or reservoirs in China stocking and fertilisation yields as much as 4000–6000 kg. ha^{-1} (Welcomme and Bartley 1998, De Silva 2003). With increasing knowledge of the ecological processes in these smaller and larger ponds there will be an increased potential to control these processes. Though this could lead to utilising larger spaces in lakes and reservoirs with similar technologies, the general tendency in aquaculture research is to exert more control on ecological processes by closing off systems from natural variation or reducing it as much as possible. High fish productivities are integral to highly fluctuating systems. Thus approaches to make use of the flood-pulse advantage could be much more promising for larger reservoir ecosystems as well as in restoration of degraded floodplains when there is a possibility to control flood-pulses.

Another step towards more closed systems comparable with more intensive forms of land based aquaculture is cage-cultures. Cage-culture is common in central and South-east Asia in countries like China, Thailand, Indonesia and the Philippines (Beveridge 1996, Beveridge and Stewart 1998). A wide range of marine and freshwater species are cultured in cages, for freshwaters including tilapia (*Oreochromis* spp.), *Pangasius* catfish, grass carp (*Ctenopharyngodon idella*) and many others. The origins of cage aquaculture could date back two millennia or so to China (Beveridge and Little 2000). In the Tonle Sap, the great lake of Cambodia, floating cages have been used for more than 100 years while in Indonesia both floating and anchored cages have been in use since the 1940-ies. More traditional cage culture production, as for instance practiced in the Tonle Sap where *Pangasias* catfish are fed with trash fish caught in the lake, is generally small in comparison to capture fisheries production. Small-scale cage-culture activities may be distinguished from the intensive cage production systems by their reliance on natural construction materials and low levels of feed inputs. Modern, intensive cage-cultures are typified by the use of synthetic, manufactured materials and commercial feed inputs. Freshwater tilapia cage-culture originated in the USA during the late 1960-ies, well after the development of the marine cultures of yellowtail (*Seriola quinqueradiata*) in Japan and Atlantic salmon (*Salmo salar*) in Norway in the 1950-ies and 60-ies (Beveridge 1996). Cage

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[16] see contribution by Welcomme for an extensive discussion of these practices: "Role of Fisheries in improving water productivity in rivers and floodplains"

cultures have the advantage above land-based systems that they do not make claims on scarce land resources. Cage cultures develop independently from, but are often closely associated with other forms of enhancement. Among the synergetic effects are stocking through escapement of cultured species from cages to the wild and through the eutrophication of the lake environment through the leaching of nutrients and excess food into the natural environment (Beveridge 1984, Beveridge and Muir 1999). The many facets of semi-intensive to highly intensive aquaculture, however, are outside the scope of this review. However, the real challenge in developing enhancement technologies is to find synergies between cultured and natural production that can enhance both whilst conserving ecological integrity and biological diversity.

8. Concluding remarks

Apart from floodplains, tropical lakes and reservoirs are already among the highest yielding aquatic ecosystems in the world on an area basis. This is due to their high biological turnover stemming from the climate, their general shallowness, and the high nutrient inputs from the surrounding catchments. But also because they are used already to varying degrees to extract production with the enhancement techniques discussed above and illustrated in Fig. 19. Vast opportunities exist for increases in productivity from a purely biological point of view, but the desired potential is a socio-cultural and political question. Any ecosystem has a limited capacity for primary production, and thus a ceiling for higher order trophic levels. The basic question is how one wants to make use of these resources. As in fisheries, where fishing mortality must substitute natural or predation mortality, any manipulation of energy pathways, for example through the enhancement technologies discussed, must also substitute another pathway. The only exception, perhaps, is when the natural productivity is increased through nutrient enhancements, but also this will create large changes to an ecosystem that are difficult and costly to reverse. There is no objective balance between the various methods and no universal rules to be followed, though methods of exposing and weighing of sustainability trade-offs are increasingly used to assist in decision making.

Ecosystem studies are mostly concerned with the relationships and fluxes of energy and material within defined groups of organisms. The universal functions in any ecosystem are: CO^2-, nutrient-, and water uptake and loss; and energy absorption, transfer, and emission. The endogenous ecosystem properties accruing from these functions are (Woodward 1993):

- characteristic dynamics of disturbance (biotic and abiotic),
- resistance to change,
- resilience following change,
- and succession.

Under these circumstances, the relevant questions may thus be: how critical is the performance of each species in maintaining the performance of the system? Or simply: how many species do we need? One might well conclude that as long as there are some plants, some consumers and some decomposers, ecosystem services would continue to be provided (Pimm 1993, but see also Naeem et al. 1994). From this perspective, the potential for increased productivity directed to human use would be straightforward. One would simply have to channel as much of the available energy as possible into palatable products. This means a simplification of the aquatic ecosystems to a point comparable with the low diversity found in the vast tracts of land used for intensive agriculture. Few, however, would probably agree with this and thats is the normative dilemma. Inland waters and reservoirs belong to the most diverse of aquatic systems and the variety and extremes of tropical lakes by far exceed those from temperate climates. Techniques such as valuation of ecosystem services are helpful in highlighting trade-offs, but cannot replace normative choices. Valuing biodiversity, for instance, is ultimately a purely qualitative exercise, and we have an obligation to conserve it. That means that our possibilities for increasing productivity in natural aquatic systems are limited.

Any method for increasing the yield or enhancing the productivity must be carefully evaluated against scarcely quantifiable trade-offs. Tentatively we would suggest that there are three main system criteria to take into consideration: scale, resilience, and origin. The ordinate axis in fig. 19 indicates the spatial dimension of our interventions. In our view, any enhancement method that will significantly affect a large system, particularly a multi-purpose and multi-use system with cascading effects must be thoroughly assessed and justified. The precautionary approach to capture fisheries and species introductions adopted in the marine environment must also be adhered to for freshwater systems. This is particularly the case with lakes of natural origin. But also the temporal scale must be taken into account as this is closely related with the natural stability or resilience of the system (Fig. 18). Most, if not all, of the methods for enhancing productivity are technically disturbances to the ecosystem. However, the more naturally disturbed (i.e. fluctuating) the system is, the more it can absorb additional sources of mortality: "Disturb an early succession, and it becomes an early succession. Disturb a climax community and it becomes an early succession stage that takes time to return to climax" (Horn 1974). Fortunately, the unstable systems are also the most productive (Figs 4, 12, 13, and 14) and perhaps also the most resilient to interventions. High fish productivities are integral to highly fluctuating systems, and approaches to make use of this variability in larger reservoirs and in degraded floodplains where there is a possibility to control flood-pulses should be developed more thoroughly.

Lastly, we could make a normative distinction between natural lakes and man-made reservoirs, as one may argue that we have not inherited our reservoirs. They are 100% artificial and therefore we should perhaps not submit them to the same standards as natural lakes, as long as the effect of our additional interventions to the watershed do not extend beyond the boundaries of the reservoirs (Fig. 18). Furthermore, man-made reservoirs, such as Lake Kariba for example, are grand-scale ecological laboratories, which provide us with a unique chance to observe and monitor the intricate pathways of nature’s response to exploitation and other enhancement techniques. Much ecological knowledge and many of the examples cited in this review are extracted from this and other man-made lakes. The results show that most fluctuating tropical aquatic ecosystems are probably more robust to human interventions than anticipated. How robust, however, we still don’t know.

9. Research needs

In this review three main categories for increased production and enhancement technologies in lakes and reservoirs were identified and classified as:

- increase the output from the available natural production
- modify the physical basis of production
- manipulate the biological basis for production

These categories constitute a range of increased biological disturbance to the system, where the possibilities and impacts of each category are scaled as illustrated in Fig. 19. Thus, depending on the objectives, there is a general trade-off between increased productivity and the impact level, ranging from natural harvesting to complete control of the productivity of selected organisms comparable with intensive land based agriculture. However, within each of the three main categories, there are possibilities that have minimal ecological impact, and it is on these that research attention should be primarily focused. We will therefore end with some general recommendations to study enhancement technologies in a broader ecological and population dynamics context.

Category 1. Increased output from the available natural production. Here the key words are harvesting level and exploitation pattern.

Compared with their importance in terms of production, productivity and livelihood dependency of the riparian fishing communities, there is a general paucity of data and lack of research on small-scale inland lake and reservoir fisheries. Instead, however, there is a significant amount of myths and misconceptions, particularly on the often high uncontrolled effort levels and perceived wasteful and indiscriminate fishing practises (Misund et al. 2002, SOFIA 2004). The latter notions are mostly deduced from the ruling paradigm that unselective fishing methods are inherently bad and will lead to both growth and recruitment overfishing. Unfortunately, however, the actual total impact of a multi-species, multi-gear fishery has rarely been investigated. Fishing the whole food web, which requires (overall) unselective methods, may actually be an ecologically sound exploitation pattern that also maximizes output (see Figs 14, 15 and 17). Moreover, in fluctuating systems the spatial and temporal dynamics of small-scale fishing effort may be highly adapted to the changing availability of fish and hence small-scale fisheries may utilise their production in a more efficient and biologically sounder way then more technologically advanced fisheries. There is therefore an urgent need:

- To remedy the general lack of quantitative information on basic fisheries information for small-scale inland fisheries on a broad scale.
- To establish the selectivity of the various gears individually and in combination and to evaluate the impact of the overall fishing pattern impact on the ecosystem.
- To investigate spatial and temporal dynamics of fishing effort in small-scale fisheries and their capacity to react and adapt to fluctuating environments

While often feared, there are in fact few - if any - examples of decreased system yields induced by effort or fishing patterns alone from fresh water systems (e.g. Jul-Larsen et al. 2003). Instead of research, however, the present national and international efforts in small-scale fisheries seem concentrated on establishing management implementations, preferably through co-management (since traditional top-down has failed), focussing on paradigmatic effort and gear control mechanisms. However, without the necessary fundamental research, these implementations will be based on reiterated dogma and may very well face the same failures as the many previous attempts to manage and ‘modernise’ the small-scale fisheries have in the past (Misund et al. 2002, Jul-Larsen et al. 2003).

Category 2. Modify the physical basis of production. Here the key words are hydrology and fluctuations.

Many lakes and most reservoirs have a seasonally fluctuating hydrology, and are intimately associated with rivers. Riverine floodplains are already acknowledged for being among the most productive aquatic ecosystems, and much of this can be attributed to the flood-pulse advantage (Bayley 1991) as described in the ‘flood pulse concept’ (Junk et al. 1989). The productivity of lakes (particularly shallow) and reservoirs should also be seen in this perspective (see Fig 13). Any outside water management that alters the flow regime or the system connectivity will have consequences for the productivity (see Welcomme’s review paper). For lakes and reservoirs more research is needed to fully understand these mechanisms and how they can be utilised to our advantage. Particularly there is a need to investigate:

- the relative impact of hydrological fluctuations in relation to fishing levels (see Table 5),
- the role of the riparian ecotone for the fish productivity (Zalewski et al. 2001)[17]
- the effects of hydrology on the pelagic ecosystems in reservoirs, in view of the assessment potential introductions of small pelagic fish species..

Lakes and reservoirs can vary from highly stable systems to highly pulsed, where most reservoirs will be in the pulsed end of the spectrum. In order to quantify this gradient we have proposed to use a ‘relative lake level fluctuation’ index (RLLF, see section 5.3) as a tool to classify different environments in terms of productivity, stability and resilience. More research is needed on the predictive power of simple physical indices for evaluating potential productivity.

Habitat modifications to enhance productivity – that include the location of culture based systems - in large reservoirs or lakes mainly take place along the coast, in the littoral areas that are often also important spawning and nursery grounds for many species. Often little is known about the role of essential habitats in the life-histories of key fish species, information that is needed to address the

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[17] In this context we also see a need for research on adaptive strategies and the adaptive capacity of people whose livelihoods depend partly on in full on fluctuating fisheries resources.

potential trade-offs between cultured and natural production as a result of habitat modifications and open water aquaculture activities. In general much more should be known of important life-history parameters of individual fish species (e.g. as mentioned in Table 6), to address implications of management (including enhancement and conservation activities).

Category 3. Manipulate the biological basis for production. Here the key words are species introductions and stockings.

All biological production is ultimately consumed within an ecosystem. Any manipulation of energy pathways for increased productivity in terms of yields must therefore substitute some other pathway. However, some food webs are not directly exploitable for human consumption, or are less desirable in terms of outputs. For example, the pelagic zone in many reservoirs has no indigenous lacustrine fish fauna and therefore remains uninhabited and under-utilised from a fishery perspective (see section 4). In such cases the introduction of low trophic level fish species in the food web for harvesting should be considered. The introduction of the pelagic clupeid Kapenta (*Limnothrissa miodon*) in several African reservoirs has significantly increased the yields without apparent negative ecological effects (Marshall 1995). The issue, however, is controversial and the impacts often remain speculative (Hall and Mills 2000), although the development of indigenous pelagic zooplankton predators in most cases is a question of (a lot of) time as many natural lakes demonstrate. There is a strong need for further investigation and documentation of the impact of introducing lacustrine species to man-made reservoirs to be weighed against the potential increase in productivity. The number of tropical reservoirs is ever increasing, which requires sober studies in the trade-offs between enhanced reservoir fisheries versus down and upstream fisheries.

Stockings of indigenous or non-indigenous fish species is an often used – or recommended – enhancement strategy in both lakes and reservoirs. Evidently, the stocking of indigenous species carries few negative connotations, but on the other hand it is rarely demonstrated that it carries any positive effect either. If a potential for population increase exists, it would most likely have happened naturally as all theory on surplus production and density dependent growth predicts (see section 6). Stocking of indigenous species, such as for example *Oreochromis niloticus* in Lake Nasser (Born 2000), can be considered as feeding their natural predators (e.g. Nile perch, which also occurs in the reservoir), which may prove to not be a very cost-effective way of improving productivity. Stocking of non-indigenous species, on the other hand, is widely used in Asian reservoirs and has usually significantly increased production (De Silva and Amarasinghe 1997, Cowx 1998, Welcomme and Bartley 1998, De Silva 2003), although sometimes not (Figure 8). The potential production of culture-enhanced fisheries is strongly linked to ecosystem productivity. The assessment of stocking and harvesting regimes therefore requires quantitative insights in the biological basis for production and associated population processes (Peterman 1991, Lorenzen 1995). In our view this insight is more often assumed than quantified, and much more work should be done on the ecological basis for success or failure of stocking to increase (or maintain!) production.

Finally, there is a paucity of studies on the dynamics of various types of enhancements and their rationale in a theoretical ecological perspective. Due to the general emphasis on the “aquaculture” attributes of enhancement techniques, research is generally aimed at increased production, productivity and other attributes of the culture system. Only rarely are population interactions; impacts of habitat change on natural populations and overall productivity; other ecosystem effects of enhancement technologies; as well as effects of ecosystems on enhancement practices (in particular the role of drivers of natural variability) studied. Today, impacts of enhancements on ecological interactions still are mostly documented on a trial-and-error basis. The current experimental management stage can only progress through research that explicitly addresses questions on potential enhancements in lakes and reservoirs in a theoretical ecological and population dynamic framework. Our report outlines the possible contents of such a framework. In addition, meta-analysis of existing experimental data and information on enhancement practices is needed, both for a better understanding and improvement of these technologies and the formulation of potentially rewarding hypotheses. We see these as very important issues for further research.

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