

Modelling the economics of ecosystem services: nutrient retention in wetlands and fisheries in Lake Victoria

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Abstract

This paper models the effect of changes in wetlands yields within the freshwater fishery of (the Kenyan segment) of Lake Victoria. Specifically, it models the nutrient retention function of wetlands as a buffer against fertilizer run-off from agriculture, and the impact of nutrient loading on the fishery. Run-off from the watershed is among the major causes of eutrophication in the lake, along with atmospheric deposition and sewage and other organic discharges from domestic and industrial activities. The ecological component of the model captures the interactions between phosphorus loading, wetland area, water quality and fish stocks. Chlorophyll-a concentration is used as a proxy for phytoplankton density, and as a measure of nutrient enrichment. The impact of this on fish stocks is then estimated using Ecopath. The economic component of the model then evaluates the effect of changes in stocks on performance in the fishery, given the regulatory regime in Kenya. We use the results to obtain an estimate of the value of the nutrient retention function of wetlands on the margins of the lake.

Key words: valuation of ecosystem services, ecological-economic interactions, wetlands, fisheries, eutrophication

JEL classification:

1. Introduction

Worldwide capture fisheries are in decline. There are two main reasons for this. One is the fact that many fisheries are still effectively open access resources, which results in the

overexploitation of those resources. The other is the effect of land-based pollution. Many freshwater and marine capture fisheries have been severely affected by sewage, nutrients, synthetic organic compounds, sediments, metals, radionuclides, oil/hydrocarbons and polycyclic aromatic hydrocarbons (PAHs) (UN, 2004). The application of fertilizers in agriculture, fossil fuel burning, land clearance and biomass burning have long been recognised as a major source of the nutrient load in freshwater, coastal and estuarine systems (Oglesby, 1977; Nixon, 1988; Vitousek et al, 1997). In extreme cases this has led to the development of large anoxic zones with negative effects on the fish and other marine organisms.

In this paper we consider the role played by wetlands in moderating the effect of land based pollution and hence on eutrophication and fishery yields. Several studies have considered the linkage between wetlands and fisheries in coastal and estuarine systems (Turner, 1982; Swallow, 1994; Barbier & Strand, 1997; Barbier & Sathirathai, 2002). All these studies focus on the ecological function of wetlands in supporting fisheries by serving as both spawning ground and nursery for fry. However, to our knowledge, there is no study of the value of wetlands in terms of their impact on water quality. Although the nutrient retention function of coastal and freshwater wetlands is known to be an important determinant of stock biomass in capture fisheries, the economic significance of this has not been evaluated.

The changes in aquatic systems that follow from changes in nutrient loading due to land-based economic activities are said to be an externality of those activities. That is, those whose activities on land damage aquatic systems are not confronted by the cost of that damage. While it is recognised that internalisation of such externalities requires an understanding of the interactions between terrestrial and aquatic activities, there are few attempts to model the problem. Early approaches either focused on simple correlations between changes in watersheds and changes in fisheries, or else identified the consequences for fisheries if the linkages were of varying strength (Ruitenbeek, 1989; Hodgson & Dickson 1998). Limnologists have investigated the consequences for freshwater aquatic systems of changes in changes in land use, vegetative cover, and

fertilizer regimes within the watershed (Postel & Carpenter, 1997; Carpenter and Pace, 1997; Carpenter and Cottingham, 1997). More recently, economists have considered the theoretical problems posed by the interaction between users of lake and catchment resources (Maler et al, 2003; Carpenter, Brock and Hansen, 1999). Nevertheless, there are few attempts to model the interactions in real systems, or to estimate the value of land-water externalities of this kind.

This paper models land-water interactions in a particular system – the Kenyan catchment of Lake Victoria – with a view to understanding the consequences of the conversion of wetlands for the lake fishery. Nutrient enrichment has a positive effect on fishery productivity in nutrient-limited environments such as oligotrophic or mesotrophic lakes (Stockner & Shortreed, 1988; Melack, 1976a; Liang *et al.*, 1981; Hoyer & Jones, 1983; Downing *et al.*, 1990; Quirós, 1990; Gomes *et al.*, 2002). However, there is also evidence that sustainable harvests of fish populations at upper trophic levels decline if the system becomes highly eutrophic (Beeton, 1969; Lee *et al.*, 1991; Caddy, 1993). Excess nutrients affect fish productivity through changes both in the amount of food available (Bootsma & Hecky, 1993) and in the quality of the habitat (Hammer *et al.*, 1993). Deoxygenated water boosts natural mortality of fish. Sedimentation negatively affects nursery grounds and may damage fish eggs. When combined with high fishing pressure, both effects can have a severe impact on fish stock biomass and fishery yields (Kemp *et al.*, 2001).

In Lake Victoria, fish production in all three riparian states has grown dramatically since the introduction of the Nile perch (*Lates niloticus*) in the early 1960s. In the Kenyan waters of the lake output grew from around 17,000 tonnes per year in the 1960s to more than 200,000 tonnes in the early 1990s. During the 1980s, *Lates* catches increased exponentially rising in few years from virtually zero to almost 60% of total yield (Okemwa, 1984; CIFA, 1988; Ogari & Asila, 1990; Ogutu-Ohwayo, 1990; Ssentongo & Welcomme, 1985). However, from 1994 fish landings have been in sharp decline, mostly due to declining catches of Nile perch. By 1998 Nile perch landings were half of those at the beginning of the decade despite increased fishing effort.

Several factors are implicated in this. Overfishing is one factor, but it is not the only one. Eutrophication, caused by nutrient run-off from agricultural land and discharges from urban settlements on the lakeshore is also an important factor, and that stems from two phenomena. One is an increase in nutrient loading due to the application of fertilizers on agricultural lands and the growth of human populations on the lake-shore. A second is a reduction in nutrient absorption by wetlands on the lake margins, largely caused by the conversion of wetlands to other uses. A number of water quality analyses over the last decades show that Lake Victoria has progressively shifted from a mesotrophic to a eutrophic state from both causes. Increasing chlorophyll-a concentrations have been reported (Ochumba & Kibaara, 1989; Gophen *et al.*, 1995; Kenya, 1999; Lung'aya *et al.*, 2000, 2001) against baseline values provided by Talling (1965, 1966) and Melack (1976b).

In this paper we model the interactions between wetlands and the fishery in the Kenyan catchment of the lake. The paper is organised in five sections. The following section describes the basic elements of model of a fishery in which productivity is affected by changes in water quality. A third section models the interactions between the wetland and the fishery. A fourth section then uses the model to evaluate the impacts of changes in the extent of the wetlands in terms of the value of output in the fishery. A final section offers our conclusions.

2. The fishery model

Whilst any Lotka-Volterra model of the dynamics of fish stocks indirectly captures the constraints imposed by the environment via the carrying capacity parameter, to date there are relatively few bioeconomic studies of fisheries that explicitly model the effect of environmental variables (Ikeda & Yokoi, 1980; Fréon *et al.*, 1993; Kasulo & Perrings, 2005). Following a similar approach to that in Kasulo & Perrings (2005), we include chlorophyll-*a* concentration (a proxy for phytoplankton density) as a measure of nutrient enrichment in a Gordon-Schaefer fishery model (Gordon, 1954; Schaefer, 1954, 1957),

allowing for a delay in the impact of water quality change on stock growth, in discrete time (Simonit & Perrings, 2004). The stock growth equation takes the form::

$$\Delta X_t = rX_tW_{t-1} \left(1 - \frac{X_t}{KW_{t-1}} - eW_{t-1} \right) - qE_tX_t \quad [1]$$

where X_t is the aggregate stock biomass at time t (tonnes), W_{t-1} is chlorophyll- a concentration at time $t-1$ (mg m^{-3} or $\mu\text{g l}^{-1}$), E_t is fishing effort at time t ('000 boat days); r is the intrinsic growth rate of the stock; q is its catchability coefficient; and e is a coefficient representing the amount by which a unit change in chlorophyll- a depresses r . Nutrient loading positively affects the growth of fish stocks up to a certain point, after which further increases in nutrient loading cause a decrease in the maximum sustainable yield (MSY), open access and profit maximising levels of effort, and stock size.

Which stock measure is appropriate depends on the fishery management regime and the set of property rights. The degree to which the Lake Victoria fisheries have been regulated or policed varies over time. Table 1 reports the steady state level of fish stock (X), catch (Y) and fishing effort (E) under three fishery management regimes: open access, maximum sustainable yield, and profit maximisation.

Equation [1] is estimated using Schnute's (1977) method. This involves transforming the Gordon-Schaefer model into a linear form and then fitting the following expression:

$$\ln \left(\frac{U_{t+1}}{U_t} \right) = r \left(\frac{W_{t-1} + W_t}{2} \right) - \frac{r}{qK} U_t - re \left(\frac{W_{t-1} + W_t}{2} \right)^2 - qE_t \quad [2]$$

which conforms to the multiple linear regression:

$$Y = \beta_1 X_1 - \beta_2 X_2 - \beta_3 X_1^2 - \beta_4 X_3 + \varepsilon \quad [3]$$

where U represents catch per unit effort (CPUE); $\beta_1=r$, $\beta_2=r/qK$, $\beta_3=re$ and $\beta_4=q$ are estimated regression coefficients; and ε is the error term.

Table 1: Maximum sustainable yield (MSY), open access (oa) and profit maximising (*) steady state solutions

MODEL 1: Standard Gordon-Schaefer model

$$\begin{aligned}
 X_{msy} &= \frac{K}{2} \\
 Y_{msy} &= \frac{rK}{4} \\
 E_{msy} &= \frac{r}{2q} \\
 X_{oa} &= \frac{c}{pq} \\
 Y_{oa} &= \frac{cr(pqK - c)}{p^2 q^2 K} \\
 E_{oa} &= \frac{r(pqK - c)}{pq^2 K} \\
 X^* &= \frac{K}{4} \left[\left(\frac{c}{pqK} + 1 - \frac{\delta}{r} \right) + \sqrt{\left(\frac{c}{pqK} + 1 - \frac{\delta}{r} \right)^2 + \frac{8c\delta}{pqKr}} \right] \\
 Y^* &= rX^* \left(1 - \frac{X^*}{K} \right) \\
 E^* &= \frac{Y^*}{qX^*}
 \end{aligned}$$

Note: p = market price of fish stock; c = cost of fishing effort; δ = discount rate.

The data used to fit the model derive from three sources. First, we use annual data on fishing effort and catch per unit effort (CPUE) for the Kenyan fisheries of Lake Victoria (Othina & Tweddle, 1999). Second, we generate a time series for water quality is generated using Ecosim (Walters *et al.*, 1997, 2000) and a dynamic simulation using Ecopath (Christensen & Pauly, 1992) as follows. Specifically, from fishery statistics for 1989 we estimate the biomass values for the same year and we use them, together with

the time trend in relative fishing effort, as starting values in a nine-year dynamic simulation. Using the Runge-Kutta 4th order integration method, the dynamic model is then fitted to time series values of catch per unit effort for the Nile perch fishery, and two observations (1994-1995 and 1997-1998) of average chlorophyll-a concentration (Kenya, 1999; Lung'aya *et al.*, 2000) converted to phytoplankton biomass measured in tonnes km⁻².

Biological inputs and diet composition data were taken from the Ecopath model for the Kenyan waters of Lake Victoria developed by Villanueva & Moreau (2002). We assume that the difference between the first simulation of the dynamic model and the model that best fits the observed data is due to variations in annual relative primary productivity alone. This seems reasonable given the importance of primary productivity in influencing fish stock dynamics in Lake Victoria. The resulting long-term forcing function for primary productivity is then used to predict annual average phytoplankton biomass for 1989-1998. These values are then converted into chlorophyll-a concentrations (Table 2) assuming a phytoplankton/chlorophyll ratio of 70 as a rule of thumb (Scheffer, 1998), although the chlorophyll-a content of phytoplankton may vary within the range 0.5-2% of the dry weight depending on nutrient status, light and temperature (Ahlgren *et al.*, 1988).

Table 2: Values of regression variable for Kenyan waters of Lake Victoria

Year	CPUE (kg boat ⁻¹ day ⁻¹)	Fishing effort (‘000 boat days)	Chla concentration (W _t) (mg m ³)	(W _{t-1} + W _t)/2
1989	180	1202	16.54	16.54*
1990	152	1387	17.63	17.09
1991	145	1496	12.55	15.09
1992	137	1606	15.25	13.90
1993	115	1862	13.13	14.19
1994	93	1862	16.02	14.58
1995	86	2007	19.25	17.64
1996	78	1971	12.00	15.63
1997	93	2008	24.36	18.18
1998	86	2190	23.01	23.68

*assuming W₁₉₈₈ = W₁₉₈₉

Parameterization was performed for both the standard and extended Gordon-Schaefer models. The estimated coefficients for both models are all statistically significant at 5% level and of the expected sign (Table 3). The goodness of fit is high for both models

($R^2=.76$ and $R^2=.67$ respectively) relative to results reported on other fisheries (cf. Hilborn & Walters 1992).

Consistent with findings by Kasulo & Perrings (2005), the model including the environmental variable fits the data much better than the standard Gordon-Schaefer model. After parameterization, the estimated model for the Kenyan fisheries of Lake Victoria becomes:

$$\Delta X_t = 0.201033 X_t W_{t-1} \left(1 - \frac{X_t}{53082 W_{t-1}} - 0.029214 W_{t-1} \right) - 0.000629 E_t X_t \quad [4]$$

The first term of the right hand side of equation [4] says that the growth of the fish stock is positively affected by chlorophyll-a concentration at relatively low levels. Fish stock growth reaches a maximum at the W_{t-1} value of 17.11 mg m^{-3} beyond which it starts to decline. At this point the maximum sustainable yield attainable is 195,368 tonnes and the fish stock 227,126 tonnes. In eutrophic conditions a further increase in primary productivity has a negative impact on the growth of the fish stock and on fish harvesting. The environmental variable influences both the growth rate at a given level of the stock (rXW), the maximum sustainable yield and the carrying capacity of the lake ($KW[1-eW]$). Steady state conditions under open access (Y_{oa}), maximum sustainable yield (Y_{msy}) and profit maximising regimes (Y^*) also change with water quality.

Table 3: Value of estimated coefficients

Coefficient	MODEL 1: Standard Gordon-Schaefer	MODEL 2: With environmental variable
Constant	2.01295 (2.990)**	–
β_1	–	0.20103 (3.062)**
β_2	-0.00696 (3.315)*	-0.00602 (3.670)*
β_3	–	-0.00587 (2.779)**
β_4	-0.00075 (3.004)**	-0.00063 (3.318)**
R^2	0.67	0.76
Adjusted R^2	0.56	0.62
p-value[F-statistic]	.0369	.0517

Note: t-ratio in parenthesis; * statistically significant at 2% significance level; ** statistically significant at 5% significance level.

3. Modelling the impact of wetlands

The primary focus of this paper is the relation between the fishery and changes in the wetlands at the margins of Lake Victoria. We model the relation between land use change and water quality, and hence between wetlands and fish stock biomass. Observed changes in primary productivity and phytoplankton composition in Lake Victoria are assumed to be the result of excess nutrient loading from the drainage basin. The model links nutrient loading and phytoplankton density (i.e. chlorophyll-a concentration) using functional forms drawn from empirical studies. The dependence of the overall phytoplankton biomass on nutrients (total phosphorus TP and total nitrogen TN) is a general feature in freshwater ecosystem and many chlorophyll/nutrient relationships have been published. Without the support of specific studies for Lake Victoria, we use the Jones & Bachmann's (1976) equation:

$$W_t = 0.0731TP_t^{1.449} \quad [5]$$

where W_t is chlorophyll-a concentration (mg m^{-3}) and TP_t is total phosphorus concentration (mg m^{-3}) in the lake.

To convert phosphorus flows in concentrations we draw on the substantial number of limnological models developed for lakes. In general, lakes are open flow-through systems whose content of a given element is determined by the dynamic balance between supply through the inflows, loss through the outflows, and internal sources and sinks (Andersen, 1997). Prediction is commonly based on a family of phosphorus mass balance models directly descending from the pioneering work of Vollenweider (1968, 1969). Under steady state conditions Vollenweider's model can be used to represent a description of overall nutrient processes in a lake and as such it can be used to evaluate or predict changes in the nutrient balance of a water body as a response to a step input, when the input changes from one constant level to another load level. By taking into account atmospheric deposition and scaling the unit of measurements the limnological expression is:

$$TP = \frac{(L_{TP} + D_{TP}) * 10^9}{Q_{lake} + \frac{s_{TP}}{H_{lake}} V_{lake}} \quad [6]$$

where TP is the concentration of phosphorus (mg m^{-3}); L_{TP} is the superficial loading (tonnes yr^{-1}); D_{TP} is the long term average atmospheric deposition (tonnes yr^{-1}); V_{lake} is the lake volume (m^3); Q_{lake} is the hydraulic superficial outflow from the lake ($\text{m}^3 \text{yr}^{-1}$); H_{lake} is the mean depth of the water body (m); and s_{TP} is the settling velocity rate for phosphorus (m yr^{-1}).

We are concerned with the nutrient retention function of wetlands. The capacity of wetlands to purify watersheds reducing nitrogen, phosphorus and other pollutant levels has been analysed in a number of studies (Nichols, 1983; Mitsch & Jorgensen, 1989; Reckhow & Quian, 1994; Richardson *et al.*, 1997; Wang & Mitsch, 2000), and has also been evaluated by the catchment scale (Mitsch & Wang, 2000; Arheimer & Wittgren, 2002; Trepel & Palmeri, 2002). At the catchment scale, predictive models have been developed to characterise the ability of wetlands to reduce point and non-point pollution from the upstream watershed.

Several studies have analysed nutrient retention by wetlands as a function of wetland area and nutrient loads (Byström, 1998; Dortch & Gerald, 1995). We use the general mass balance model presented by Kadlec & Knight (1996) assuming that hydraulic flow through and out of the wetland is equivalent to the water inflow:

$$L_{TP}(A) = L_{in} \exp\left(\frac{-k_{TP}A}{Q}\right) \quad [7]$$

where L_{TP} is the phosphorus outflow from the wetland to the main lake (tonnes yr⁻¹); L_{in} is phosphorus inflow to the wetland (tonnes yr⁻¹); Q is water inflow to the wetland (m³); A represents wetland area (m²); and k_{TP} is the areal removal rate constant (m yr⁻¹).

By combining equations [5], [6] and [7] we obtain the general expression for the environmental variable which influences fish growth and fishery yields. The environmental variable W , chlorophyll-a concentration, can therefore be represented as a function of nutrient loading (L_{in}), wetland area (A) and a series of constants or long term averages:

$$W_t = .8034 * 10^{12} \left(\frac{L_t^{in} \exp\left(-\frac{k_{TP}A_t}{Q}\right) + D_{TP}}{Q_{lake} + \frac{S_{TP}V_{lake}}{H_{lake}}} \right)^{1.449} \quad [8]$$

Notice that this expression assumes that all the phosphorus loading from the watershed is flowing through wetlands. In most of cases this will overestimate the nutrient retention function of wetlands. More complexity could be added to the model by considering hydraulic inflow (Q) as variable, taking into account changes in precipitation patterns. But we do not add this here.

In applying the model to the Kenyan fishery, and watershed, of Lake Victoria we use the long term average of 1460 tonnes yr⁻¹ for atmospheric deposition (COWI, 2002),

$5376 \times 10^6 \text{ m}^3 \text{ yr}^{-1}$ for the hydraulic inflow (Balirwa & Bugenyi, 1988), the areal removal rate constant (k_{TP}) of 12 m yr^{-1} (Kadlec & Knight, 1996), and a settling velocity for total phosphorus (s_{TP}) of 16 m yr^{-1} (Chapra, 1975). We also assume an average depth of 12 m and a volume of $5.3664 \times 10^{10} \text{ m}^3$ for the Kenyan sector of Lake Victoria, and that the hydraulic outflow is compensated ($Q_{lake}=0$) by inflowing water from the Ugandan and Tanzanian side of the lake with the same concentration of phosphorus. This assumption is known in the engineering literature as the continuously stirred tank reactor (Reckhow & Chapra, 1983) and is equivalent to consider the lake's waters as completely mixed.

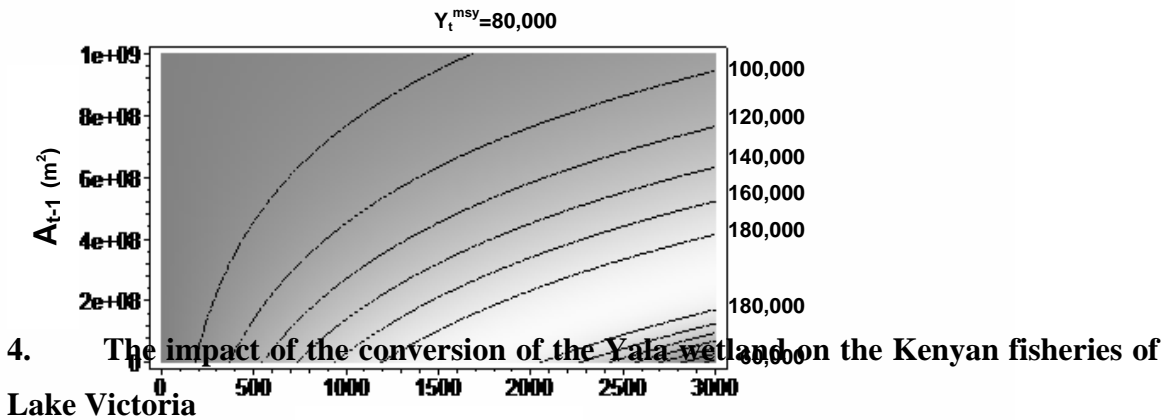
The predictive power of equation [8] can be tested by comparing predicted and observed values of chlorophyll-a concentrations. Given long term averages for both atmospheric deposition and superficial inflow of phosphorus (COWI, 2002) the predicted value of $W=18.85 \text{ mg m}^{-3}$ is close to the long term (1989-1998) average of 16.97 mg m^{-3} from the values estimated using the simulation package in Ecopath (Table 2), and well approximates the average value between inshore observations of $10.7\text{-}38.1 \text{ mg m}^{-3}$ (Kenya, 1999), 31.4 mg m^{-3} (Ochumba & Kibaara, 1989) and offshore measurements of $6.3\text{-}14.1 \text{ mg m}^{-3}$ (Kenya, 1999) for the Kenyan waters of Lake Victoria.

Given [8] we can calculate the changes in the steady state level of fish yield under various management regimes (Y_{msy} maximum sustainable yield, Y_{oa} open access, Y^* profit maximising) corresponding both to the level of phosphorus load at $t-1$ into the wetlands and the area under wetlands at $t-1$. These steady state solutions can then be represented by a surface. An example is provided for the case of the steady state catch under maximum sustainable yield regime for the Kenyan fishery of Lake Victoria in Figure 1.

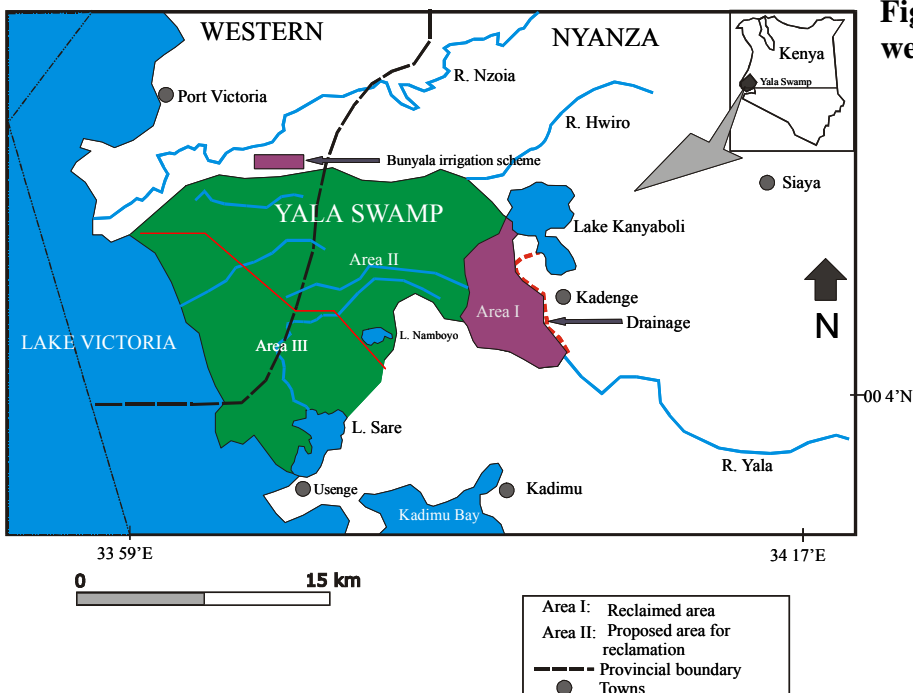
Without at the moment considering the impact of changes in the extent of the wetlands, the yield under maximum sustainable yield regime (and the profit-maximising regime) would peak at a nutrient loading of around $1550 \text{ tonnes yr}^{-1}$ (Figure 1). Since actual loading of phosphorus from the Kenyan basin is currently around $1925 \text{ tonnes yr}^{-1}$ (COWI, 2002), well above the turning point, we would expect the lake to move towards a eutrophic condition and fishery yields to decline. Any further increase in loading will

accordingly reduce fishery yields in any of the three management regimes. It is in this context that we consider the importance of the wetlands at the margins of the lake.

Figure 1: Fish yield (t/yr) under MSY regime as function of wetland area and superficial loading of phosphorus for the Kenyan fishery of Lake Victoria

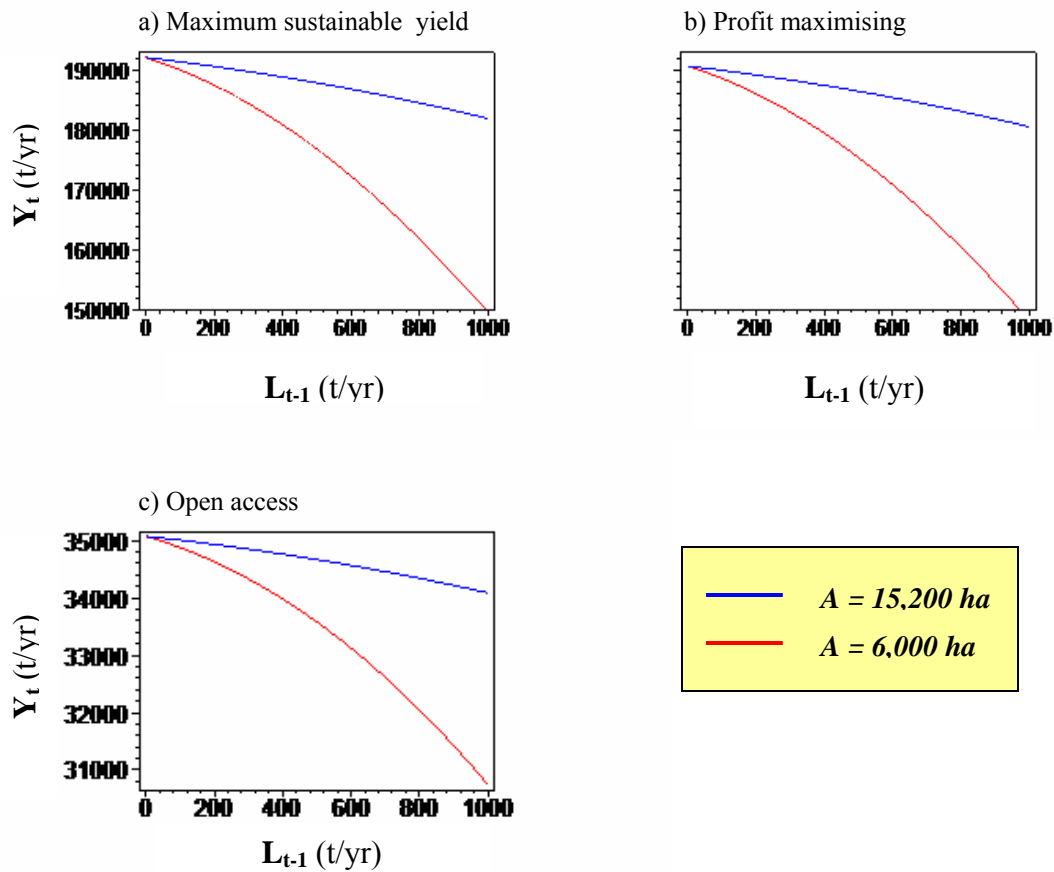


We are interested in evaluating the externality of wetland conversion in Lake Victoria, focusing on the Yala swamp – one of the largest wetlands in the Kenyan basin of Lake Victoria. The swamp has already been heavily affected by human development and much of the remaining area has been demarcated for ‘reclamation’ since the mid 1960s. After 2,300 ha (Area I in Figure 2) of the original 17,500 ha were drained in the 1960s, a further 9,200 ha (Area II) were scheduled for conversion to agriculture in the Lake Basin Development Authority Five Years Plan 1989-1993.



The next step is to model the impact of changes in the extent of the wetland under this and other reclamation programmes. We assume (a) constant values for A , (b) a water discharge of $1114 \cdot 10^6 \text{ m}^3 \text{ yr}^{-1}$ from the Yala river (Balirwa & Bugenyi, 1988), (c) an average of $102 \text{ tonnes yr}^{-1}$ of phosphorus loading from the Yala catchment (COWI, 2002), and (d) accounting for the long term atmospheric deposition and phosphorus loading from the rest of the Kenyan watershed (COWI, 2002). We find that conversion of Area II will have a moderate negative impact on the steady-state path of the Kenyan fishery under any possible management regime. This is illustrated in Figure 3.

Figure 3: Prediction of steady-state yield paths for the Kenyan fishery under different management regimes before ($A=15,200 \text{ ha}$) and after ($A=6,000 \text{ ha}$) reclamation of Area II of the Yala wetland



The impact on both fish stocks and yields, given the present loading of phosphorus from the Yala watershed, translates as a direct economic loss¹ of up to US\$0.7m per year, depending on the fishery regime (Table 4). At a discount rate of 5 per cent, this implies that the value of the converted wetland (its social opportunity cost) is US\$14.7m. Notice, though, that the loss of ecosystem services is increasing in the level of nutrient loading into the wetland. If nutrient loading into the wetlands grows at the same time as the wetland is converted, eutrophication of the lake and direct losses to the fishery will be accelerated. Moreover, while this is a first approximation of the value of the nutrient retention function of the wetland, it ignores other ecosystems services such as groundwater recharge, carbon sequestration or habitat provision. Hence the opportunity cost of the wetland that is scheduled to be converted, defined in terms of its nutrient

¹ Assuming on average that the market price of the fish landed is 508.55 US\$ per ton.

retention function only, is a lower bound of its value. Comparison with estimates of the value of the converted land, approximated by the sale price of that land, provides a simple check on the efficiency of the conversion plan. Based on the simplifying assumptions used to in this paper, conversion at less than US\$1600 per hectare is unlikely to be efficient.

Table 4: Potential economic loss to the Kenyan fishery due to reclamation of Area II of the Yala wetland under different management regimes

	Steady state values (tonnes)	Steady state values after reclamation (tonnes)	Difference (tonnes)	Economic loss (US\$/yr)
Xmsy	224,777	223,965	- 812	—
Xoa	21,595	21,595	—	—
X*	205,447	204,649	- 798	—
Ymsy	191,348	189,968	- 1380	701,799
Yoa	35,000	34,867	- 133	67,637
Y*	189,933	188,555	- 1378	700,782

Note: X and Y are respectively fish biomass and yield under maximum sustainable yield (msy), open access (oa), and profit maximising (*) regimes.

5. Conclusions

The modelling problem addressed in this paper is the integration of nutrient retention in wetlands and the dynamics of a freshwater fishery. Globally, the Millennium Ecosystem Assessment has concluded that ecosystem services of this sort are declining due to the conversion of wildlands for agriculture, forestry, industry and domestic dwellings (MA, 2005). In order to understand the economic significance of changes in ecosystem services we need to be able to model the interactions between economic activities that depend on particular services, and changes in those services. Wetlands provide a range of ecosystem services of which nutrient retention is particularly important in mediating land-water interactions. The integrated model here includes both a fishery component adapted to include the effects of changes in nutrient loads, and a wetland component to explain the absorption of passing nutrients.

One result of the limnological models of the behaviour of shallow lakes subject to nutrient loading, is that the oligotrophic and eutrophic states are both locally stable. As nutrients are added to oligotrophic shallow lakes there comes a point at which they flip

into a eutrophic state. Once in a eutrophic state, however, they are subject to hysteresis. That is, they cannot be induced to return to an oligotrophic state by reducing the loading to the level that caused the flip in the first place. Loading has to be reduced far below that level and held there for a long time (Carpenter & Pace, 1997; Carpenter & Cottingham, 1997). This has important implications for policy. If policies affecting nutrient loading – whether through wetland conversion or the application of fertilizers – allow the lake to flip into a eutrophic state, it may not be possible to induce a return within a sensible time frame (Maler et al, 2003).

The fishery component of the model reported in this paper does not have this property. The effect of changes in nutrient loading will induce changes in fish biomass that depend on the initial level of loading and the initial state of the system. In general, however, a reduction of nutrient loads when the lake is in a eutrophic state will lead to an increase in fish biomass. Similarly, the nutrient retention function of wetlands is reversible. If the wetland area or biomass is increased nutrient retention will also increase. In practice, wetland conversion may be irreversible for practical political reasons, but it is not modelled as such.

The model nevertheless enables us to estimate the value of the nutrient absorption externalities of wetland conversion, and to project the consequences of alternative wetland conversion strategies. Wetlands do provide a number of other ecosystem services, but in this case nutrient absorption may in fact be the most important. The effects of wetland conversion are also much wider than the effects on the commercial fishery in the lake, although it is arguable too that the effects on the fishery are more important than the effects on other sectors.

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