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Qualitative models to predict impacts of human interventions in a wetland ecosystem

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The large shallow wetlands that dominate much of the South American continent are rich in biodiversity and complexity. Many of these undamaged ecosystems are presently being examined for their potential economic utility, putting pressure on local authorities and the conservation community to find ways of correctly utilising the available natural resources without compromising the ecosystem functioning and overall integrity. Contrary to many northern hemisphere ecosystems, there have been little long term ecological studies of these systems, leading to a lack of quantitative data on which to construct ecological or resource use models. As a result, decision makers, even well meaning ones, have difficulty in determining if particular economic activities can potentially cause significant damage to the ecosystem and how one should go about monitoring the impacts of such activities. While the direct impact of many activities is often known, the secondary indirect impacts are usually less clear and can depend on local ecological conditions.

The use of qualitative models is a helpful tool to highlight potential feedback mechanisms and secondary effects of management action on ecosystem integrity. The harvesting of a single, apparently abundant, species can have indirect secondary effects on key trophic and abiotic compartments. In this paper, loop model analysis is used to qualitatively examine secondary effects of potential economic activities in a large wetland area in northeast Argentina, the Esteros del Ibera. Based on interaction with local actors together with observed ecological information, loop models were constructed to reflect relationships between biotic and abiotic compartments. A series of analyses were made to study the effect of different economic scenarios on key ecosystem compartments. Important impacts on key biotic compartments (phytoplankton, zooplankton, ichthyofauna, aquatic macrophytes) and on the abiotic environment (nutrients and sediment resuspension) were observed through model analysis. These models results do not indicate a definite relationship between activity and a possible impact, but a potential impact that can be further studied and modelled. Likewise, the model is not intended to be an end in itself, but as a tool to help focus further ecological study, monitoring and modelling. In the real world of wetland management, it is not always possible to conduct extensive (and expensive) analysis of all the principal ecological compartments. In the same manner, the construction of larger and more complex models for resource management usually needs to be focused to those areas most likely to effect resource quality or ecosystem functioning. In this light, the development of qualitative models was considered as a first step to help researchers and decision makers focus their efforts (and economic resources) in an intensive ecological sampling programme and the construction of predictive models.

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The wetland ecosystems that dominate much of the South American continent are rich in biodiversity and complexity. They remain some of the most pristine wetlands in the world, due to their remoteness and the low population density. However, due to the liberalization of investment barriers and the need to generate exportable income, new pressures for economic development and resource utilization have arisen. Many of these ecosystems are presently being considered for their potential economic utility, putting pressure on the local authorities and the conservation community to find ways of correctly utilising the available natural resources without compromising the ecosystem functioning. Contrary to many northern hemisphere wetlands, there have been few long term ecological studies of the these areas. There is often a lack of quantitative data to construct and validate ecological models. As a result, it is difficult to determine the effects of modifications in particular ecosystem components on the remainder of the ecosystem. While direct impacts of most economic activities are well known, the secondary indirect impacts can be specific to local ecological conditions.

In environmental management, the use of ecological modelling to assist in decision-making is well accepted. Most modelling approaches require a significant data set for model construction and validation. The result is a predictive instrument, which describes the behaviour of a system with precise quantitative statements. However, in the absence of long term monitoring and data, such approaches may not be feasible. Another approach is to examine the system through the interactions between its variables. Aquatic ecosystems can be understood as a network of interactions where the multiple pathways can cause unexpected results to emerge (Carpenter and Mitchel 1993). While these concepts are well understood, few modelling approaches based solely on the interactive structure of ecosystems exist and these (Levins 1975, Hirata and Ulanowicz 1984, Ulanowicz and Abarca Arenas 1995) examine trends and system evolution rather than changes in a particular parameter. Physical and trophic chain based modelling techniques (Ross et al. 1993, Walters et al. 1997, Okey and Pauly 1999) have found a great use in marine and freshwater ecosystem analysis. These modelling approaches are excellent tools for analysing particular scenarios and their effects on trophic balances and fisheries management.

In environmental studies where limited quantitative data is available, the use of network based qualitative approaches can be a helpful tool. The correct use of these models can indicate potential feedback and secondary effects of direct action on a single or more model compartments, based on ecological observations and local knowledge. The results from such a model are clearly not quantitative but useful nonetheless to indicate important indirect consequences (Bodini 1998). Once identified, such potential consequences can lead to more clear management strategies and focused monitoring efforts to control negative impacts. The technique utilised in the present analysis is called loop modelling and is based on the construction and analysis of signed digraphs. In the paragraphs that follow, there is a brief introduction of loop analysis to assist the reader in understanding the model output. For a more in-depth explanation, see Puccia and Levins (1985).

Signed digraphs

The signed digraph (Fig. 1) is a model consisting of variables linked by lines that indicate their relative relationship (positive, negative, none). In the present model, large circles define the variables of the model and are expression of their actual biomass, abundance or concentration (as in the case of nutrients). The links between variables are drawn to describe the trophic relations between them. An arrow, that departs from one variable (S1) and ends on one other (S2), indicates that the latter receives some benefit from the former. A line with a small circle including a dash indicates the opposite situation: that one variable (S2) produces a negative effect on the growth of another variable (S1). The case of a prey-predator system is described by two variables connected by a link containing both symbols (Fig. 1a). A self-damping link (on S1) is also present in Fig. 1a, as a line and circle connecting the variable to itself. Self-effects are related to density dependent phenomena that influence growth of the species on which it is present. If a species acts on its own growth rate by some other element that is not represented explicitly in the model, a self-damping loop is also necessary. Lower elements in the trophic web are usually dependent on other materials not represented in the model and therefore are usually self damped.

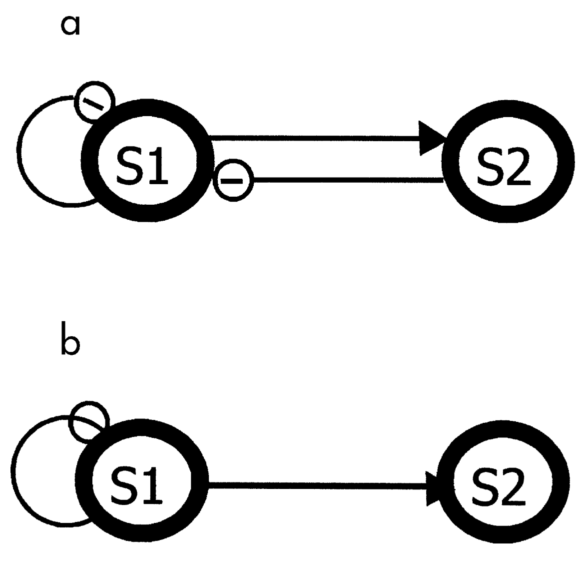

Fig. 1. Symbols and interrelations between two species (S1 and S2), utilised in loop analysis.

The second illustration (Fig. 1b) represents another type of interrelationship that is present in the current model between abiotic and biotic variables. This relationship is observed when the mere presence of one item positively impacts the equilibrium of another variable, which does not elicit any reciprocal effect. One example of this could be the presence of submerged vegetation in providing refuge for a particular fauna species with respect to open water. In this case the vegetation provides a positive benefit to this particular population while not receiving any direct effect itself. The importance of vegetation in maintaining the population structure in shallow lakes has been demonstrated through biomanipulation experiments (Meijer et al. 1995).

Appropriate links reflect actual trophic and physical relationships between model variables. Usually, a series of digraphs is constructed until a final model is found that best represents the ecosystem under study. After the construction of a model that reflects the observed ecological relstionships of the system, the stability of the model is examined utilising stability criteria based on the nature of the feedback at each level of the model and the entire model in general. A stable model (and ecological system) will be dominated by negative feedback. If a model of a known stable system demonstrates instability, the interrelations chosen to represent the model are re-evaluated, further analysis and further model development is necessary to describe the system.

When a model is constructed and the stability is determined, one can begin to examine the potential effect of the modification of one variable on the equilibrium values of the other variables of the model. In this way, one can examine how the modification of a particular ecological compartment could effect other compartments of the model ecosystem. It should be noted that these results are purely qualitative, indicating an eventual increase or decrease in the equilibrium concentrations. The determination of the relative (positive or negative) modifications in the equilibrium concentrations of the model variables begins by identifying the possible feedback paths between each secondary variable and the modified variable.

It should be noted that in most systems, there are numerous pathways between two variables and often times modifications to one variable can have both negative and positive feedback effects on another variable. In the present ecosystem, the direct positive effect of the nutrient concentration on phytoplankton density is positive, whereas there is a also a negative feedback on phytoplankton through the aquatic vegetation variable which imparts a negative effect on phytoplankton (through allelopathic exudates and increased settling). Therefore in the case of increased nutrient concentration, phytoplankton receives both positive and negative feedback. An examination of the total number and relative strength of each feedback is made to determine the overall impact on the equilibrium of the affected variable.

To determine the effect on the equilibrium value of one variable as a result of a change in a parameter of another variable, we need to consider all the possible paths between these two variables, the complementary paths that do not include the path variables and the overall feedback of the entire system. For further explanation of the mathematics involved in the calculation of the equilibrium change in the variable, see the Appendix and Puccia and Levins (1985).

The study area

In this paper, we explore the relationships between ichthyofauna, aquatic vegetation and sediment resuspension in two large shallow lakes within a large wetland area in Argentina, the Esteros del Ibera. This area is the site of an EC sponsored research and development study dedicated to developing management tools for large wetland areas in South America. Models and scenarios were constructed to study the impacts of large scale regional modifications in economic activities, population density, transportation and energy production on wetland resource quality and wetland ecosystem integrity. Physical, chemical, plankton, benthos, ichthyofauna, waterfowl, terrestrial and aquatic vegetation characteristics of two shallow lagoons were monitored for a 1–2 yr. period. One of the first steps in the project was to examine future development possibilities and determine where potential impacts may arise, thereby focusing monitoring and modelling efforts on key compartments of the ecosystem.

The Esteros del Ibera, located in the province of Corrientes in Argentina, represents one of the most important wetland complexes in South America. The entire area covers > 12 000 km^2, of which nearly 60% are permanently inundated. The macrosystem consists in a vast mosaic of sandy plains, low hills, and an intricate complex of marshes, swamps and shallow lagoons. The Esteros system is rain and groundwater fed, with no active incoming river. The interrelation between permanently and seasonally flooded wetland ecosystems supports a diversified community of wildlife typical of neotropical seasonal savannahs: capybara *Hydrochaeris hydrochaeris*, marsh deer *Blastocerus dichotomus*, otter *Lutra longicaudis*, yellow anaconda *Eunectes murinus*, caimans *Caiman yacare* and *C. latirostris*, and piranhas *Serrasalmus* spp. In the present study, two large shallow lagoons are being studied by a multidisciplinary group of researchers. They are Laguna Ibera (area 52 km^2, average depth 3.2 m) and Laguna Galarza (area 15 km^2, average depth 2.3 m). The two lagoons share many of the same physical characteristics (large, permanent shallow lagoons with a seasonal water level variation of ca. 1 m) but each has different ecological characteristics and are subjected to varying anthropogenic pressures.

Laguna Ibera has a large local community (> 300 people) and a growing diversified economic activity (ecotourism, rice cultivation, forestation). In this lagoon, there is a historically high density of macrofauna which previously provided the main economic resource for the local community of hunters. From descriptions from local hunters and preliminary measurements, it appears that L. Ibera has widely varying water quality, in particular affecting turbidity, water colour and pH. Laguna Galarza has a much smaller local community (< 50 people) with a lower human activity induced pressure as economic activities are more traditional with most local estancias dedicated to livestock and small scale rice farming.

The Esteros del Ibera wetland has historically been subjected to little developmental pressure. Activities were limited to trapping and hunting, mostly for capybara, caiman and marsh deer. Local persons were mostly hunters who utilised low technology methods and stayed on the lagoons and marshes for several weeks. For several years, beginning in the 1980s, there was a Provincial attempt to create a natural reserve. However the actual control over this vast area was limited due to financial and organisational constraints and poaching continued throughout most of the region. During the last few years, several areas have been effectively protected within the overall reserve, two of these areas are the study lagoons L. Ibera and L. Galarza.

The natural isolation has helped conserve the wetland integrity but future development plans for the region threatens to create strong impacts on the area. Management and conservation efforts require integrated and innovative tools to insure that the ecosystem is not irreversibly damaged. Agricultural (rice) development, aquaculture, forestry with exotic species and increased tourism in the area could bring about dramatic changes to the entire ecosystem if their impacts are not assessed and their development is not properly planned. While some attention has been given to limit direct impacts of development activities on particular (charismatic) fauna of the wetlands, many of the proposed activities could have important impacts on the chemical and physical characteristics of the wetlands, modifying the structure that supports the unique ecosystem. It is hoped that the use of qualitative models can assist in highlighting feedback mechanisms and pre-emptively indicate where monitoring efforts should be concentrated.

It is obvious that the best development to maintain the ecosystem would be no development at all. However such a purest approach is not possible as the region needs to create economic activity for its population. Additionally, the main economic activity of the small communities within the wetland has been eliminated (hunting), causing related social and demographic consequences. In this light, the best approach is to promote a development that is socially, culturally, environmentally and economically acceptable and sustainable. One possible tool to investigate secondary impact of growing development pressures is the development of qualitative models, assisting researchers and decision makers to focus their efforts and resources on particular ecological studies and modelling.

A large number of potential loop models were created and compared with observed and historical data of the ecosystems under study. The objective of this examination was to qualitatively examine what the potential effects of several small scale economic activities could be on key characteristics of the lagoons. The variables used in the model are: nutrients (considered those that would effect vegetation growth), aquatic macrophytes (rooted emergent and submersed aquatic vegetation), phytoplankton, resuspension of lagoon sediment (consisting of fine organic material), zooplankton, small planktivorous fish, piranha and benthivorous fish. While these variables will describe only a small part of the complex ecosystem, they were considered the minimum necessary to examine the interrelationships between several direct effects from potential economic activities that were selected in scenario workshops with local and regional experts. The economic activities that were examined are: increases in ecotourism, large scale rice farming and the introduction of sport fishing and fish farming. These were selected after meetings with local persons and regional authorities as being the most important activities that would impact the wetlands.

"Ecotourism" has been demonstrated to be one of the key economic opportunities in remote areas of Latin America (Ecuador, Brazil, Costa Rica). Large wetland and forest areas that in the past were left undeveloped for lack of resources and infrastructure are looked upon as economic outlets to tap into the growing ecotourism industry. In the present expansion of western and national tourism industries, such unique ecosystems have advantages that can be capitalised on by the host countries, tourist operators and the tourists themselves. The importance of tourism revenue is particularly important in developing countries as national economies suffer from a severe balance of payments problems. The notable increase in the last two decades of the ecotourism industry has made local and regional governments positively re-evaluate their development schemes, placing more importance on promoting on this new travel trend. Large intact ecosystems have a clear advantage in terms of the variety and extent of unspoiled nature. Data for several countries that have growing ecotourism industries follow (Cater 1994; Table 1).

However, the overall benefits of these new activities are mixed. While ecotourism can provide an excellent opportunity to attract foreign exchange for the preservation of natural systems and wildlife, there is no doubt that tourism, as any economic activity can pose a threat on the very resources on which it depends. Tour groups leave garbage behind them in pristine areas, tour boats create acoustic and wave damage along coastlines, hikers trample fragile undergrowth, increased demand on local infrastructures modify resources (water, transport, waste treatment) as well as the cultural balances in local communities. In Costa Rica, where ecotourism has been very successful, many environmental impacts have been ambiguous, with more popular and accessible areas absorbing impacts beyond

Table 1. Economic growth of the ecotourism industry in developing countries (GNP: Gross National Product).

	Tourism receipts 1981 (US$ millions)	Tourism receipts 1990 (US$ millions)	Tourism receipts as %GNP 1981	Tourism receipts as %GNP 1990
Belize	8	91	4.5	24.8
Costa Rica	94	275	3.6	4.8
Ecuador	131	193	1.0	1.8
Kenya	175	443	2.5	5.9
Madagascar	5	43	0.2	1.6

their natural carrying capacity. Such damage is usually related to problems of overcrowding, water pollution, trail erosion and changes in wildlife behaviour (Weaver 1994). In the Esteros del Ibera, the potential growth of ecotourism is based on the presence of a number of charismatic fauna species (marsh deer, caiman, neotropical otter, capybara, black howler monkeys, brocket deer, maned wolf, yellow anaconda) and in particular the spectacular diversity of waterfowl.

These latter species are present in both lagoons and has been found to exceed 400 species of birds. The most common species are: the American anhinga *Anhinga anhinga*, a diverse guild of herons and their allies (*Ardea cocoi, Egretta alba, E. thula, Syrigma sibilatrix, Butorides striatus, Nycticorax nycticorax, Botaurus pinnatus, Isobrychus involucris, Tigrisoma lineatum*), the neotropical cormorant *Phalacrocorax olivaceus* and kingfishers (*Ceryle torquata, Chloroceryle amazona, Chloroceryle americana*). These species are attracted to the lagoons by the density of fish present in a water with a high transparency (Secchi depth 70–100% in littoral lagoon areas, data from autumn 1999). While there is a very diversified community of waterfowl, the species density is relatively low, perhaps due to the low nutrient content and primary production of the principle lagoons.

Another important tourism related species are the caiman found in the Esteros, *Caiman yacare* and *Caiman latirostris*, the former being the most common and is widely distributed. Caiman are found in most water bodies and marshes throughout the Esteros. The presence and quantity of littoral vegetation is a key element in the survival of the caiman as it provides a support for the prey of juvenile caiman, a reproduction area and resting base. Due to the large number of variables involved, no direct relationship has been published between vegetation density and caiman population but it would appear that the presence of large vegetated areas favours a larger caiman population.

Rice production was, until recently, limited to small scale farms with a marginal use of the lagoon waters. As such, the relative impact on lagoon water levels and the possible infiltration of pesticides or back flushing of fertilisers was limited. Long canals with pumps were dug to the lagoons from the rice fields which were at a higher elevation than the Esteros. In recent times, with the formation of the Mercosur and the reduction of property and trade restrictions, there is a massive increase in investment in the region primarily dedicated to agriculture (rice) and silviculture. A number of proposals have been presented for large scale (> 10 000 ha) rice plantations which would utilise lagoon waters and could have significant impacts if poor material management or unfavourable weather conditions prevail (heavy rains during or after the fertiliser or pesticide application). Increased nutrient runoff would significantly alter the present nutrient conditions. Furthermore, the removal of large water quantities could temporarily lower lagoon levels, increasing the occurrence of wind generated resuspended sediment modifying the light regime for aquatic macrophytes.

Due to the presence of high quality, low use waters in the wetland, the introduction of aquaculture has been repeatedly suggested as a possible local income source. Such activities could entail a wide range of possibilities from extensive fish farming for selected species, to the introduction of particular species for sport fishing, to the harvesting of the local species. The local communities do not depend on the fish for food as their main diet consists of beef which is available for a low cost. Some local recreational fishing is done, but the dominant fish (piranha) is held in low esteem by the local population. The introduction of fish farming in either enclosed or open areas represents one possible economic activity. The fish biomass produced could be sold for export or used as a protein supplement for livestock. The introduction of larger predator species for sport fishing is another possibility. Such species would have to survive the competition and co-habitation with the piranha, unless these latter were eliminated (such wholesale biomanipulation is not uncommon in some western European, North American and African lakes; Meijer et al. 1995). A final possibility could be the harvesting of the small tropical fish for home aquariums. The impacts of each activity are further explored below.

Model development

A series of signed digraphs were created and examined, utilising information obtained from field observations, information from local persons, literature data and descriptive information from regional experts in similar ecosystems.

Models which did not reflect the trophic and ecological combinations found in both Laguna Ibera and Laguna Galarza were discarded and a final basic model was determined. The model is represented in Fig. 2. The model is directed mainly towards the extensive littoral areas of the lagoons, in which macrophytes and phytoplankton compete for nutrients and the highest density of fish are claimed to be present.

The model begins with a negative feedback loop between sediment resuspension and rooted aquatic vegetation. In the study lagoons, it has long been noted that water is less turbid in the area of aquatic vegetation. Secchi depths increase from 80 to 260 cm in the highly vegetated lagoon and canal areas with respect to the unvegetated areas. This is a result of a number of self-reinforcing phenomena that are represented by the line with two negative symbols (circles with a dash). Macrophytes absorb wave energy, reducing the erosive-like forces of the passing wave on the lagoon floor, reducing the resuspension of sediments. Turbulence within macrophyte stands is also strongly reduced, which promotes faster resettling of resuspended particles. Furthermore, macrophyte roots in thick stands can partially hold down sediment.

With respect to the effect of resuspended sediment on vegetation, turbid water limits the light available for macrophyte growth in light limited environments. Resuspension not only increases turbidity but settling particles of suspended sediment may also cover plants, reducing light and nutrient availability. Additionally, loose unconsolidated sediment presents a poor substrate for vegetation exposed to wave action allowing for their uprooting. These effects can cause alternative steady states in lagoons with strong external inputs, with a steady vegetated clear state and a turbid vegetation-less state. The study lagoons have, to date, maintained a single relatively stable state with significant littoral vegetation and a vegetationless centre body. The presence of vegetation reinforces itself while diminishing the possibility for the resuspension of sediments. On the contrary, in turbid lakes, resuspended sediment acts as a deterrent for vegetation growth. Both variables have negative self loops as both have external factors, not included in the model, that influence their growth. For vegetation these factors include light and temperature, whereas for resuspension these include the presence of currents, wind and activities of the local fauna (herbivores and birds) and man.

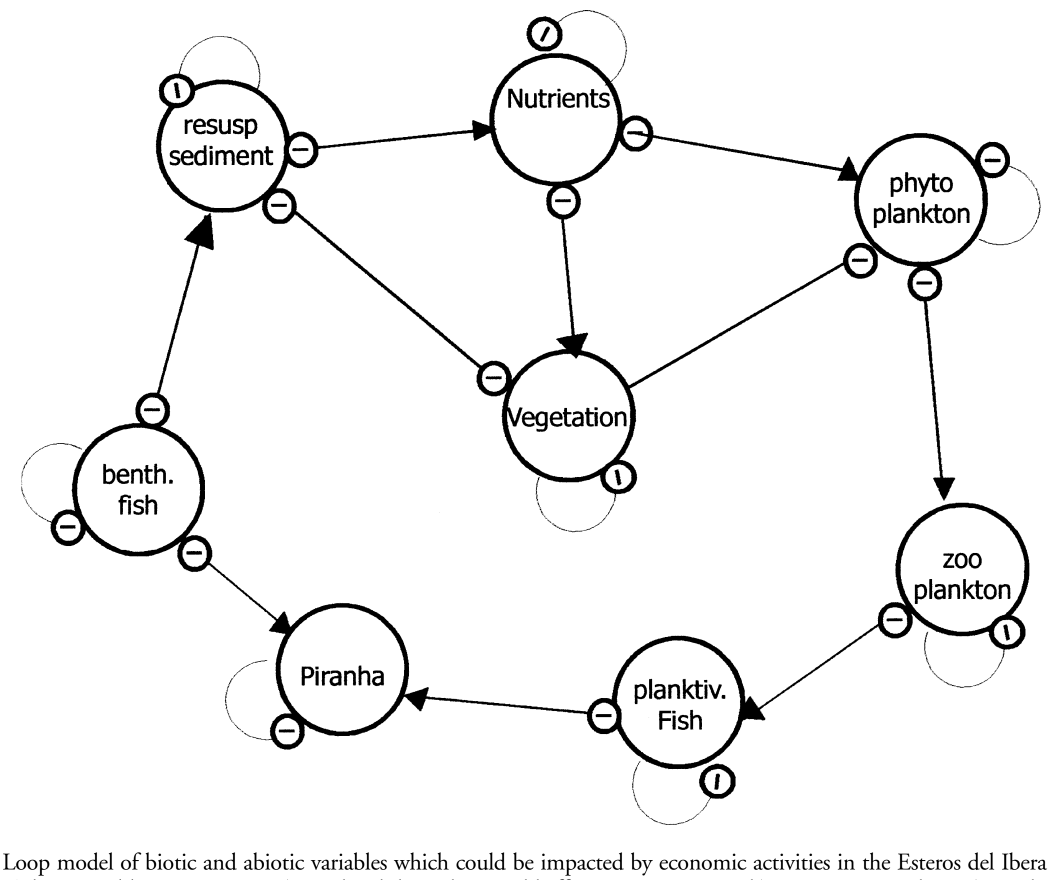

Fig. 2. Loop model of biotic and abiotic variables which could be impacted by economic activities in the Esteros del Ibera wetland lagoons. These variables are: nutrients (considered those that would effect vegetation growth), aquatic macrophytes (rooted emergent and submersed aquatic vegetation), phytoplankton, resuspension of lagoon sediment (consisting of fine organic material), zooplankton, small planktivorous fish, piranha and benthivorous fish.

The concentration of nutrients in the water body is influenced by both resuspension as well as the presence of phytoplankton and macrophytes. Unlike terrestrial plants, many submerged macrophytes has an uptake of nutrients through their shoots as well as their roots. Macrophytes are considered here to include their associated periphyton biomass which also utilises the nutrients present in the water. Resuspension of sediment and water movement (Wetzel 1983) make formerly unavailable nutrients available to vegetation as well as moving nutrients from nutrient rich areas to nutrient poor areas of the lagoon. The relation of macrophytes and phytoplankton with the nutrient concentration is a competition like relationship with the presence of nutrients benefiting both variables that compete with each other for their availability. The limiting nutrient for phytoplankton and macrophytes in the study lagoons has yet to be quantitatively determined, but low nitrogen levels have been frequently found in vegetation stands in shallow lakes (Scheffer 1998).

Non-nutrient related negative effects of vegetation on phytoplankton are also important in shallow lagoons. Shading by standing macrophytes has been reported to reduce algal abundance (Wetzel 1983) and depends upon the vertical distribution of the plant biomass. Also important are the emission of allelopathic substances in macrophyte stands that suppress some phytoplankton, in particular cyanobacteria which appear to be important in the lagoon waters studied (Alinamos pers. comm.). Another important mechanism in reducing the phytoplankton growth in macrophyte stands is related to the reduction of water movement within the vegetation stands, thus increasing settling losses of plankton in the shallow water and reducing the potential resuspension of settled plankton. All these three effects are summed in the digraph as a single negative impact from the vegetation to the phytoplankton variables. The light limitation of phytoplankton on the macrophytes was not included in the model as this impact would be very limited due to the low phytoplankton concentrations found in the preliminary study and reported in the literature.

It should be noted that the model does not include, as a main variable, floating macrophytes which would also negatively impact on phytoplankton as well as submerged macrophytes. Floating macrophytes were not considered as they have a secondary impact on resuspension and are limited to particular sheltered areas of each lagoon.

The standard predator-prey trophic chain between phytoplankton and zooplankton, planktivorous, and benthivorous fish populations and the piranha is described in the lower part of the model. While the relationship between these variables is much more complex, the predator-prey symbols are sufficient to describe their interrelations. The zooplankton receive a benefit from the phytoplankton who are negatively affected by the presence of the zooplankton. The density of zooplankton can be an important factor in controlling the concentrations of phytoplankton and maintaining clear lagoon water. The zooplankton variable is self-damped as the species that seem dominant in the lagoons (rotifers and copepods) are omnivorous. The phytoplankton variable is also self-damped as other factors (light, temperature) are important in its growth.

The small and medium size planktivorous fish (Clupeidae, Tetragonopteridae, Poecilidae, Ciprinodontidae), that are often seen in the littoral areas of the lagoons, link the zooplankton variable to the piranha variable. These are important species in the plankton driven trophic chain between the primary production and the top predators. Within the lagoons, there are other variables that effect their population (i.e. waterfowl) making them self damped within the present model.

Piranhas, *Serrasalmus* spp., are voracious predators which strongly control the growth of ichthyofauna species more desirable for their commercial value. The piranhas may represent an important historical deterrent in the development of potentially damaging economic activities in the lagoon (e.g. fish farming and large scale recreational tourism). Within the model the piranha variable is the top predator consuming both planktivorous fish as well as benthivorous fish. The variable is self-damped as other factors are important in controlling its population (piscivorous species such as caiman, otter and birds as well as piranha cannibalism).

Large benthivorous fish species are often very important in the nutrient recycling in oligotrophic lakes, both through faecal pellets emission but more importantly through indirect mechanical agitation of the lake floor, which can significantly increase sediment resuspension in shallow lakes. The benthivorous fish community forages by sucking in sediment, retaining food particles through a gill-raker system. The effect of the foraging increases the resuspension of non-retained sediment particles with a resultant increase in the water turbidity. In biomanipulation experiments in the Netherlands, the reduction of stock of benthivorous fish from 600 kg ha^{-1} to 200 kg ha^{-1} resulting in an almost instantaneous increase in transparency, largely due to a drop in the concentration of inorganic suspended solids. In experimental pond experiments, the concentration of suspended solids decreased linearly with fish density. In European lakes, several benthivorous species were found to suspend five times their own body weight per day (Scheffer 1998). There is a significant community of these fish in the study lakes (Erythrinidae, Rhamphichthyidae, Pimelodidae), resulting in a positive link from the benthivorous fish variable to the resuspended sediment variable.

Studies in Finnish and Swedish lakes indicate that lakes without piscivorous fish have large benthivorous fish populations with many small individuals, whereas in larger lakes with piscivores have the small benthivorous fish populations consisting of few large individuals (Brönmark et al. 1995). The voracious predation pressure by the dominant piranha population is most likely an important factor controlling fish related resuspension thereby maintaining the highly transparent waters of the Esteros lagoons and canals.

Based upon the above ecological information, numerous models were examined and a final digraph model was selected. Next, a positive parameter change to each variable was examined according to a potential impact from a present or proposed economic activity. Based on the pathways between this variable and the other variables in the model, the change in an equilibrium concentration of each model variable can be calculated. The result is the qualitative effect of a parameter change of a single variable on the equilibrium state of the other model variables. A positive result indicates that the resultant effect on the equilibrium concentration or population of a particular species is positive (increase of abundance or biomass), whereas a negative sign would indicate that the equilibrium concentration or population would decrease respect to the pre-impact situation.

For each parameter change to a single variable, there are a number of possible paths from the impacted variable to the examined variable. A comparison of these loop paths is made to determine if the overall impact is negative or positive. In the absence of information on the relative strength of the loop paths, the equilibrium effect is considered to be related to the number of paths that link the variables. If the number of positive loops is three times more numerous than the number of negative loops, the overall equilibrium effect is considered positive. For example, if there are 6 positive and 2 negative loops correlating the planktivorous fish population to an increase in the concentration of phytoplankton biomass, the overall impact on the fish population is considered most probably positive in relation to positive parameter change on the phytoplankton. If the number of positive and negative loops is similar, the relationship remains ambiguous. For example, if there are 4 positive loops and 7 negative loops relating the benthic fish biomass to a positive parameter change in the piranha population, the impact cannot be determined until more information is available on the individual 11 paths. A weak relationship signifies that the number of paths in one direction are more than double but less than three times the number of paths in the other direction. A zero describes no relationship between variables. The results for the above model are presented in Table 2.

Examining a parameter change to each variable, one can estimate the resultant equilibrium state of the remaining variables and predict the secondary impacts of particular activities in the lagoons.

Increases in the resuspension of sediment could result from increased tourism activities or changes in the hydrological regime of the lagoon. The recent development of ecotourism on Laguna Ibera has increased the number of motorised boats present on the lagoon as well as the size of the average motor. The impact of high horsepower outboard motors (40 hp) on the lagoon ecosystem is multifold, but one impact in littoral zones (where the tourist related macrofauna are most present) will be an increase in the sediment resuspension.

This effect can be seen in Table 2, where an increase in the resuspension of sediment will have a positive effect (increase) on the plankton driven trophic chain and the nutrient concentrations. The equilibrium biomass of benthivorous fish should decrease. The effect on the aquatic macrophyte density is unclear as there are both positive effects from the increased nutrient concentrations but direct negative effects from the increased turbidity (sediment and phytoplankton). To further clarify the equilibrium effect, it would be necessary to determine if macrophyte growth was light limited (negative effect) or nutrient limited (positive effect). If the vegetation were light limited, the increase resuspension and phytoplankton would reduce the ability of the vegetation to survive and reproduce. This has been reported in shallow lakes in the Rift Valley Lakes in Kenya (Aloo pers. comm.), where an increase in sediment concentrations from up basin over grazing has caused significant reduction of littoral aquatic vegetation. A possible reduction in aquatic macrophyte density could have important implications on macrofauna (caiman, otter) and

Table 2. Prediction table for qualitative model for feedback between system variables in the neotropical wetland (Esteros del Ibera). Model variables which have been affected include: nutrients (considered those that would effect vegetation growth), aquatic macrophytes (rooted emergent and submersed aquatic vegetation), phytoplankton, resuspension of lagoon sediment (consisting of fine organic material), zooplankton, small planktivorous fish, piranha and benthivorous fish.

Affected node:	Resuspen.	Phytopl.	Nutrients	Acq. Veg.	Plank. fish	Piranha	Benth. fish	Zooplankt.
Input node:								
+ → Resuspen.	+	+	+	?	+	+	–	+
+ → Phytopl.	+ weak	+	?	–	+	+	–	+
+ → Nutrients	–	–	?	+	– weak	– weak	+ weak	– weak
+ → Acq. Veg.	–	–	– weak	+	–	–	+	–
+ → Plank. fish	?	?	– weak	?	?	?	?	?
+ → Piranha	–	–	– weak	+ weak	– weak	?	?	?
+ → Benth. fish	+ weak	?	+ weak	?	?	?	?	+ weak
+ → Zooplank.	–	–	?	+	?	?	?	?

waterfowl, both important species for tourism. If the species of macrophyte were nutrient limited increased resuspension could increase the equilibrium density of the aquatic macrophytes.

The increase in lagoon nutrient concentrations from anthropic activities such as tourism facilities or agricultural fertilisers is an important potential modification to the lagoon equilibrium. A larger tourism activity, together with the resulting modification on the local economy could lead to significant increases in the wastewater nutrient additions to the lagoons. Large scale intensive agricultural activities would increase the presence of nutrients in the local groundwater and increase the possibility of nutrient runoff arriving into the lagoon. Furthermore, intensive aquaculture activities would require the addition of nutrients to the fish ponds connected to the system whereas extensive activities that included harvesting could remove nutrients from the lagoon systems.

The key feedback mechanism in this case is the nutrient uptake competition between phytoplankton and vegetation and consequently a negative feedback between vegetation and phytoplankton. It is interesting that an increased nutrient concentration would lead to increased macrophyte density, and a probable reduction in the phytoplankton biomass. This will be the case when the negative effect of the aquatic macrophytes on the phytoplankton is significant, leading to an over reduction in the plankton trophic chain. Therefore, the equilibrium values of the entire chain phytoplankton → zooplankton → planktivorous fish → piranha populations could be reduced.

As these effects are a combination of both positive and negative feedback (hence the weak symbol), it would be important to further study the individual links. However an increase in vegetation density in oligotrophic lakes with increased nutrient load has been reported (Scheffer 1998). An obvious beneficiary in this effect would be the benthivorous fish population which would suffer from less predation by the lower population of piranha. Important impacts on macrofauna and bird populations would result from modifications in the fish community were to occur. Similarly, the density of emergent littoral vegetation is a key factor in maintaining the present ecosystem structure.

Another interesting observation is the lack of a clear equilibrium effect of increased nutrient runoff on the nutrient concentration itself. As there is both an increase in aquatic vegetation and a decrease in sediment resuspension, the increased runoff may not necessarily result in increased equilibrium concentration. One possible result could be alternating vegetational states in lagoons in relation to nutrient inputs that have been described for two Swedish shallow lakes (Blindow 1992), with hysteresis between a steady vegetated clear state and a turbid vegetation-less state.

Another result of interest is the effect of modifications in the density of the aquatic macrophytes on the other variables. In this case, such impacts could be related to the reduction of littoral zone vegetation by tourism development or the physical damage of vegetation by high boat traffic. Both impacts are presently very limited, but could be important if future development is not controlled. The results in Table 2 are based on a positive parameter change and we would like to examine a negative parameter change to vegetation, therefore it is necessary to reverse the signs of the results. By reversing the sign of the parameter change, the signs of the resultant changes in the equilibrium concentrations will also change, e.g. resuspended sediment then becomes positively affected.

The resulting equilibrium values have important consequences for the wetland functional value. Most importantly, there would be an increase in nutrient concentrations, both directly from the reduced nutrient uptake by the vegetation as well as indirectly from an increased resuspension. Similar observation have been hypothesised for tropical shallow lakes in Uganda, where vegetation removal has been determined to reduce the nutrient assimilation capacities of littoral wetland areas (Kansiime et al. 1994). There would also be a positive increase in the equilibrium concentration of phytoplankton related variables. Such modifications could have important impacts on local fauna, as increased resuspended sediment and phytoplankton would reduce transparency, negatively affecting fauna species depend on clearer water for fishing. Benthivorous fish populations would decrease through increased pressure from the piranha population.

Another important result of the model is the equilibrium predictions for modifications made to the piranha population. Large scale manipulation of the ichthyofauna community for commercial purposes is not unheard of. Such procedures include killing the entire fish stock with rotenone, netting out selective species or adding a new non-autochthonous species that negatively affects one or a group of native species through predation or competition. Large scale lake manipulation is used to promote aquaculture and sport fishing industries and could find a place in proposed economic activities. The African Great Lakes are important examples of potential catastrophic changes of new species introduction to the historic community structure (Wilson 1993).

A negative parameter change to the piranha population (increased mortality through selective continuous capture or the introduction of an antagonistic species) would have positive effects on the resuspension and phytoplankton (reversing the signs in Table 2). The resultant increased turbidity would negatively impact waterfowl density and water quality. The impact on the nutrient concentrations is weakly positive as the increased resuspension would bring more nutrients into the water column and there are less macrophytes to take up those nutrients, but the increased concentrations of phytoplankton will have an opposite effect. To better define the potential equilibrium effects on the nutrient concentrations, more information is necessary on the benthivorous fish – resuspension link and the phytoplankton – nutrient link. In the deeper Laguna Ibera, it is probable that the effect on nutrient concentrations would be less evident as fish related resuspension is of less importance and vegetation may be more light limited than nutrient limited allowing for phytoplankton to dominate nutrient uptake. In the shallower Laguna Galarza, with generally lower nutrient and chlorophyll concentrations, resuspension is more important and vegetation effects on phytoplankton are stronger, resulting in possibly increased sensibility to increased nutrient availability.

An important secondary negative effect on aquatic macrophytes would result from the increased piranha mortality. This is the result of the negative effects of increased resuspension as well as the negative competition like effects resulting in the changes in the plankton driven trophic chain.

Regarding the fish populations, one would expect to see reduced piranha population and increased benthivorous fish population. However, there are number of conflicting feedback that make unclear the equilibrium populations of these variables. Potential increases in piranha prey (feedback from the increased resuspension through the plankton variables) could have a positive effect on the equilibrium piranha population (perhaps increasing reproduction rate to offset the increased mortality) which might offset the continuous capture. The equilibrium effect would depend on the strength of the nutrient feedback loop with respect to the self loops of the piranha. As such, any biomanipulation work would require thorough evaluation of these feedback loops before proceeding. It should be noted that many biomanipulation experiments which resulted in short term successes fail over time as unforeseen secondary effect lead the aquatic ecosystem to reach an equilibrium different than that desired.

Zooplankton are a key link into the plankton driven trophic chain and important in controlling phytoplankton growth. Impacts to the zooplankton density could result from agricultural activities. This is particularly important if adverse weather conditions or poor water management cause the infiltration of irrigation water containing pesticides into the lagoons. Pesticides are known to have negative effects on the zooplankton density (Ware 1994). Note in Table 2 that a negative effect to zooplankton would be related to a positive effect in resuspension and phytoplankton. The positive impact on the phytoplankton density is an obvious result of positive effects on the benthivorous fish population and negative effects on the vegetation biomass. The reduction in macrophyte density would also negatively affect a number of important fauna populations that use macrophytes for physical support and feeding.

The model presented above is only one of a number of models that were constructed to represent the study ecosystem. To demonstrate the robustness of the model developed, a similar model is presented below to highlight how slight variations of the model may give different results (Fig. 3).

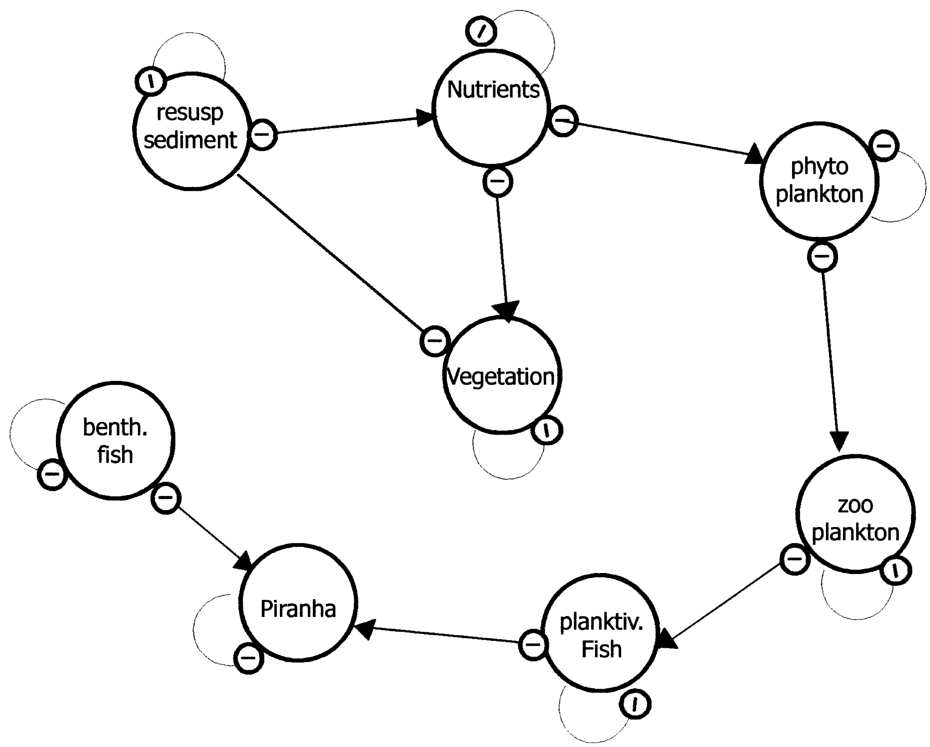

Fig. 3. Alternative model using the same biotic and abiotic variables as utilised in Fig. 2. These variables are: nutrients, aquatic macrophytes (rooted emergent and submersed aquatic vegetation), phytoplankton, resuspension of lagoon sediment, zooplankton, small planktivorous fish, piranha and benthivorous fish.

In deeper lakes the effect of benthivorous fish on the concentration of sediment in the water column is not significant as resuspension depends on more significant wave energy (wind speed and fetch). In such lakes the vegetation is light limited and does not cover a significant part of the lake floor. Therefore the impacts on phytoplankton concentration and sediment resuspension are limited (while the impact of the sediment on the vegetation remains; Fig. 3). The results of this deep water model are described in Table 3, differences from the shallow water model are marked with an asterisk (*).

Major differences can be seen in the equilibrium concentrations of most variables for parameter changes to the nutrient concentrations and piranha populations. The impact of an increase in nutrient concentrations has a clearly positive effect on the entire phytoplankton based trophic chain as well as the aquatic macrophytes. This is due to the removal of negative links between the vegetation and the phytoplankton and resuspension. We should note that this is based on an oligotrophic conditions in which the negative effects of eutrophication are not present.

A parameter change to the piranha population would now result in a clear modification of the plankton based trophic chain and a clearly negative effect on the benthivorous fish population. Aquatic macrophytes would benefit as there should be a reduction in the phytoplankton concentration through increased predation pressure by the zooplankton.

The removal of the negative feedback link from the vegetation to sediment resuspension together with the elimination of the benthivorous fish – resuspension link removes all but a direct self effect from the resuspension variable, hence the vertical column of 0 (no impact) of the variables on resuspension. Hence, the modifications of these seven variables do not effect the resuspension of lake sediments in this deeper lake.

Conclusions

The sustainable utilisation of wetland resources is a complex task, in which long term monitoring and ecological study are essential to correct decision making. However, in the developing areas, there is often an urgent need to create economic development without the necessary understanding of the impacts of these activities on the ecosystem functioning and resource quality. As a result, decision makers cannot make informed decisions and often lack ideas even on where to begin looking. To successfully maintain the biodiversity and functional values of these ecosystems and satisfy local development needs, there is a need to develop innovative analysis instruments. As ecological and socioeconomic modelling is growing in acceptance for management purposes, there is a need to develop and integrate the numerous approaches already available. One helpful instrument for examining the interrelationships between key ecological variables in ecosystems in which there are limited quantitative data can be qualitative loop modelling.

The development of qualitative models helps highlight complex feedback responses that are difficult to incorporate in quantitative model, in particular where there are limited data and few comparable ecosystems. In this paper, we have described a model that relates potential effects of increasing economic activities on the fundamental physical and trophic characteristics of two shallow lagoons in the Esteros del Ibera wetland system. Interesting secondary effects were found regarding the impacts of particular economic activities on nutrients, plankton, ichthyofauna, increase resuspension of lagoon sediments and macrophyte density. The activities analysed were increased agricultural use of surrounding lands for rice production, increased ecotourism and the introduction of aquaculture. Other activities, not currently considered, could be examined using the same model.

Table 3. Prediction table for an alternative qualitative model for feedback between system variables in the neotropical wetland (Esteros del Ibera). Model variables which have been affected include: nutrients (considered those that would effect vegetation growth), aquatic macrophytes (rooted emergent and submersed aquatic vegetation), phytoplankton, resuspension of lagoon sediment (consisting of fine organic material), zooplankton, small planktivorous fish, piranha and benthivorous fish. The asterisk indicates where the equilibrium change differs from the original model. Differences from the shallow water model are indicated by (*).

Affected node:	Resuspen.	Phytopl.	Nutrients	Acq. Veg.	Plank. fish	Piranha	Benth. fish	Zooplank.
Input node:								
+ → Resuspen.	+	+	+	?	+	+	–	+
+ → Phytopl.	0 *	+	–	–	+	+	–	+
+ → Nutrients	0 *	+ *	+ *	+	+ *	+ *	– *	+ *
+ → Acq. Veg.	0 *	–	–	+	–	–	+	–
+ → Plank. fish	0 *	+ *	–	–	+ *	+ *	– *	– *
+ → Piranha	0 *	–	+ *	+ *	–	+ *	– *	+ *
+ → Benth. fish	0 *	– *	+	+ *	– *	+ *	+*	+
+ → Zooplank.	0 *	–	+ *	+ *	+ *	+ *	– *	+ *

Based on the model, large scale agricultural activities such as increased rice production using lagoon waters were seen to not only potentially affect nutrient concentrations directly but have impacts on the balance between macrophyte and phytoplankton densities. Likewise the entrance of pesticide contaminated water would have a direct effect on plankton abundance and a more important effect on overall turbidity by increasing equilibrium concentrations of both resuspended sediment and phytoplankton as well as decreasing macrophyte density. Modifications of the lagoon turbidity would have important consequences throughout the trophic web as well as affecting important fauna (piscivorous) and waterfowl populations. Reductions in the aquatic macrophyte density would have important negative impacts on the macrofauna which inhabit the littoral area of the lagoons.

Massive withdrawal of lagoon waters for rice production could effect the lagoon water levels. Water level plays a key role in maintaining the equilibrium between vegetated areas and nonvegetated areas of the lagoons. Short-term withdrawals could decrease the seasonal water transparency as there would be an increase in wave driven sediment resuspension on open wind exposed areas. According to the model, such resuspension would cause increases in the plankton driven trophic chain and decrease the macrophyte density. It should be noted that on the leeward side of the lagoon, photosynthesis would benefit from increased light availability in deeper zones during the draw down period. Depending on the duration of the water level change as well as weather (wind) conditions and vegetation conditions, the net overall effect can be determined. The most probable effect would be one in which overall turbidity increases and there would be long term negative effects on vegetation density of the lagoon.

Ecotourism is heralded as a possible best compromise to attract foreign exchange and create economic revenue while preserving the natural environment. Due to the currently limited tourism presence, there is a rather limited impact on the wetlands. Small side businesses are growing and there are signs that the local population is beginning to get involved. It is important to note that all such growth is very recent and the continued uncontrolled growth of tourism could lead negative impacts on the nutrient load in the lagoons as well as damaging the littoral macrophytes. Such modifications in the ecosystem could jeopardise the very uniqueness and biodiversity that tourists come to visit. According to the model, equilibrium effects of such modifications would have conflicting impacts on trophic and water quality (turbidity) values. To further analyse these impacts, additional analysis and modelling is necessary.

Increases in high-horsepower boat traffic may increase sediment resuspension leading to secondary effects on phytoplankton concentrations and fish populations. The resultant increased turbidity would reduce macrophyte density, which would be further reinforced by the mechanical destruction of the boats on the vegetation shoots and leaves. The presence of vegetated areas is important for a number of charismatic species (caiman) as well as waterfowl diversity. Vegetated clear water is an important factor in maintaining bird diversity in wetland systems.

An unregulated increase in the number of tourists who stay in the lagoon communities would cause increased pressure on the present day infrastructure as well as increases in the amount of wastewater that arrives to the lagoon. The presence of many affluent tourists may also favour local immigration and modify consumption patterns in the local communities. All of which would increase the nutrient loading into these oligotrophic lagoons. The model shows that increased nutrients would increase the rooted aquatic vegetation and have a negative impact on the plankton driven trophic chain. The relative strength of this latter impact is not clear but one key mechanism was evidenced through the model, that being the multiple negative feedback of aquatic macrophytes on phytoplankton. Such a relation will exist as long as the lagoons do not become eutrophic, at which point other mechanisms would become dominant.

The opposing secondary effects of these two impacts (increase resuspension and increased nutrients) cannot obviously be purely summed but must be considered separately. Each may have different spatial and temporal effects. As a result of the model, certain observations can be made that could be incorporated into a local monitoring plan. One interesting option would be to utilise selected species of fish or waterfowl as indicator species within a locally based management plan to monitor changes in vegetation density and effects from increased turbidity.

Other potential impacts of increased ecotourism activities are related to direct harvesting in the fish community. Limited fishing of piranha for tourists consumption in not likely to cause significant changes in fish population structure. However the model shows that lowering the piranha density will have secondary effects on increasing turbidity (resuspension and phytoplankton) which combined with other impacts by increase boat traffic (damages vegetation stands, increased resuspension) could have seriously negative impacts on water quality and fauna habitat.

The introduction of some form of aquaculture or sport fishing is a low priority development option in the region. The effect of aquaculture on nutrient concentrations could have unexpected results on the macrophyte density as well as decreases in the planktivorous and piscivorous fish populations where one would normally expect increases. The key feedback mechanism was found to be the negative links from the aquatic macrophytes to the plankton that are particularly important in shallow lagoons.

Sport fishing would require an elimination of the piranha population or the introduction of an aggressive competitor to the piranha. Similar whole lake manipulations occurred at the turn of the century in many of the African Rift Valley lakes, leading to the present day near-absence of native species in these large shallow lakes. In the present study area, biomanipulation (continuous fishery pressure or the introduction of an antagonistic species) directed at decreasing the top predator species (piranha) was found to give very unclear results, including the possibility that equilibrium concentrations of the affected species could actually increase. The introduction of any new species in this unique ecosystem should be avoided and the model further highlights that the equilibrium results of such manipulations would be difficult to predict.

All economic activities are based on utilising (economically) free ecosystem services and as such consuming the available ecological resources. Correct management of such activities should consider the effect on the "equilibrium" status of the ecosystem as well as the system's carrying capacity according to the principles of sustainability. The basic challenge in using such an approach in natural systems lies in considering the complex feedback mechanisms between ecosystem components. For which, any reductionist model that strives to describe more than a small part of the system is doomed to fail. However, through the correct use of modelling, insights may be gained into the overall functioning of the ecosystem and key relations may be identified which help focus further study and monitoring (Puccia and Hull 1988).

It should be noted that the qualitative modelling approach utilised in the present work is considered a first step in the study of ecosystem interactions. As such, it is a useful tool to focus field work and other modelling efforts where little quantitative data are available. In the present project, numerous ecological modelling approaches were used to more specifically study the specific interactions between the environment and the fauna populations. One important result of the qualitative analysis was the identification of the aquatic vegetation as a key variable in maintaining the actual ecosystem quality. As a result, further study of the temporal distribution of the wetland vegetation was made using satellite sensors in collaboration with the Argentina Space Agency (CONAE).

Wetlands have mechanisms and feedback that are not adequately explained by present ecological paradigms (Mitsch and Gosselink 1993). As transitional areas, wetlands present a number of difficult problems related to their management and study. When selecting parameters for monitoring, often times historic quantitative data are missing or they are inadequate. In these cases, field observations, bibliographic information and local knowledge can be utilised to create qualitative models that bring to the light previously unconsidered connections. This new information then becomes fundamental in management decisions and monitoring programmes. In the present study of the wetlands of the Esteros del Ibera, loop analysis was found to be a useful instrument in understanding the interrelationships between wetland variables and to give indications for the construction of a long term monitoring plan.

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Appendix. For a better understanding of the loop model construction, stability criteria and equilibrium effect calculation, see the original text by Puccia and Levins (1985). The calculation of the change in the equilibrium value of the X_j as a result of a change in variable X_i is given by the following equation:

$$\frac{\partial X_j}{\partial c} = \frac{\sum_{i,j} \left(\frac{\partial X_i}{\partial c}\right)\left(p_{i,j}\right)\left(F^{comp}\right)}{F_n}$$

where the variable being changed is dX_i/dc , each possible path from X_i to X_j is $p_{i,j}$ and the complementary path of each $p_{i,j}$ is F^{comp}. The overall feedback for the entire system is F_n, which for a stable system should be negative. As there may be a number of pathways between X_i and X_j, there are an equal number of complementary paths F^{comp}. It is the sum of the effects through each pathway that determines the overall effect. The sum of the products of dX_i/dc, $p_{i,j}$ and F^{comp} for each possible path determines the overall effect on X_j. For any loop model with n variables, there are n points of entry for a parameter change, one for each variable. A table of predictions can be constructed that demonstrate how each variable will change as a response to a change in itself or any other variable.