Tropical Lake Ecology Assessment
With Emphasis on Changes in
Salinity of Lakes
Project No.SAA-140714
Final Technical Memorandum # 7
Impact Determination

Prepared for:
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ANNEX

1.0 INTRODUCTION

The Panama Canal Authority (ACP) is currently performing a series of studies to assess the feasibility of a new set of locks, alternative systems to raise and lower vessels, and upgrading the navigation channel to prepare a Master Plan for the Modernization and Expansion of the Canal. Part of these studies includes the analysis of risks to increase the salinity of Lake Gatun. This may occur as a consequence of increased traffic, and anticipated structural modifications, which include lateral water saving basins and an additional set of locks to accommodate larger Post-Panamax vessels. Lake Gatun is adjacent to the locks on the Atlantic side of the Canal and is separated from the Pacific side by Gaillard Cut (Corte de Culebra), Lake Miraflores, and the Pedro Miguel and Miraflores locks.

Within this context, ACP retained URS Holdings, Inc. (URS) for the execution of the contract for the Tropical Lake Ecology Assessment with Emphasis on Changes in Salinity of Lakes. More specifically, under this agreement, URS shall recommend the maximum salinity levels, which may be tolerated in the lakes mentioned above. The salinity standards must consider the current procedures for treatment of potable water in Panama and must also maintain the biological integrity of freshwater ecosystems.

The terms of reference specify several intermediate products in the form of technical memoranda. In this context, this is the seventh technical memorandum, which deals with the potential impacts on the biota and ecology under proposed scenarios for salinity level increases in the Lake Gatun ecosystem.

1.1 Objective

Based on the previous paragraphs, the objective of this seventh technical memorandum is to present the potential changes that may occur, in the biological community, as salinity levels increase in Lake Gatun. A second objective of this document is to identify the limitations of the information database available and to outline a program to fill those information gaps.

1.2 Background

Interest in potential changes in the salinity content of Lake Gatun and their biological implications has been associated with the need for canal expansion for several decades. These concerns may have reached a peak when the idea to pump seawater to meet navigation demands was considered during the early 1970's by the Panama Canal Commission. Scenarios for salinity

levels as high as 15 ‰ were considered for Lake Gatun at that time. Environmental concerns related to the increase in salinity levels at that time were related primarily to two main issues: the changes in the biological community in Lake Gatun, where the primary freshwater species will likely disappear, and the passage of biological species from one ocean to the other.

When one looks at the issue of migration from one ocean to the other, the main concern is the disruption of the trophic relationships and the risk of impacting the population of economically important species. In addition, evolution of marine species which have been separated during 4-5 million years will be altered. In this regards, a truly freshwater body such as Lake Gatun represents a salinity barrier for the majority of marine species, which would die during the prolonged period required to cross the lake. Consequently, the increase of salinity levels, to the values indicated before (15 ‰), would eliminate the barrier effect for a significant number of species.

Those concerns brought about a significant effort, in the 1970's, to collect and interpret existing information as well as to conduct a field reconnaissance in order to determine what potential changes could be anticipated. The reconnaissance was conducted by a multi disciplinary that collected some new data and provided insights about the possible effects of increasing the reservoir's salinity. Practically all the documents that were produced by that effort indicated that data was not adequate for a forecast of changes in the biological community of Lake Gatun and/or the biological communities on either ocean. Those documents also provided guidance on research that should be conducted in order to increase the confidence of the potential prognosis. Unfortunately the research efforts have not been implemented and most of the information gaps identified three decades ago are still present. Must of the relevant documents have been described in a previous report (Technical Memorandum No. 2). Reference will be made to those information sources, but they will not be described herein again, only the most important elements of that information will be highlighted.

Currently, the anticipated changes are not as significant even in the event that a significant expansion of the Canal is implemented. This is primarily due to ACP's desires to keep Lake Gatun as a truly freshwater ecosystem, without affecting the lake's water as a potable source and minimizing impacts to biological community. Consistent with that desire, expressed in the terms of reference for this job, the absolute maximum salinity level recommended as a standard in this effort (see Technical Memo No. 3) is 0.5 ‰. In addition, it's worth nothing that we are also recommending an action level or "red alert", which is only 50% of that value. Therefore the anticipated increase of salinity levels in the reservoir's water is going to be small and the

reservoir will continue as a truly freshwater ecosystem that provides an effective salinity barrier to inter oceanic migration.

Consequently, this document deals more with the second issue of concern, which relates to the biological effects of salinity over the biological community of Lake Gatun. In this regards it is important to point out that the information generated in the 1970's is not as relevant since the anticipated changes are much subtle than then considered. The previous analyses considered the potential changes between a truly freshwater ecosystem and a completely brackish water one.

In order to have a better understanding of the biological community of Lake Gatun and the potential changes, which could be brought about by an increase in salinity, the ACP recently initiated an effort with the University of Panama to document and to monitor the presence and relative importance of biological species in the freshwater ecosystem. Unfortunately, this effort is at its initial stage and the information is still very limited.

1.3 Structure

This Technical Memorandum has been organized in a manner that is consistent with the objectives of the document and that will allow a clear and concise presentation of the relevant information, and its significance. The structure of the document is briefly discussed in the next paragraphs.

Introduction. This introductory section contains a general description of the work to be carried out by URS as well as the objective, and structure for the Technical Memorandum. In addition, background narrative that explains the activities performed prior to this effort and the nature and general limitations of the available information.

Conceptual Model of Lake Gatun. The section on conceptual model of Lake Gatun uses the energy circuit language symbols to represent the main structural elements and processes existing and occurring in Lake Gatun. The resulting diagram and the associated text play the role of a baseline condition and is useful to organize information and identify the main information gaps.

Potential Changes in the Biological Community. This section uses the information available to identify the potential effects of increasing the salinity levels in the waters of Lake Gatun. Changes are discussed per functional categories with reference to specific taxonomic groups whenever this is appropriate and information is available at that level of detail.

Simulation Model of Lake Gatun. This section describes how the limited information available may be used to represent in the computer the behavior of the Lake Gatun ecosystem. The sections explains the simulation process, how data are used and combined into equations to represent changes in the living and non-living components of the system, and also how flows of energy and materials connect them. Simulations represent the reservoir ecosystem under current conditions and explore the potential changes, which may occur over time if salinity levels increase in the water of the reservoir.

Needed Research. This sections provides suggestions to support additional research to determine the relative importance of energy and material inputs to Lake Gatun ecosystem as well as the standing crop and seasonal variation of the more important storages and the flows between them. The purpose is to measure the reservoir metabolism to better understand what changes an increase in salinity may bring about.

Conclusions. Finally, this section presents basic conclusions and recommendations applicable to Task 7 of the project (Potential Impacts on the Biological Community of Lake Gatun).

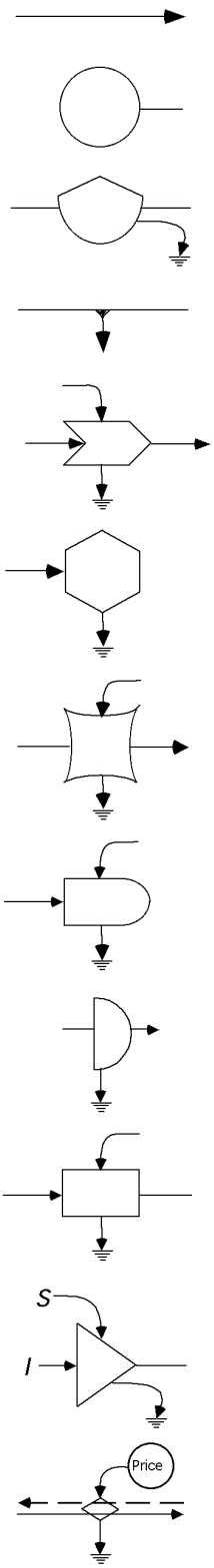
2.0 CONCEPTUAL MODEL OF LAKE GATUN

Lake Gatun is a tropical meromictic reservoir with a surface area of about 410 Km^2, and a mean depth of 12.9 meters. The average water detention time is slightly over 1 year and the reservoir is considered to be a meso-euthrophic freshwater body, with an estimated phosphorous loading of 0.14 g/m^2.yr. The water level in Lake Gatun fluctuates as a consequence of water inputs from the contributing watershed, direct rainfall, and discharges from Lake Alhajuela and water outputs for ship transits, potable water supply, hydropower generation water level control releases and evapotranspiration from the lake ecosystem to the atmosphere. The maximum water level (26.67 masl) is determined by the spillway associated with Gatun Dam and the minimum water level (23.89 masl) is ultimately determined by navigation draft requirements and the elevation of the existing locks.

In order to understand the ecosystem of Lake Gatun and the potential changes that may occur as a consequence of the anticipated changes in salinity, an ecosystem diagram and model may be useful. The conceptual model may be used to summarize what we know about the reservoir and to identify the main information gaps. The ecosystem diagram was prepared using the energy circuit language symbols (Figure 1), which have been used extensively for ecosystem diagramming and modeling. The conceptual diagram of Gatun Lake (Figure 2) shows a somewhat aggregated food-web influenced by the flows of water and salt introduced as a result of the operation of the locks system.

This diagram indicates the main relationships of the ecosystem with the rest of the world, as well as the relationships between its main components. The diagram frame establishes the limit between the reservoir ecosystem and the outside world. On the outside there are several forces, flows and switches, which directly affect what goes on in the ecosystem. Between the forcing functions we can mention solar radiation, atmospheric gases, wind, rain, runoff, the oceans, birds, and fishing. In addition the diagram depicts the decisions made by ACP, which control fluxes of water to pass ships, produce potable water, generate electricity, and maintain the water level in the lake under safe conditions.

Inside the reservoir we can see a complex matrix of physical and biological elements represented by the several energy circuit language symbols. Two big tanks represent the water and the sediments in Lake Gatun, the big bullet shaped symbol represents the primary producers, the organisms that are able to take the energy of sunlight and convert and store it in the form of chemical energy in biomass.



Energy circuit: A pathway whose flow is proportional to the quantity in the storage or source upstream.

Source: Outside source of energy delivering forces according to a program controlled from outside; a forcing function.

Tank: A compartment of energy storage within the system storing a quantity as the balance of inflows and outflows; a state variable.

Heat sink: Dispersion of potential energy into heat that accompanies all real transformation processes and storages; loss of potential energy from further use by the system.

Interaction: Interactive intersection of two pathways coupled to produce an outflow in proportion to a function of both; control action of one flow on another; limiting factor action; work gate.

Consumer: Unit that transforms energy quality, stores it, and feeds it back autocatalytically to improve inflow.

Switching action: A symbol that indicates one or more switching actions.

Producer: Unit that collects and transforms low-quality energy under control interactions of high-quality flows.

Self-limiting energy receiver: A unit that has a self-limiting output when input drives are high because there is a limiting constant quality of material reacting on a circular pathway within.

Box: Miscellaneous symbol to use for whatever unit or function is labeled.

Constant-gain amplifier: A unit that delivers an output in proportion to the input *I* but is changed by a constant factor as long as the energy source *S* is sufficient.

Transaction: A unit that indicates a sale of goods or services (solid line) in exchange for payment of money (dashed line). Price is shown as an external source.

Figure 1: Symbols of the Energy Circuit Language and their meaning

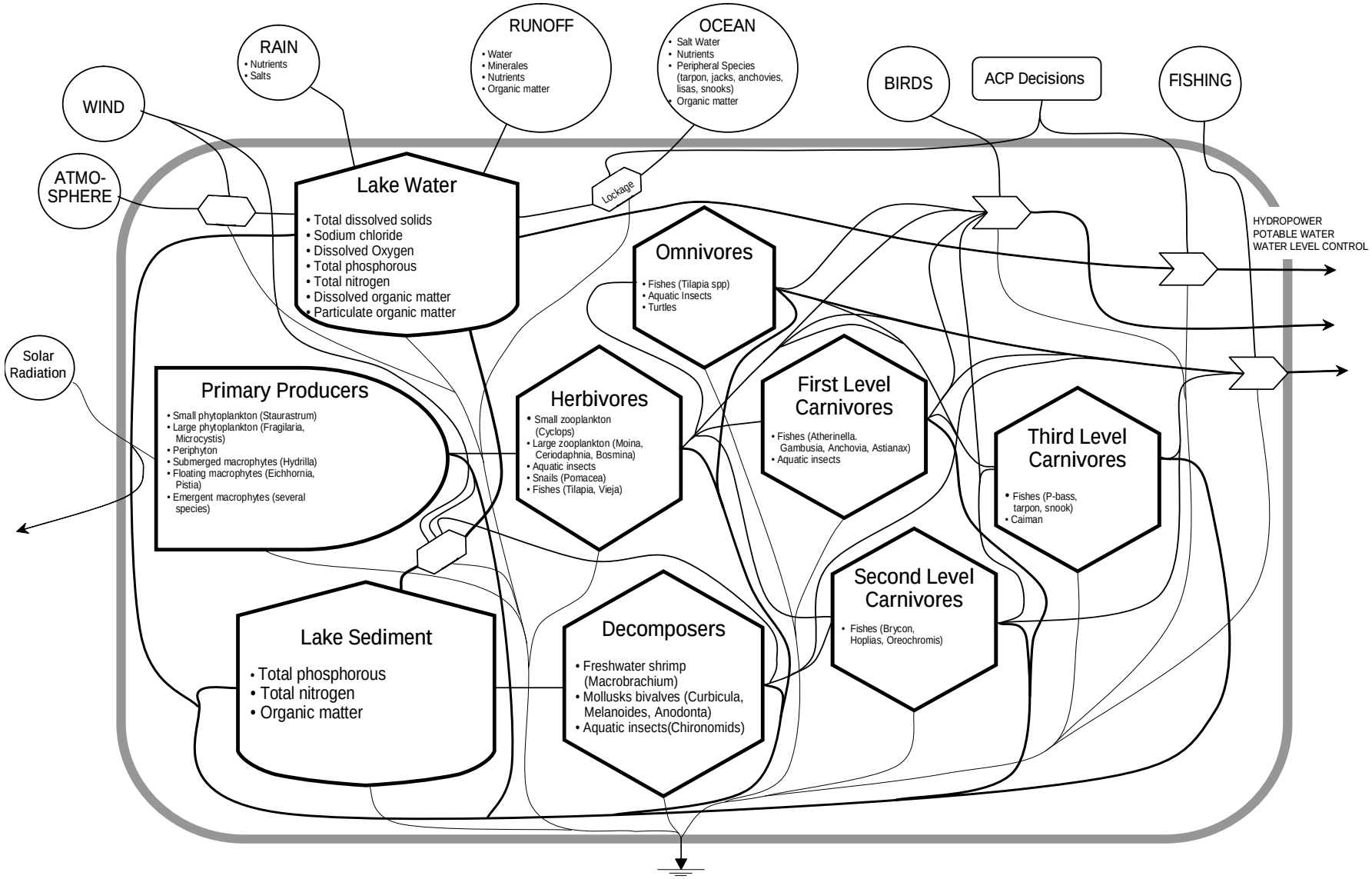


Figure 2: Conceptual Model Diagram of Lake Gatun.

The hexagon shaped symbols represent several levels of consumers, which depend for their survival from the energy incorporated into the food web by producers upstream. Depending on their feeding habits these may be herbivores - those that feed directly on primary producers, decomposers – those feeding on organic matter (detritus) flowing or accumulated in the ecosystems, carnivores – those eating other consumers, and omnivores – which typically have a more diverse diet.

2.1 Physical Components and Processes

Several flows are important for the ecology of the Lake Gatun reservoir including those of water, gases, dissolved and suspended minerals and organic matter, and sun light among others. Giving its nature of aquatic ecosystem, water storage and flows play a central role and serve as the transportation mechanism for other flows of energy and materials to occur.

The average storage of water in the reservoir is about 4.5 billion cubic meters. The main source of this water is the runoff from the associated basin (The Panama Canal Watershed), including the portion of this watershed that is further regulated by Lake Alhajuela. A smaller source of water is pluvial water falling directly over the lake surface. The main output of water from the reservoir is the operation of the locks for passing vessels from one ocean to the other. Other outputs include potable water, hydropower, discharges for reservoir level control, direct evaporation from reservoir surface, and transpiration by floating and rooted aquatic plants.

A very significant difference between flows of water going in and out of the reservoir is the degree of control that humans, in this case ACP management decisions have over them. Most outflows are controlled by decisions taken by ACP management, as indicated in the diagram (Figure 2). However, the possibilities of controlling the flows going in the reservoir are quite limited, at this time.

Reservoir water contains a great variety of dissolved and suspended matter, both living and non-living. A list of the most important ones, from the perspective of reservoir metabolism and the potential changes caused by increased salinity levels, is included in the diagram. Similarly, flowing waters carry dissolved and suspended materials and living organisms. As indicated in the diagram water inputs from runoff and rain bring into the lake nutrients and other minerals, as well as dissolved and suspended organic matter. This matter is also carried when water flows out of the system. Lake waters also interact with the atmosphere and there are flows of atmospheric gases, primarily oxygen and carbon dioxide, going in both directions (indicated with

bi-directional arrow in the model). Kinetic energy of the wind creates waves and influences the magnitude of the exchange.

Another two-way flow is shown between the reservoir water and the oceans, which occurs with every ship that goes through the locks. Although the net flow of water is toward the ocean, certain amount of ocean water gets its way into the lake, carrying salts and marine species with it. Finally, a third two-way flow is shown between reservoir water and sediment. Particles in the water column are constantly settling to the bottom, however, sediments are re-suspended by water movements such as wave action, as well as by the mechanical action or organisms stirring them. In addition nutrients stored in the sediments are taken up by rooted aquatic plants, such as hydrilla, and eventually released in the water column when the plants die off or are eaten by herbivores.

Solar radiation is important for the entire ecosystem as it drive the photosynthetic machinery. As shown in the diagram, a portion of the solar energy is reflected away from the system. Light is absorbed by plants growing on the reservoir or enters the water column where it is absorbed by water, particles (living and non-living), and dissolved substances.

2.2 Biological Components and Processes

The main biological processes occurring in the reservoir are primary production and respiration. **Primary producers** take a portion of the energy in solar radiation, transform it into chemical energy, and store it in the form of biomass through the process of photosynthesis. Primary producers present in the reservoir include phytoplankton species (large and small), periphyton species, submerged macrophytes (hydrilla), as well as floating and emergent aquatic plants. The biomass produced by these organisms is grazed directly by herbivores or the dead plant material flows as detritus.

Among the **herbivores** the diagram shows several species of zooplankton (large and small), the apple snail that feeds primarily on hydrilla, some fish species ("vieja" and one of the species of tilapia), which feed primarily on the periphyton attached to hydrilla. In addition, several aquatic insect species feed primarily on hydrilla and other floating and rooted aquatic plants.

Among the **carnivores**, the diagram includes three levels. The first level carnivores include primarily small fish species in genus such *Atherinella*, *Gambusia*, *Astianax*, and *Anchovia*. The latest is a marine species that enters the reservoir and has been reported as one of the dominant food item for the top carnivore in the system, Peacock bass (*Cichla ocelaris*), representing over

25% of its diet[105]. In addition to these fish species, a variety of aquatic insects may also be in the first level of carnivores. In the second level we find predominantly fish species particularly those from the genus *Brycon, Hoplias*, and *Oreochromis*. Finally, in the third level of carnivores we find the top predators of the system including species such as the peacock bass mentioned before and some marine fish species that tolerate freshwater such as tarpon, snook, and jack. In addition the caiman population in the reservoir may be included in this category.

Among the **omnivores**, those consumers with a more diverse food intake, we can mention the fresh water turtles, a few fish species (tilapia) and some of the aquatic insects. Finally, a group of consumers known as **decomposers** take advantage of the energy stored in dead organic matter that tends to accumulate in the bottom of the reservoir. It may be important to note that in addition to the organic matter from photosynthesis in situ the reservoir receives a significant amount of organic matter from its associated watershed. In most fresh water ecosystems this input is very significant and consequently, the detritus food chain tends to be a very important portion of the overall reservoir metabolism. Some of the species in this category come from the freshwater shrimps (*Machrobrachium* sp), several species of mollusks (*Curbicula, Melanoides, Anodonta*) and aquatic insects (Chironomids).

The last processes included in the diagram depict the constant removal of species from the ecosystem. This takes place primarily as a result of fishing by human and birds. Fishing by humans is predominantly focused on the top carnivore, the peacock bass. However, other species also included are tilapia, the freshwater shrimps, and some of the mollusks. Birds such as egrets, kingfishers, and terns feed on a diverse array of fish and other organisms. Particularly notorious is the feeding of the snail kite on the population of apple snail, which in turns feeds primarily on the aquatic plant hydrilla (*Hydrilla verticillata*).

3.0 POTENTIAL CHANGES IN THE BIOLOGICAL COMMUNITY

As mentioned before the increase anticipated in the salinity levels of Lake Gatun under current plans for the expansion and modernization of the canal is significantly smaller than those under consideration during the 1970's when the majority of the specific information on the issue was generated and analyzed. The intention of ACP is to maintain the reservoir as a freshwater ecosystem without significantly affecting the biological community and continue using its water, in addition to passing ships, for potable water supply. Consequently, the changes in salinity levels that are expected to occur over time are in the order of one or two tents of a part per thousand (0.1 – 0.2 ‰). It is important to point out that this is the worst case scenario since the action level or red alert for the system has been set to 0.25 ‰. Therefore, if the red alert is reached near the locks, the average salinity in the lake will be significantly smaller than that.

Although these changes may not dramatically alter the nature of the food web in the reservoir certain changes among species and/or dominant groups may occur. Given that salinity changes modify the osmotic balance between internal and external fluids on both sides of the cellular membrane, it is in general expected that smaller organisms will be more easily affected than larger ones given the larger surface are per unit volume.

Unfortunately, little research has been done about the ecology of the reservoir and most data available to precisely anticipate potential impacts is fragmentary, at best. However a brief discussion about what may occur in each functional group is presented below. In this discussion several sources of information are taken into account, however, the recent sampling conducted by a team from the University of Panama is used extensively since it provide the only semi-quantitative information available.

3.1 Phytoplankton

As pointed out in Technical Memorandum No. 2, several groups of algae could be affected by an increase in salinity. According to Weers[28], any increase in salinity would cause the destruction of small unicellular algae, and consequently the Dinoflagellates and Euglenoides of Lake Gatun, such as *Peridinium umbonatum* F. Stein, *Dinococcus bicornis* (Woloszynska) Fott and *Ceratium hirundinella* (O.F.Müller) Bergh, could disappear. This statement is consistent with the fact that none of the groups are represented in the more brackish waters of Lake Miraflores.

However, a comparison of the data collected from Lakes Gatun and Miraflores by the University of Panama team does not indicate significant differences between the dominant groups of

phytoplanktonic algae in both lakes. In both cases the dominant groups include blue-green algae (primarily *Microcistis aureginosa*), diatoms (primarily *Aulacoseira granulate* and *Fragilaria crotonensis*), and green algae (particularly several species of *Staurastrum* sp).

It is important to point out that the sampling conducted by the research team used 80 microns mesh. Although this is a standard procedure for limnological research it is also known that the smaller algal groups such as those mentioned above will be under represented by this collection and counting process. On the other hand, it is known that the importance of the smaller components of the phytoplankton is greater than what their biomass suggest due to the shorter turnover time of their populations.

In summary it is possible that a decrease in the smaller groups of phytoplankters may occur but their overall importance in the reservoir metabolism are unknown. One could speculate that smaller algae, with fast turnover are not as important as food item, but they are releasing significant amount of oxygen that is used to oxidize allochthonous and autochthonous organic matter in different compartments of the ecosystem. Additionally one could think that a portion of the critical nutrients (primarily phosphorous) might be held tightly in the biomass of the small organisms.

Consequently, the decrease in small algae in the phytoplankton could cause a reduction of the dissolved oxygen content in water column, particularly in those pools that are more protected from the effect of the wind and waves. A second effect could be a slight increase in nutrients (phosphorous) available to larger algae and therefore an increase in their biomass. This will tend to reduce light penetration and concentrate photosynthetic activity in a thinner layer of water. Both trends mentioned in this paragraph will move the appearance of the reservoir water to a more eutrophic like conditions, including a potential deterioration of water quality indicators.

In order to provide more elements for this analysis as well as for modeling purposes in the future it will be important to increase the algae collection efforts and to measure the metabolism of different portions of reservoir. Primary production of the planktonic community and the entire reservoir can be evaluated by measuring oxygen evolution in light and dark bottles and the entire water body (diurnal curve). Bioassays may also be conducted, at different salinities, to correlate the amount of chlorophyll with the intensity of primary production as an indicator of photosynthetic efficiency, which is expected to be greater in the smaller algae.

3.2 Other Producers

Forecasting the changes in other producers' biomass is even less feasible than phytoplankton. Most of the macroscopic aquatic plants show an ample distribution within a significant range of salinity levels. Hydrilla, which is probably the single most producers in the reservoir, tolerates salinities[1] as high as 9-10 ‰. According to Pasco[32], the species *Pistia stratiotes* L. and *Eichhornia crassipes* (Mart.)Solms, present a salinity tolerance ranging between 1 and 10 ppt. Other species present at Lake Gatun, such as *Lemna minor* L., *Azolla caroliniana* Willd., and *Salvinia auriculata Aubl*., among others, are also know to have similar ranges of tolerance to changes in salinity. Two marginal macrophytes that are known for their tolerance to salinity (*Fuirena umbellata* Rottb. and *Oriza latifolia* Desv.) were reported for Lake Gatun.

3.3 Zooplankton

The most complete review of the zooplankton is that described by Hurlbert[44]. In this work he suggests that the decrease of *Diaptomus leoninicollinus* may have been cause by small changes in salinity (0.01 to 0.1 ‰). Based on this work one would expect that the relative abundance of cladoceran and rotifers to decrease and cyclopoids and calanoids copepods to increase. The only semi quantitative data from the University of Panama sampling efforts in years 2003 and 2004 does not include comparative data from Lake Miraflores. The abundance of rotifers, as documented by the 2003 sampling campaign associated with the environmental studies conducted in support of deepening of the navigation channel, already suggest a very low density of rotifers in the zooplankton community of Lake Gatun.

3.4 Benthic Organisms

Three groups were mentioned as important in the benthos of Lake Gatun, crustaceans (primarily freshwater shrimp), mollusks, and aquatic insects and none of the species listed are reported as having a high sensitivity to small changes in salinity levels of the overlaying waters. The review of decapods (shrimp, lobsters, and crabs) prepared by Lawrence Abele[49] suggest that marine species could colonize the reservoir if salinity goes to 10 ‰ or more. However, there is no indication that changes will occur at the smaller increases currently under consideration.

Regarding the mollusks, the review by Michael Greenberg[48] points out the remarkably low number of freshwater species and that significant salinity increases (10 ‰ or more) may lead to massive mollusks growth and formation of reefs in certain areas of the reservoir. However no

[1] The Western Aquatic Plant Management Society. http://www.wapms.org/plants/hydrilla.html

indication of these changes exists for the much smaller salinity levels currently anticipated for Lake Gatun. Although the apple snail (*Pomacea flagellata*) is not a truly benthic organism it is worth mentioning it here since it is associated with the hydrilla mats, has been reported from a wide variety of salinity ranges and no changes are expected in its populations as a consequence of the slight increases salinity herein indicated.

Finally, the same is true for aquatic insects. The reviews prepared by Boreham[46] and Hogue[24] suggest that insects of medical importance insects may increase in higher salinities but their review are based on much higher changes than are now under consideration.

3.4 Icthyofauna

The more dynamic portion of the Lake Gatun biological community has probably been that of fish species. Particularly dramatic changes were observed after the colonization of the reservoir by the Amazon cichlid, *Cichla ocellaris* (peacock bass), as has been documented by Zaret and Paine[85]. Since the arrival of the peacock bass other species that have colonized the lake waters including at least two species of tilapia. Furthermore there are reports[2] that "guapotes" (probably *Cichlasoma*[3] *dovii* and *C. managüensis*) are already in the reservoir.

Although the evolution of fish populations under the slightly modified salinity levels is unpredictable at this time, it is obvious that those fish species that are primary freshwater species are the ones that are at higher risk of being affected. They have a very narrow tolerance to changes in salinity and will have a more limited ability to adapt. Among these primary species there are several species of the Characidae, Hypopomidae, Cichlidae, Heptateridae, and Loricaridae families. The individual of these primary freshwater species were included in Table 2.10 of Technical Memorandum No. 2. Given the importance of these species in the food web of the reservoir, their disappearance would likely have a profound impact in the trophic structure of the entire ecosystem and shall be avoided, if possible.

However, we believe that with the anticipated modest changes in salinity levels future changes in the icthyofauna of Lake Gatun will probably depend more on other factors than salinity. The genus *Cichlasoma* and *Cichla* are both typical of freshwater ecosystems but have been reported to withstand high salinity levels. Shafland[106] reported an upper salinity tolerance of 18°/oo, experimentally determined, for peacock bass. Martin and Bermingham[107] suggest that the salinity

[2] Rigoberto Gonzalez, personal communication.

[3] Some authors refer to these species as members of the genus *Parachromis*.

tolerance of Cichlasoma is partially responsible for its wide distribution from Texas to Central America.

One of the unanswered questions about the Panama Canal Ichthyology is the absence of the bull shark (*Carcharinus*) from both lakes, Gatun and Miraflores. Although, the shark goes freely into freshwater ecosystem in many parts of the Americas and it has been reported in the locks, there are no reports of this species in the reservoirs. Possibilities that the bull shark will establish a presence within Lake Gatun with the slight increases in salinities under consideration are completely unknown. However, the fact this species has not been reported in Lake Miraflores may suggest that it probably will not. At higher salinity levels Zaret[26] considers that peacock bass could disappear, and a much greater importance, at the top carnivores' level, could be played by tarpons, snooks, and sharks.

4.0 SIMULATION MODEL OF LAKE GATUN

The energy circuit language is used to diagram systems to gain understanding of flows, components and processes of interaction as the first step in developing simulation models. Each symbol is rigorously defined mathematically, and therefore, the drawing of a diagram in essence yields a set of simultaneous equations that can be programmed to simulate behavior.

4.1 Model Overview

Systems diagrams include a system frame that separates the system under study from the rest of the world and through which driving energies pas and materials and energy are exported. Diagrams are organized to show the flows of materials, energy and information from left to right an explicitly incorporate the energy laws and hierarchical principles of system organization. Lowest quality components are shown on the left and the flows of energy matter and information are 'upgraded" into higher and higher quality components as they flow up the hierarchy to the highest quality components on the right side of the diagram. At each step in the hierarchy, energy is transformed form one type to another (ie from phytoplankton, to zooplankton, to planktonic fish to carnivorous fish, etc) and the total amount of energy decreases due to thermodynamic losses. The necessary thermodynamic losses of energy at each step are shown exiting the bottom of the diagram the heat sink symbol.

The process of modeling a system begins with the construction of a complex system diagram of the components (also known as state variables), flows of energy, material and information between them and processes of interaction. The complexity is then aggregated to a fewer number of compartments and interconnecting flows in such a manner as to retain functional relationships of components of interest, but simplifying organization. The aggregated diagram is then used as the basis for computer programming and numerical values are assigned to pathways and state variables

Figure 3 shows a systems diagram of the simulation model of Lake Gatun that emphasizes the effects of increased salt concentrations on ecosystems components. The model aggregates the Lake Gatun food web into trophic levels and shows more detail at the lower end of the food web than at the higher end.

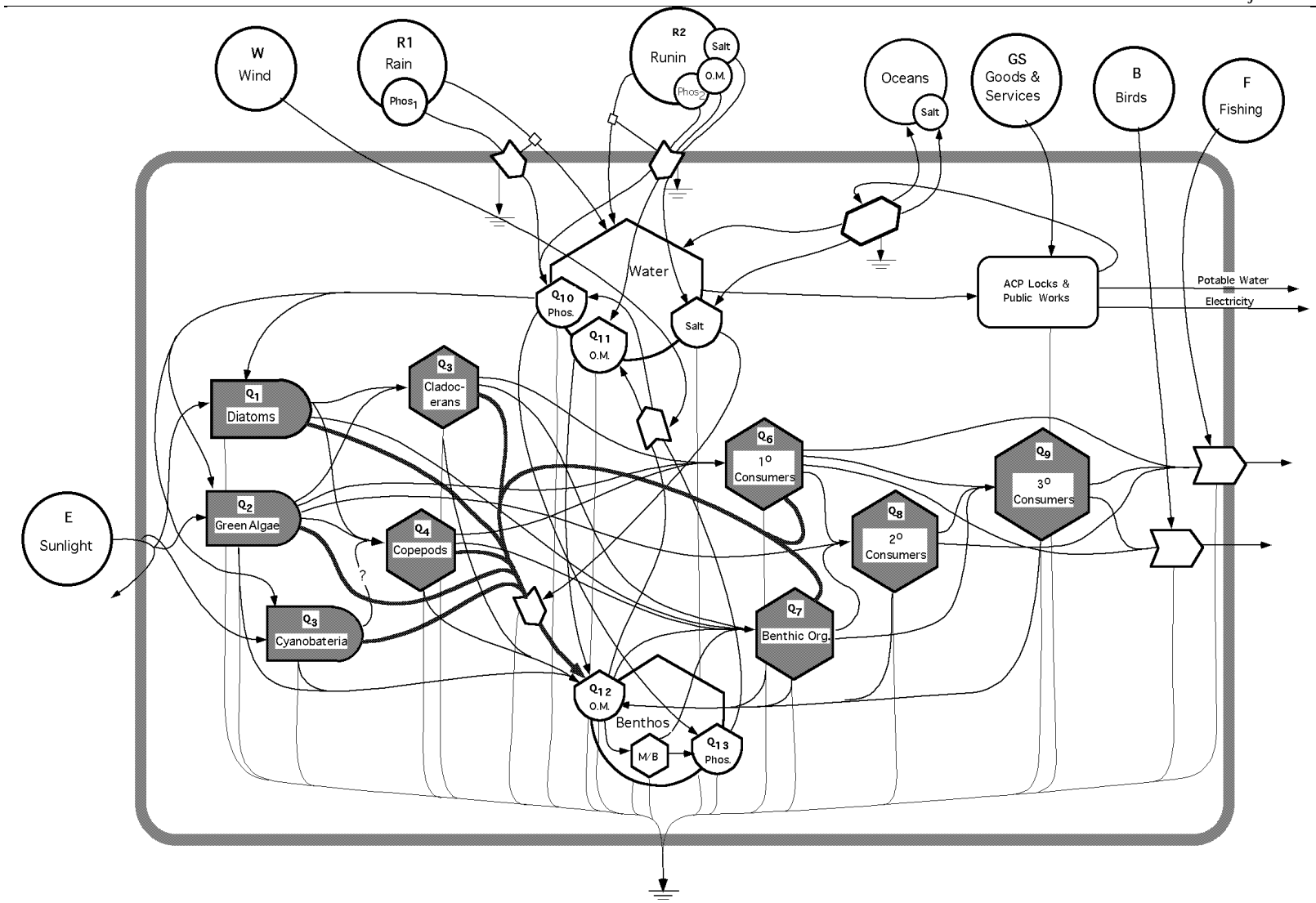


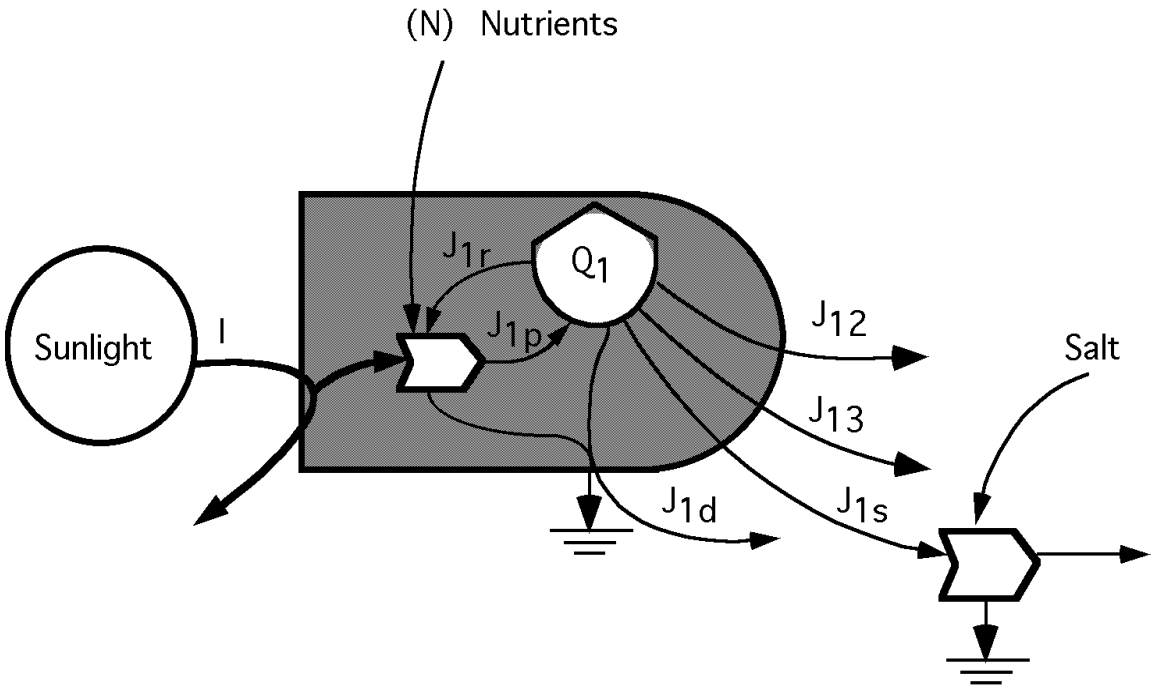
Figure 3. Systems diagram of the Lake Gatun salinity effects simulation model. Since the lower end of the food web will experience greater effects from expected salinity changes, more detail in the number of compartments is shown for the primary trophic levels, while the higher end of the food web has more aggregation, since few if any effects will be experienced by these higher order trophic levels.

Since the expected changes in salinity will affect the phytoplankton and zooplankton communities to a greater degree than the higher trophic levels we have concentrated our efforts on these lower level compartments. The model does not include macrophytes and is primarily a pelagic model. The model is run for one year time intervals using different salt concentrations and average climatic conditions taken from the decade beginning in 1990. Model simulation output is displayed as of affected state variables over a one year time interval.

The model includes three primary production compartments representing diatoms, green algae, and blue-green algae (cyanobateria). Each of these compartments has differing sensitivities to increases in salinity. The next level in the food web is represented by two zooplankton compartments representing cladocerans and copepods. The zooplankters are followed by primary consumers and benthic organisms; each of these compartments exhibit decreasing sensitivities to increases in salinity. In this model, higher trophic level consumers are not sensitive to anticipated increases in salinity in Lake Gatun. Birds and humans harvest higher trophic levels.

4.2 Component diagrams and equations

Shown in Figures 4 and 5 are system diagrams of primary production and consumer level state variables respectively. The system configuration and equations in Figure 4 apply to all phytoplankton compartments while those in Figure 5 apply to all consumer compartments. Pathways into and out of each state variable are numbered to reflect component interactions. The first number in the subscript is the component number while the second number or letter designates the pathway of interaction. Primary production pathways are labeled with a “p” and respiration pathways are labeled with an “r”. Similarly, increased respiration due to salinity increases are represented with an “s”. Pathways between two components carry the numbers of both components. The first number is the component where the pathway originates and the second number is the component where it ends. The figures also include the generalized differential equations for each of the components.

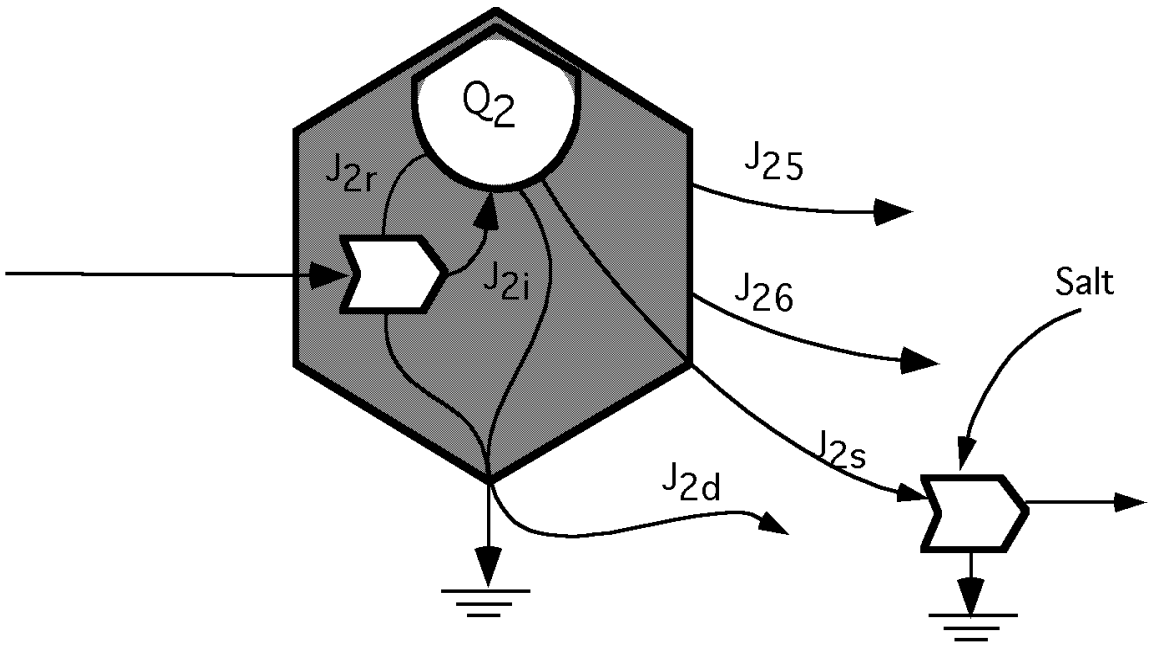


$$dQ1/dt = J_{1p} - J_{1r} - J_{1d} - J_{12} - J_{13}$$

where:

$$J_{1p} = k_{1p} * I * N * Q_1$$
$$J_{1r} = k_{1r} * I * N * Q_1$$
$$J_{1d} = k_{1d} * Q_1$$
$$J_{12} = k_{12} * Q_1 * Q_2$$
$$J_{13} = k_{13} * Q_1 * Q_3$$
$$J_{1s} = k_{1s} * Q_1 * S$$

Figure 4. Detailed diagram and equations for plankton state variables.



$$dQ2/dt = J_{2i} - J_{2r} - J_{2d} - J_{25} - J_{26} - J_{2s}$$

where:

$$J_{2i} = k_{2p} * I * N * Q_2$$
$$J_{2r} = k_{2r} * I * N * Q_2$$
$$J_{2d} = k_{2d} * Q_2$$
$$J_{25} = k_{25} * Q_2 * Q_5$$
$$J_{26} = k_{26} * Q_2 * Q_6$$
$$J_{2s} = k_{2s} * Q_2 * S$$

Figure 5. detailed diagram for the consumer state variables

4.3 Evaluated pathways

The table in Annex 1 lists each of the forcing functions (driving energies), state variables, and pathways of the Lake Gatun model. State variables are designated as Qs with a subscript (ie Q1, Q2, Q3, etc), while flows are identified with 'Js" and a subscript (ie J1, Jp, J13, etc). Values in the table represent data collected from the literature or estimates of values based on literature averages.

4.3.1 Primary Production of Phytoplankton

<u>Phytoplankton growth rate</u>

Phytoplankton growth rate is influenced primarily by light and nutrient concentration (equation 1). To simplify growth equation we do not include temperature effects. Input parameters for the growth equations are given in Table 1. The phytoplankton growth equation is as follows:

$$\mathbf{m = m_{max} * * q_L * q_N} \qquad (1)$$

Where:

m_{max} = maximum growth rate
q_L : effects of light on growth
q_N : effects of nutrients on growth

I. q_L ~ Effects of light intensity on phytoplankton growth

We use the Steele formulation[108], which is one of the most commonly used photoinhibition relationships:

$$\mathbf{q_L = I/I_S * exp(1-I/I_S)} \qquad (2)$$

Where:

q_L= relative photosynthesis
I: light intensity
I_S: optimum (saturating) light intensity

II. q_N ~ Effects of nutrients on phytoplankton growth

We assume that phytoplankton growth is phosphorus-limited.

$$\mathbf{q_N = P/(P+k_{sa})} \qquad (3)$$

Where:

P= ortho-P concentration
k_{sa} = Michaelis-Menten half-saturation constant[109]

Phytoplankton grazing rate

Grazing rate is dependent on the abundance of zooplankton and phytoplankton and feeding rate of zooplankton as follows:

$$\mathbf{G = F_{clad}*Z_{clad}*X + F_{cop}*Z_{cop}*X}$$

Where:

G = zooplankton grazing rate
F_{clad} = cladocerans filtering rate (ml/ind-day)
Z_{clad} = cladocerans concentration (# of individuals per L)
F_{cop} = copepods filtering rate (ml/ind-day)
Z_{cop} = copepods concentration (# of individuals per L)
X = phytoplankton concentration (mgC/L)

4.3.2 Phytoplankton settling rate (death)

Settling rate describes the portion of the phytoplankton biomass that sinks out of the water column. We assume settling rate is constant throughout the year.

4.3.3 Plankton competition

Three different phytoplankton compartments are shown in the model: diatoms, green algae, and the cyanobacteria. While each has differing sensitivities to salinity increases, an important interaction between species results from the ability of the blue-greens to capitalize on nutrient enrichment and dominate the water column competing with the diatoms and green algae for available light. This is shown on the system diagram with the pathway for blue-greens capturing light from available light prior to the diatoms and green algae. Under conditions of nutrient enrichment not only are blue-greens favored because of their faster growth rates and nutrient assimilation, but they also compete better for available light.

4.3.4 Spreadsheet Simulation Model

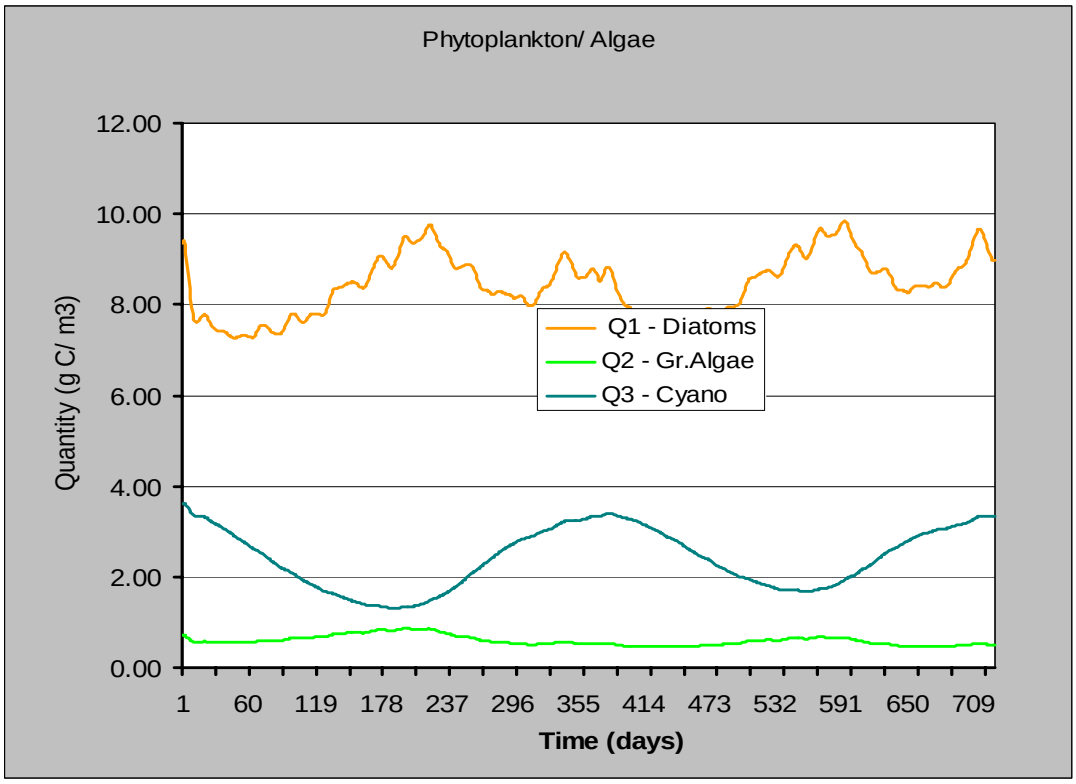
The Lake Gatun model is simulated using an EXCEL spreadsheet. There are three separate sheets in the EXCEL model: 1) the model, 2) a spreadsheet that calculates sunlight, rain and runin, and 3) a spreadsheet that is used to calculate the pathway coefficients. The model run is for 2 years, the same input data is used for each year (ie. the driving energies are repeated in the second year). This done to make sure there are transient behaviors that are not seen in a single year simulation.

Table 1. Input parameters for the phytoplankton growth model.

Parameter	Symbol used	Value/Equation
Maximum phytoplankton growth rate	m_{max}	1.7/day; 1.85/day
Solar radiation	SR	Variable
Saturating light intensity	IS	300 Ly
P concentration	P	Variable
Michaelis-Menten half-saturation constant for phytoplankton growth	k_{sa}	20 ugP/L ; 30 ugP/L
Cladocerans filtration rate	F_{clad}	3.8 ml/(animal*day)
Copepods filtration rate	F_{cop}	1.4 ml/(animal*day)
Cladocerans concentration	Z_{clad}	Variable
Copepods concentration	Z_{cop}	Variable
Phytoplankton concentration	X	Variable
Phytoplankton settling rate	S	0.18/day ; 0.11/day

4.3.5 Simulations Results

The graphs in Figures 6 through 8 are simulation results for the base condition over two years. Graphed separately are: 1) diatoms, green algae and cyanobacteria, 2) benthic organism and primary consumers, 3) secondary and tertiary consumers, and 4) organic matter and phosphorus in the water column and benthos. There are annual fluctuations in populations of organisms in the lower trophic levels driven primarily by fluctuations in rainfall and secondarily by changes in sunlight energy.



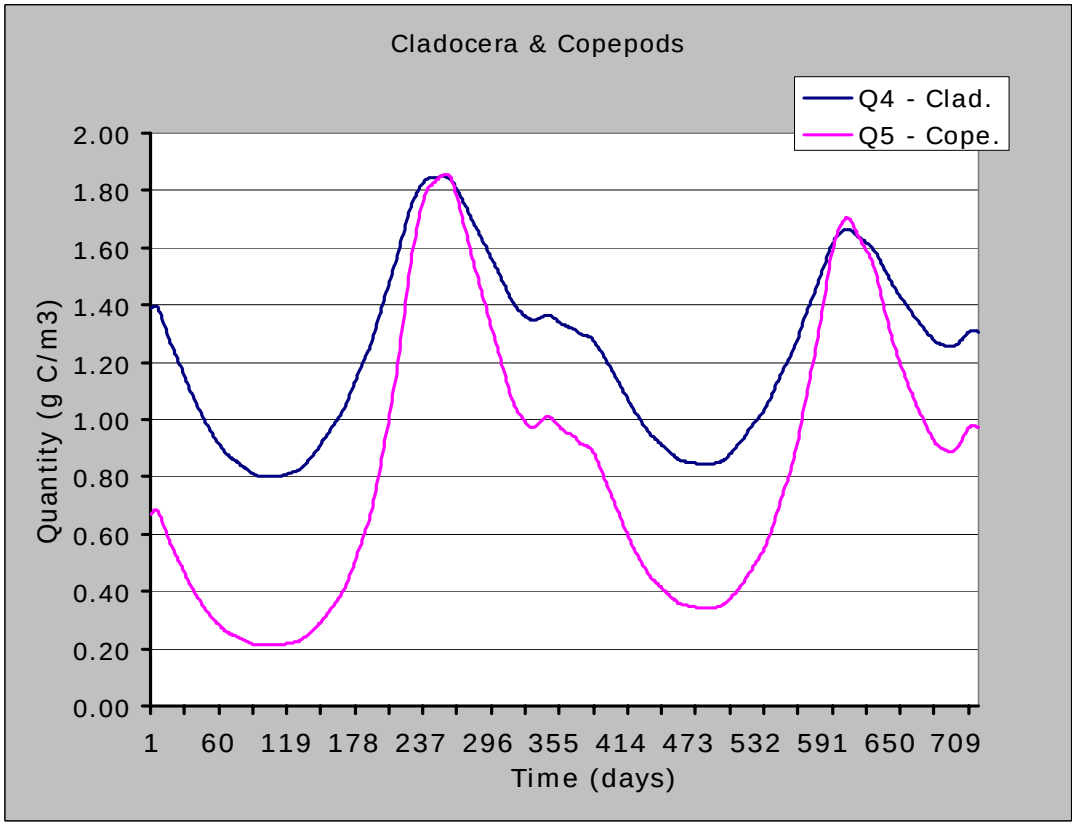
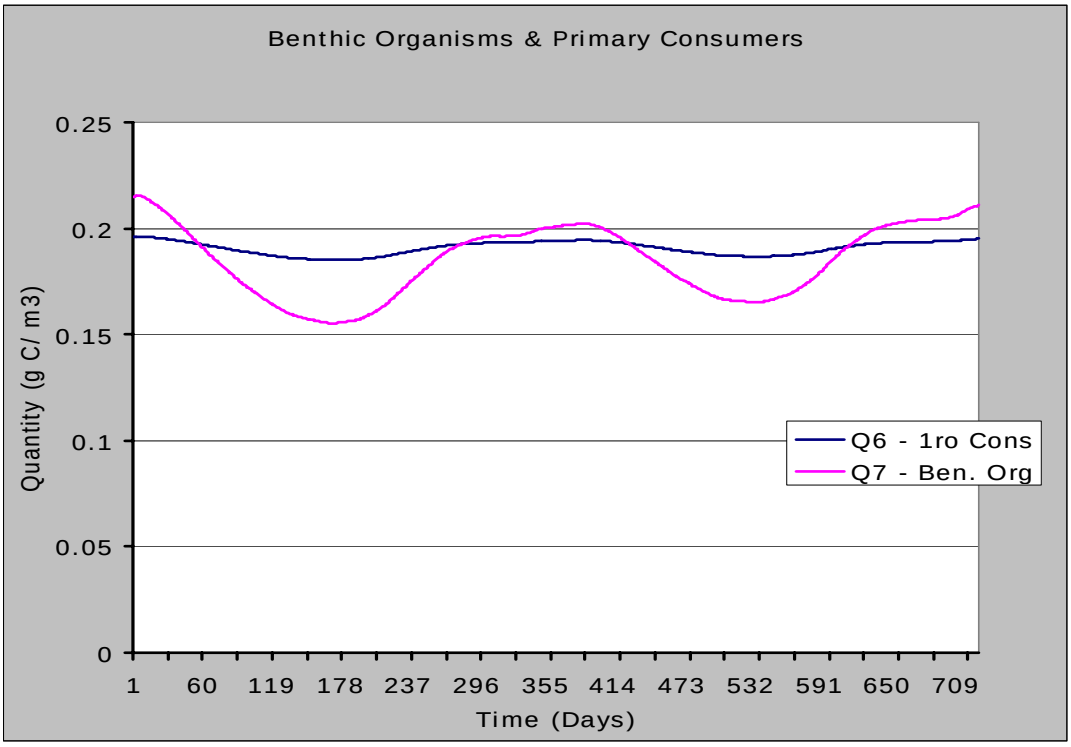


Figure 6. Simulation results for the base condition, showing graphs of phytoplankton (top) and Zooplankton (bottom)



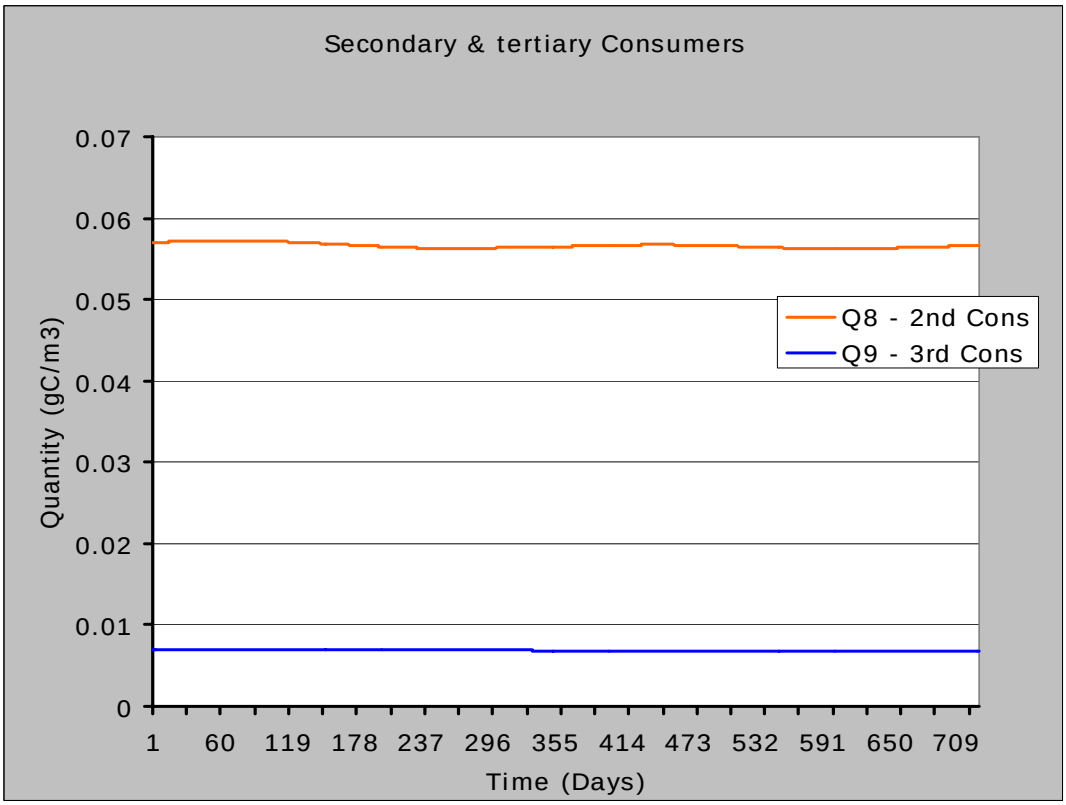


Figure 7. Simulation results for the base condition, showing graphs of benthic organisms (ben.org) and primary (1o) consumers top) and secondary(2o) and tertiary (3o) consumers (bottom)

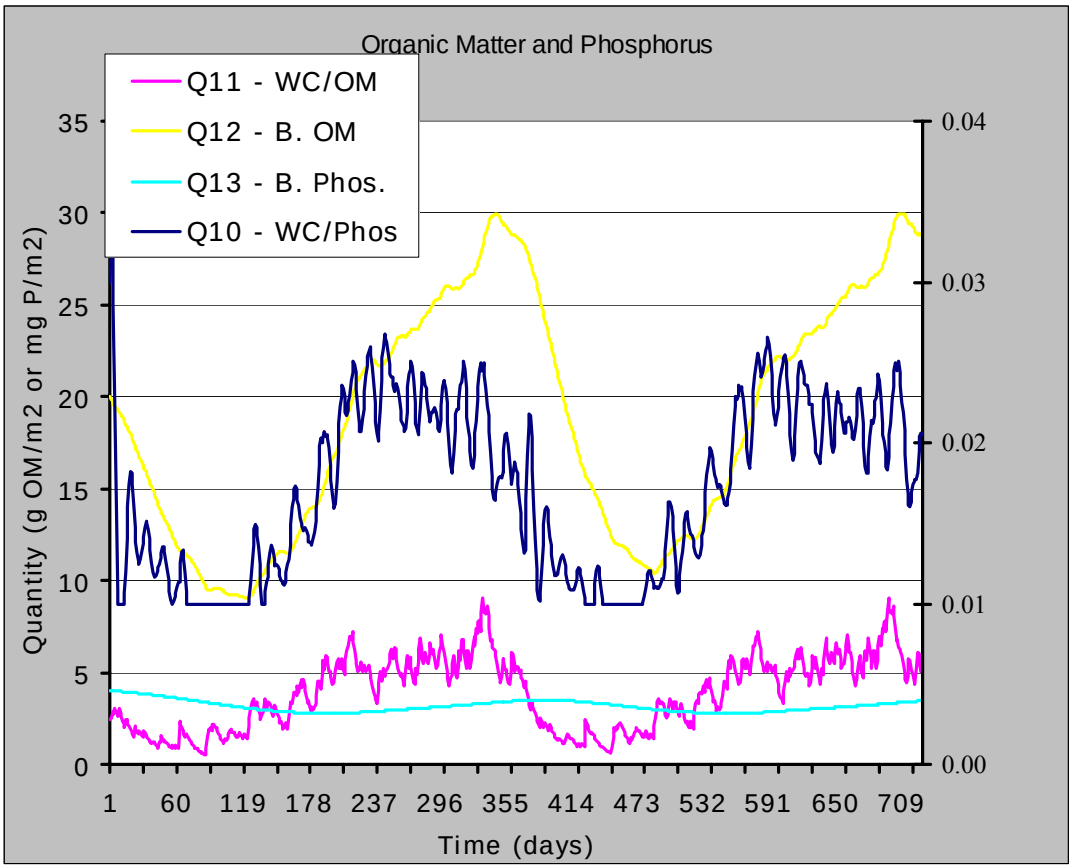


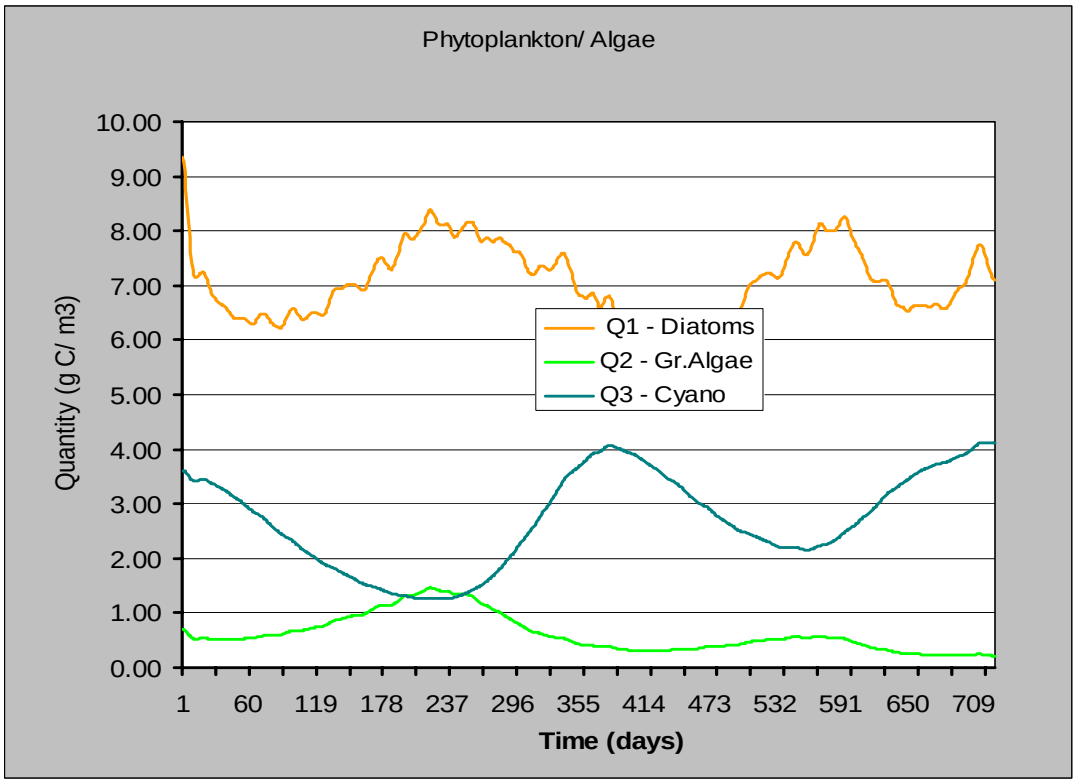
Figure 8. Simulation results for the base condition, showing graphs of organic matter and phosphorus in the water column (WC) and benthos (B).

The salinity effects were then simulated as an additional respiration or metabolic cost for dealing with the altered osmotic balance that increases linearly. Affected most by the increased salinity are the green algae and diatoms. The respiration of green algae is modeled to increase by 75% when the salinity is at 500 mg/l, while that of diatoms increases by 72%. On the other hand, respiration of blue-green algae increases only by 5%. Other organisms affected by the increased salinity are cladocerans (22%) copepods (9%) and primary consumers (5%). Benthic organisms and secondary and tertiary consumers are not affected by salinity in the model. The graphs in Figures 9, 10, and 11 are simulation results when salinity is raised to 250 mg/l and the graphs in Figure 12 thru 14 display the simulation results when salinity increases to 500 mg/l.

The results from these simulations show that the dominance from diatoms decreases and they become similar in importance to blue–green algae as salinity increases. Blue-green algae show marked increases in total biomass over the 2 year simulation both, at the 250 mg/l and the 500 mg/l model runs. All components of the ecosystem are affected by the increased salinity including those whose respiration is not directly augmented. Zooplankon compartments have higher amplitudes of fluctuation and there is a shift from cladocerans to copepods.

Primary consumers and benthic organisms decrease in total biomass primarily as a consequence of less production and food being available to them. Their decrease seems to be more dramatic than one would expect, but this is probably due to the fact that only the pelagic portion of the ecosystem is being modeled. Secondary and tertiary consumers are also affected but do not show the extreme changes seem in the lower trophic levels.

Even non living elements of the system show a change. Particularly interesting is the observed increase in phosphorus in the water column, which will have significant implications in the water quality in the lake. Although the change at the intermediate salinity level (250 mg/l) is not noticeable, when the salinity reaches 500 mg/l there is a significant trend to increased levels of phosphorous in the water column.



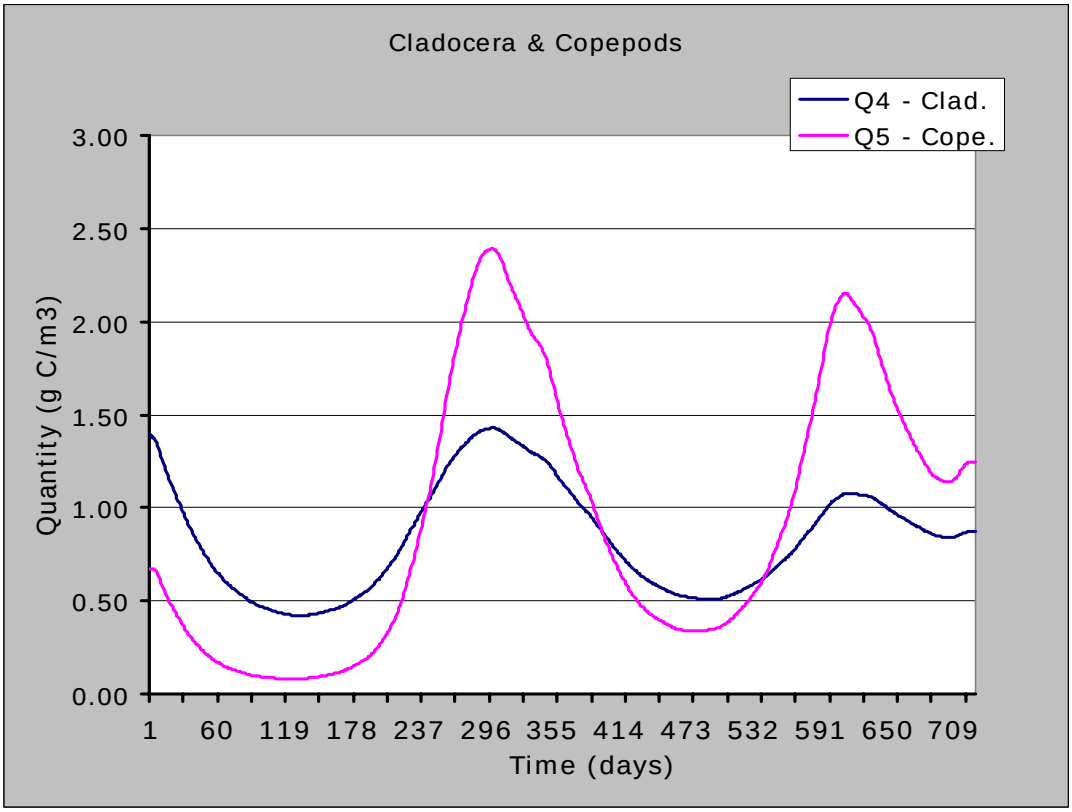
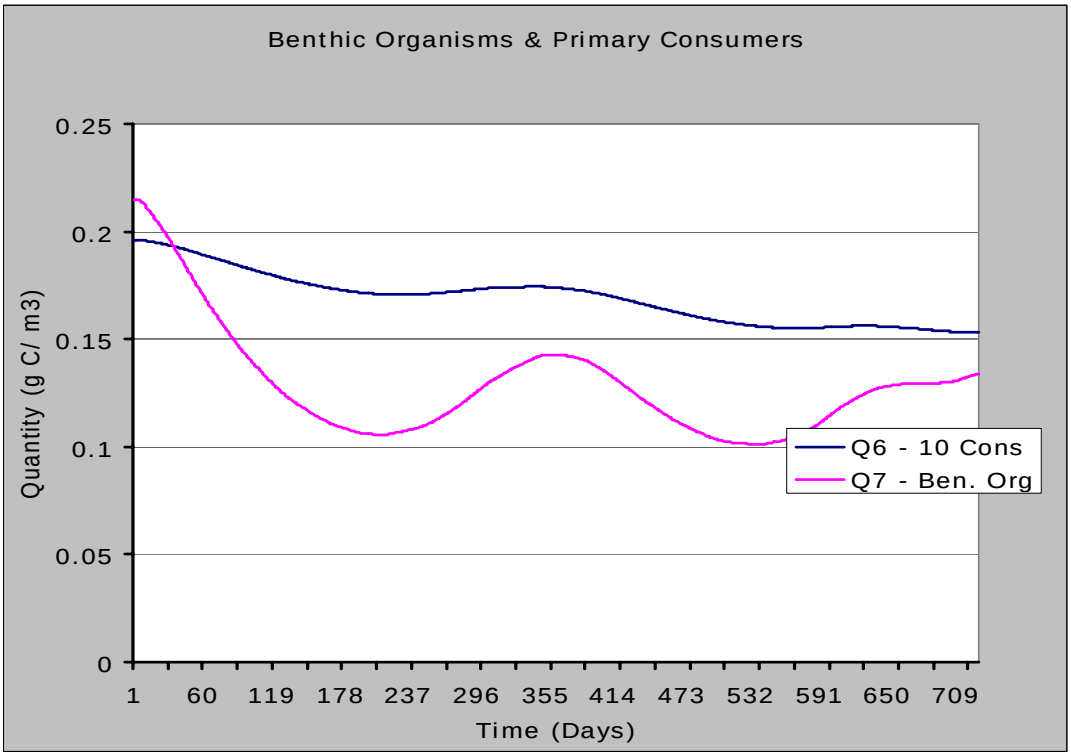


Figure 9. Simulation results for the simulation run with increased salinity (250mg/l), showing graphs of phytoplankton (top) and Zooplankton (bottom)



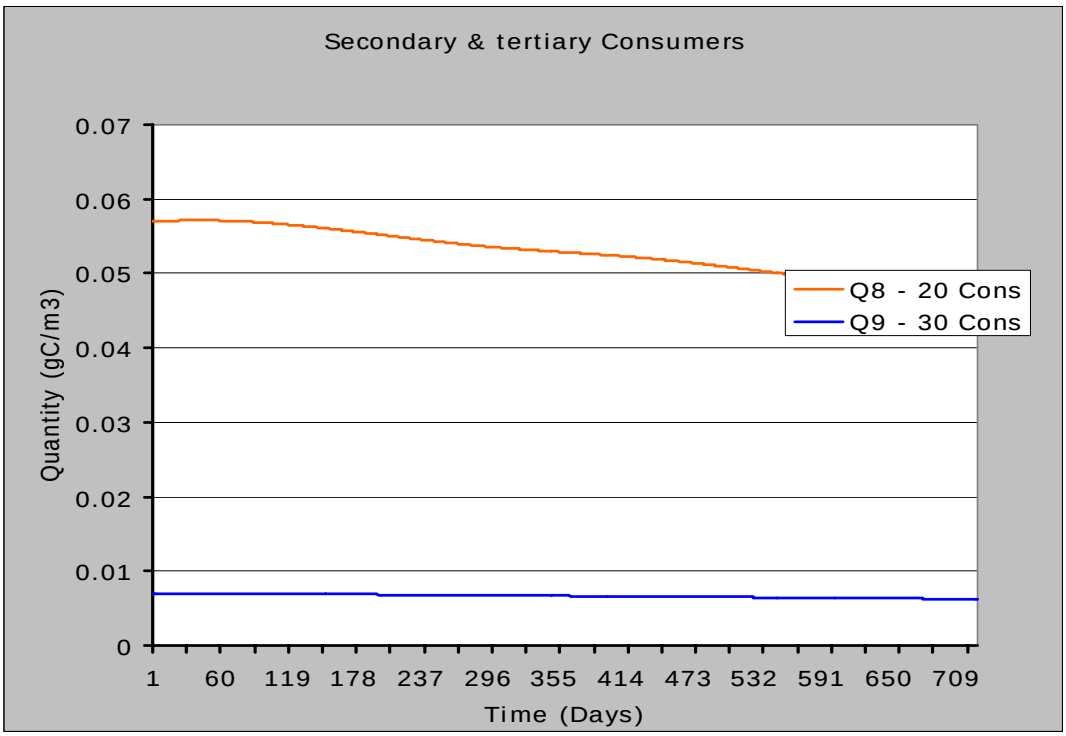


Figure 10. Simulation results for the simulation run with increased salinity (250mg/l), showing graphs of benthic organisms (ben.org) and primary (1ro) consumers top) and secondary(2do) and tertiary (3ro) consumers (bottom)

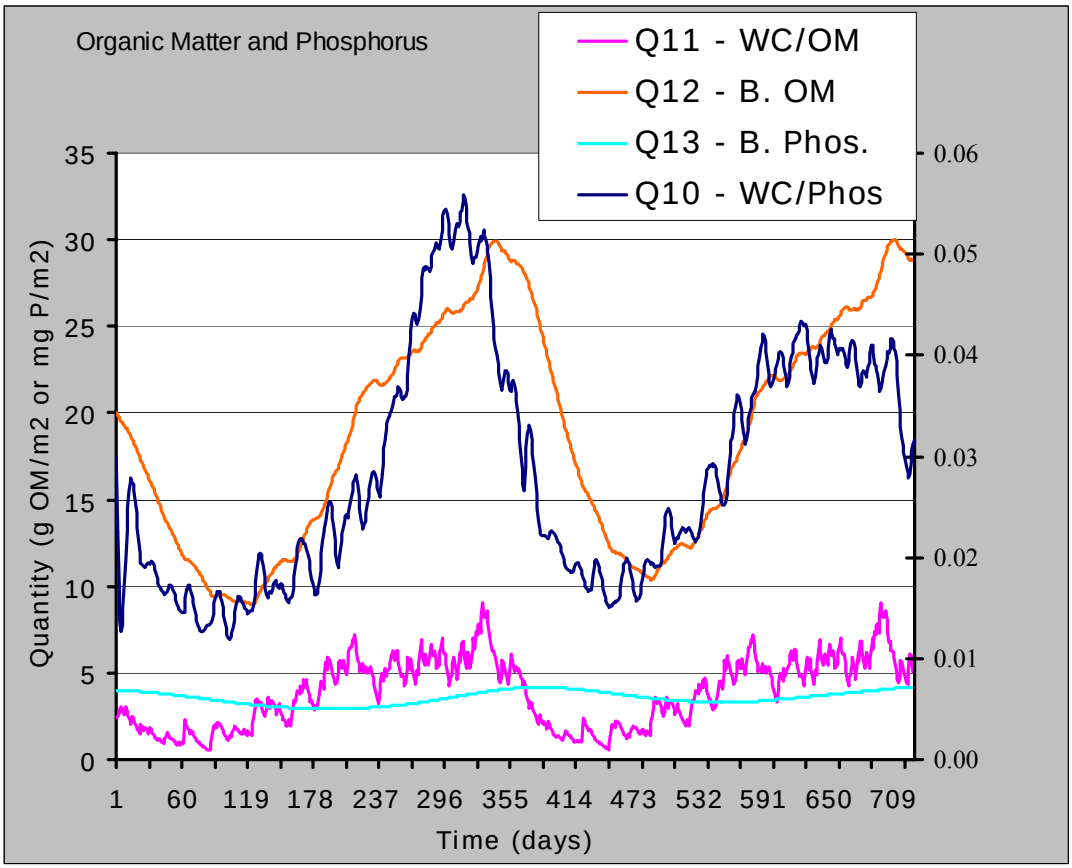
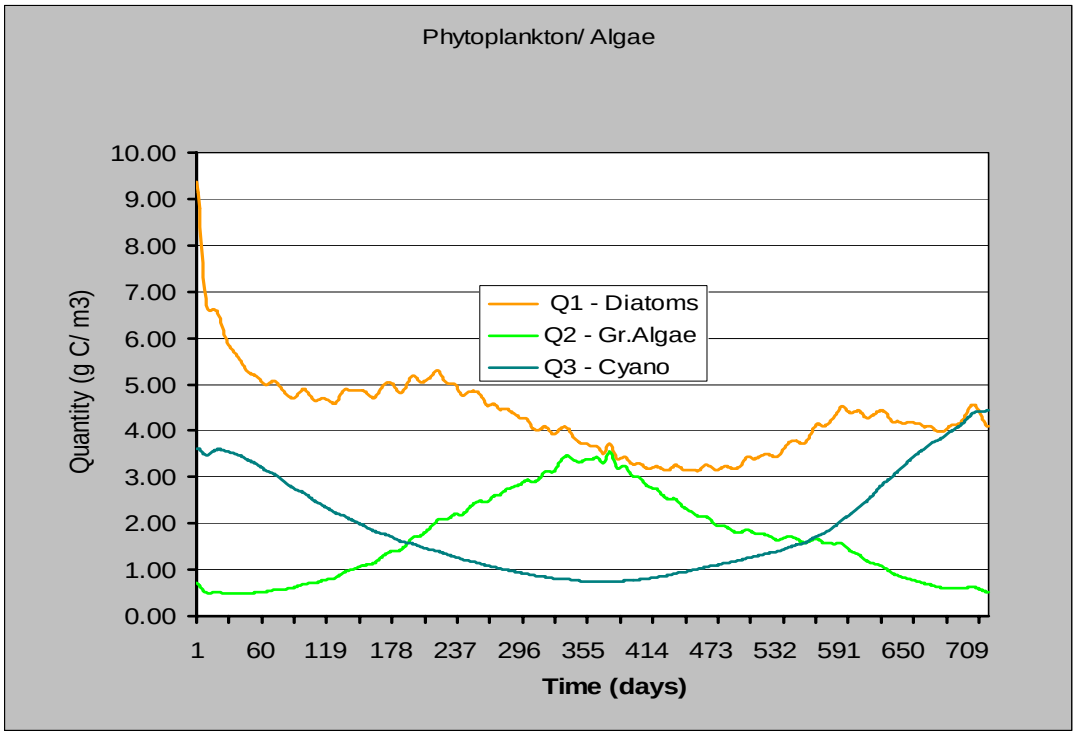


Figure 11. Simulation results for the simulation run with increased salinity (250mg/l), showing graphs of organic matter and phosphorus in the water column (WC) and benthos (B)



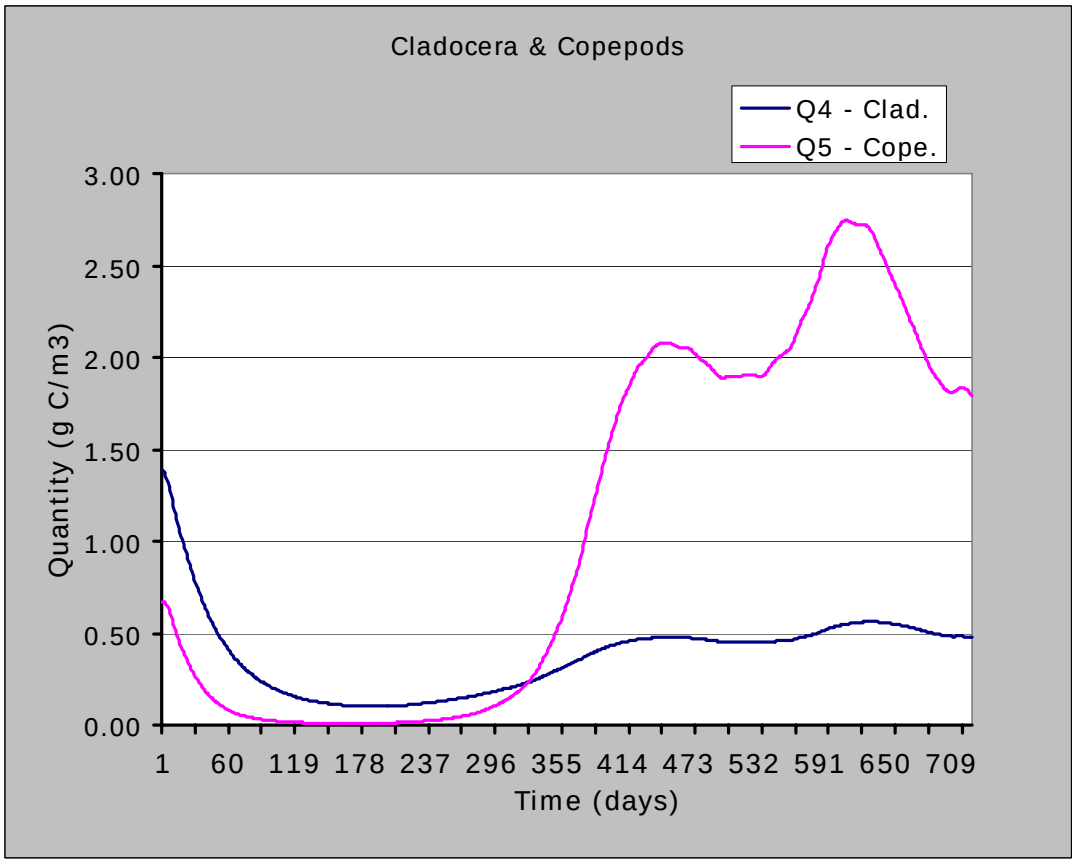
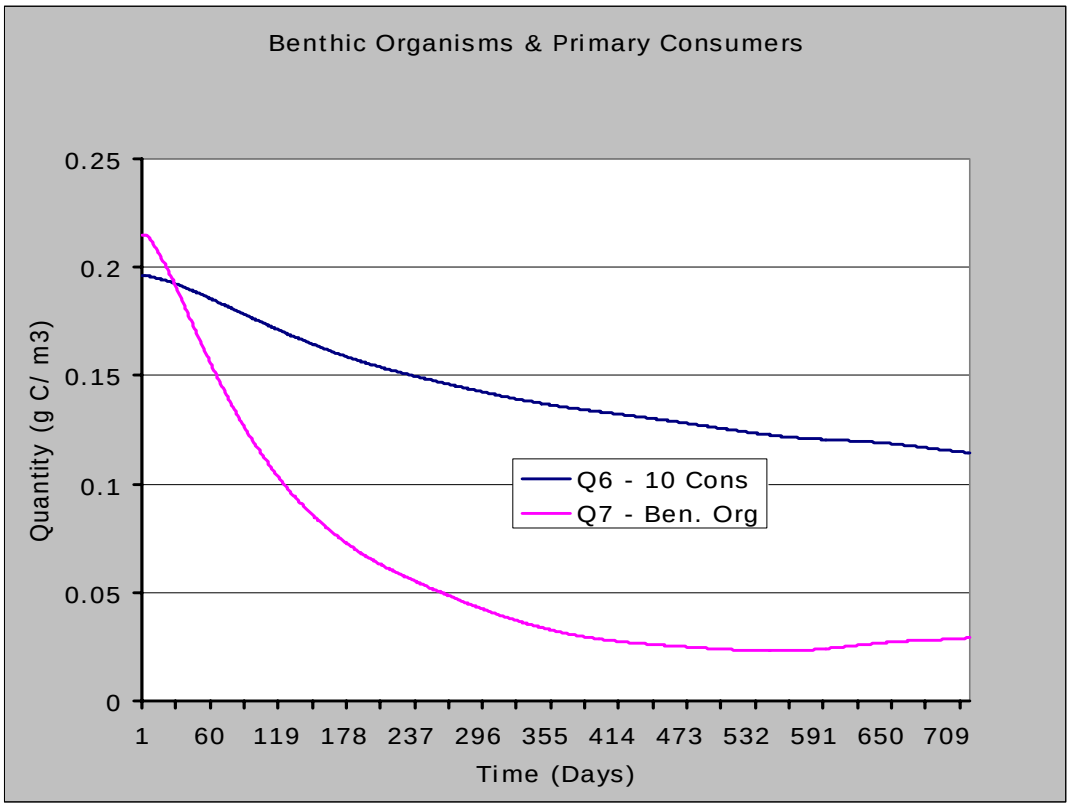


Figure 12. Simulation results for the simulation run with increased salinity (500mg/l), showing graphs of phytoplankton (top) and Zooplankton (bottom)



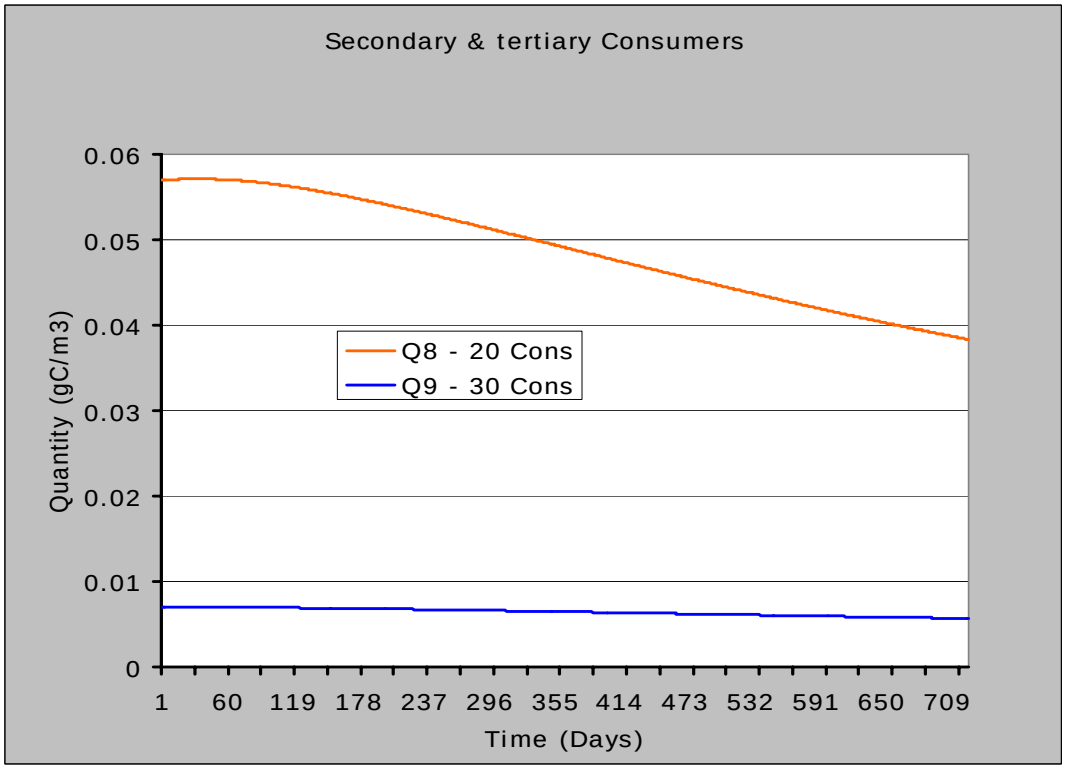


Figure 13. Simulation results for the simulation run with increased salinity (500mg/l), showing graphs of benthic organisms (ben.org) and primary (1o) consumers top) and secondary(2o) and tertiary (3o) consumers (bottom)

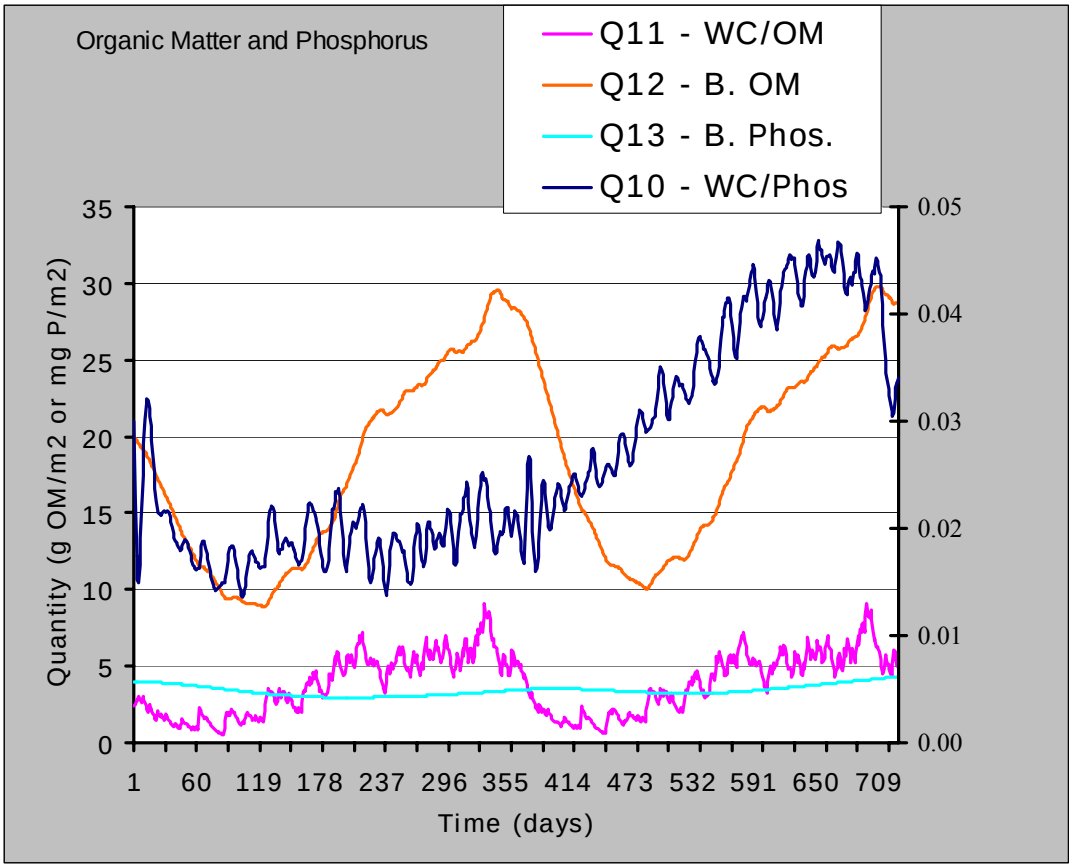


Figure 14. Simulation results for the simulation run with increased salinity (500mg/l), showing graphs of organic matter and phosphorus in the water column (WC) and benthos (B)

5.0 SUGGESTED RESEARCH

The two previous sections, sections 3 and 4, deal with the changes that may be anticipated in the ecosystem of Lake Gatun and the modeling of the metabolism of this ecosystem. Using our judgment and the information available we conclude that the impacts of the small salinity increase, that are anticipated (under 0.2 $^{o}/_{oo}$), will be minor and that the food web in the lake will not change significantly. Our judgment suggest that there may be an apparent switch towards a more eutrophic like conditions based on the hypothesis that the smaller algae may be affected more by the small changes in salinity. There decrease may lead to less oxygen in the water column, more nutrients available for the growth of larger algae, and decreased levels of light penetration in the water column.

All the changes mentioned above will tend to increase the total portion of biomass that flows through the detritus way rather than the herbivore-carnivore grazing path. This will transfer more energy to the sediments, where most of the ecosystem respiration is likely to be taking place at the time. This metabolic displacement may increase the abundance of certain groups such as the chironomids (water midgets), which would be undesirable for the reservoir based tourism. These water midgets have significant impact on communities around Lake Nicaragua, where there are known as “sayules”.

At the higher throphic levels the potential changes are smaller in terms of species composition, although the transfer of more energy to the sediment may slightly decrease the total fish production in the lake. This will probably be compensated by higher levels of biomass in some of the decomposers groups, such as freshwater shrimps and some of the mollusks.

We have made the point that available information is not enough to make predictions about the effects of salinity on the biological community, with a high degree of certainty. Consequently, this section suggests a series of data gathering activities that we envision should take place in parallel with additional modeling efforts to better understand the reservoir metabolism and its community structure. We anticipate that this information gathering, guided by the parallel modeling effort, shall take the understanding of the reservoir ecology to a point that makes the identification of potential impacts a more reliable undertaken. The nature of the data gathering activities is described in the paragraphs below.

5.1 Establish and Energy Budget for Lake Gatun

The first step should be to measure the main energy flows available to the biological community in Lake Gatun. Although several sources of energy contribute in different ways to this budget, we are particularly interested in those sources of chemical energy stored in organic matter that can be used directly as food by living creatures in the reservoir. There are basically two categories of organic matter that can be identified based on the location where it was originally synthesized. External sources (allochthonous organic matter) include that coming from biomass that was originally synthesized out of the reservoir and carried to it by water, wind and other means. Internal sources (autochthonous organic matter) include organic matter coming from the biomass that was originally synthesized by the primary producers existing in the reservoir.

As mentioned before, the energy budget for most freshwater ecosystem is dominated by external sources of organic matter, both dissolved and particulate. This organic matter is incorporated to the food web through a variety of mechanisms ranging from species of bacteria, which are able to take advantage of the energy in the dissolved organic matter, to fish, reptile, and even aquatic mammal species that eat pieces of fruits, flowers, leaves and insects among other creatures that fall on the water surface. A significant proportion of the particulate external organic matter normally settles to the bottom and is incorporated into the food web via the detritus pathway.

On the other hand, internal sources may be split at least into the biomass produced by the planktonic community and that produced by aquatic macrophytes and periphyton. A significant proportion of the organic from biomass produced by macrophytes may settle to the bottom of the ecosystem, as plants die off, and also enter the food web via the detritus chain.

Consequently, the first important piece of information has to do with the proportion of the total organic matter available to reservoir consumer that comes from internal sources versus that coming from external sources. This energy source is not likely to be affected by salinity changes since it is produced outside the reservoir. The total amount of organic matter can be estimated by measuring the concentration of dissolved and particulate organic matter in the discharge of rivers and stream that enter the reservoir.

The next important piece of information is the amount of biomass that is actually produced and consumed in the reservoir by the planktonic community and by the entire lake. Although several techniques are available to measure photosynthesis, probably the most efficient way to approach the magnitude of production and consumption of organic matter in the reservoir is by measuring the metabolism of oxygen at least at two levels of detail.

The first level is aimed to evaluate the magnitude of production and respiration in the planktonic community and uses a technique known as the **clear and dark bottles technique.** This technique measures the changes in dissolved oxygen in pairs of clear and dark bottles that are suspended at various depths in the water column. The oxygen concentration in the bottles, which are filled with water taken from the same level they are suspended at, changes as a result of the photosynthesis and respiration. Both processes occur simultaneously in the clear bottle and, therefore, it measures the rate of net primary production. On the other hand, inside the dark bottle only respiration occur since light is blocked from entering and, therefore, the dark bottle measures the rate of respiration of the planktonic community. Adding the values obtained for net primary production and respiration one can estimate the rate of total photosynthesis occurring in the planktonic community. These measurements should be taken at several times during the day and correlated with the solar radiation during the period of time the bottle were suspended in order to properly extrapolate to the daily rates of primary production and respiration. In addition, several stations shall be included in these measurements to evaluate the range of variation production and respiration may show across the various pools and sections of reservoir.

The second level of oxygen metabolism that can be used to estimate the rates of production and respiration is that of the entire reservoir, by means of the **diurnal oxygen curve technique**. The approach in this case is to estimate the amount of net primary production by measuring the increase of oxygen in the water column during the day time hours, when photosynthesis exceeds respiration. On the other hand, respiration is measured by the decrease of oxygen during the night time hours, when only the respiration process is active. Similarly to the previous technique, the sum of the two values provides an estimate of the total daily gross photosynthesis of the entire reservoir. It is important to record the oxygen levels in the water inflow as well as to estimate the amount of oxygen exchange with the atmosphere due to wind and wave action during the period of observation, to make adjustments and increase the accuracy and precision of the estimates.

Finally, it is important to note that a comparison of the two techniques may provide a good idea of the amount of production coming from the phytoplankton and from aquatic macrophytes, particularly hydrilla and periphyton. This is due to the fact that the diurnal oxygen curve measures the total lake metabolism, while the clear and dark bottles techniques measures that of the planktonic community only.

We suggest that this type of measurements be made in Lake Gatun every quarter during the first year and then every semester. In order to measure the lake metabolism we estimate that level of effort shall include one principal researcher and two teams of two trained biologists each during

one week for the fieldwork; and two weeks of the principal researcher and one assistant for data organization and analysis. It is important to point out that during the fieldwork the teams have to be in the water for periods of about 30 hours to measure the metabolism of oxygen during the day and night time. Alternatively, continuous oxygen measuring equipment can be used to obtain the diurnal evolution of oxygen concentration at different depths and locations in the reservoir. In addition, support will be required for transportation in land and in water and for laboratory analysis.

5.2 Measuring the Standing Crop of the Main State Variables

The second step in the set of suggested measurements should be the evaluation of existing values of standing crop in the several compartments of the ecosystem, primarily the living components. This should include the species composition and total biomass at each of the trophic levels considered in the simulation model. These values should be measured using a variety of appropriate techniques, recommended for each of them, to obtain the amount of energy that is present per unit area of the ecosystem. The detailed description of each technique is beyond the scope of this work, but the work shall be implemented by a team of aquatic biologist.

These measurements shall be taken at the same general time that is used for measuring the main metabolic process of production and respiration as described in the previous section. The purpose is to understand the interactions between the several species in each trophic level in a quantitative base. For this portion of the study a team of three senior biologists and three assistants may be required for a week to conduct the field work and for as long as three weeks for the identification of species and estimation of biomass from samples collected.

5.3 Salinity Bioassays

One of the main information gaps for a reliable analysis of potential impacts to the biological community in Lake Gatun is the sensitivity of the current species to salinity changes and the ability of potential colonizers to compete with indigenous ones under a range of realistic salinity values. This information will be more useful and reliable if it is collected in situ, and in order to obtain it we suggest a series ob bioassays that could be conducted in aquaria in laboratory conditions and partially submerged in the water of the reservoir. The later are particularly valuable to better discriminate between the effects of temperature and light conditions that may vary in the laboratory, when compared with the same parameters in the reservoir.

These bioassays shall be run with enough number of replications for a sound statistical analysis and must include at least 3 levels of salinity between the existing conditions and the maximum

value of 0.5°/oo. The bioassays shall be conducted to determine the succession of phytoplankton and zooplankton species, if any, as salinity increases. Salinity increments must be induced by using water coming from the locks or the approach channels in both entrance, Atlantic and Pacific. Finally, toxicity levels shall be conducted for all primary species to determine if they are at risks at the anticipated salinity levels.

The level of effort for the bioassays includes three researchers and their assistants for 50% of their time during one year. In addition, materials, equipment and transportation will be required to collect water, sediment, and living organisms as required for the tests.

5.4 Illustrative Budget

An illustrative budget required to conduct this research is outlined in Table 2 below. This budget assumes that a principal investigator will be from abroad and that several local biologists will be hired locally. The anticipated total cost is slightly over eight hundred thousand dollars and cover the first three years of operation. This budget includes time for the principal investigator to continue developing the simulation model of Lake Gatun and to provide enough direct supervision of field work and analytical work to be responsible for the overall effort.

The budget also assumes that the main team of researchers will be local biologists and that the bulk of biological assistants efforts will be provided by biology students who will in addition prepare their thesis or graduation project from this effort.

Other direct expenses include travel an per diem for the staff as well as anticipated expenses for local transportation and logistics as well as a lump sum for equipment.

Table 2. Illustrative Budget for the Execution of the Data Gathering Activities

		Año 1		Año 2		Año 3		TOTAL	
Labor (hours)	Rates	units	value	units	value	units	value	Units	value
Principal	130	480	62,400	240	31,200	240	31,200	960	124,800
Aquatic Biologist	50	960	48,000	480	24,000	480	24,000	1,920	96,000
Phytoplankton Expert	50	480	24,000	240	12,000	240	12,000	960	48,000
Zooplankton Expert	50	480	24,000	240	12,000	240	12,000	960	48,000
Ichtyologist	50	960	48,000		0		0	960	48,000
Crustacean Experts	50	960	48,000		0		0	960	48,000
Mollusk Experts	50	960	48,000		0		0	960	48,000
Assistant Biologists	10	7,000	70,000	2,000	20,000	2,000	20,000	11,000	110,000
Support Satff	20	4,000	80,000	1,500	30,000	1,500	30,000	7,000	140,000
Subtotal Labor		16,280	452,400	4,700	129,200	4,700	129,200	25,680	710,800
Travel & Other Expenses									
Air Travel - Rnd trip	750	4	3,000	2	1,500	2	1,500	8	6,000
Perdiem - day	145	40	5,800	20	2,900	20	2,900	80	11,600
Local Transp - day	100	80	8,000	40	4,000	40	4,000	160	16,000
Boat – Days	200	30	6,000	15	3,000	15	3,000	60	12,000
Copies - page	0.10	800	80	400	40	400	40	1,600	160
Color Copies - page	1	100	100	100	100	100	100	300	300
Equipments	25,000	1	25,000	0	0	1	25,000	2	50,000
Subtotal T&O Expenses			47,980		11,540		36,540		96,060
Total per Year			500,380		140,740		165,740		806,860

6.0 CONCLUSIONS

Very little quantitative data are available to properly evaluate the changes that may occur in Lake Gatun as a consequence of increases in salinity in the order of one or two tents of a part per thousand. We believe that changes in the relative abundance of species are most likely to occur at the lower trophic levels particularly phytoplankton and, to a lesser degree, zooplankton. The analysis of the information in reports and scientific literature allows a few generalizations to be made.

- Even small salinity increases may negatively affect the smaller algae in the phytoplankton community.
- Although not well documented the role of these small algae may be important to maintain low levels of nutrients (phosphorous), and high levels of dissolved oxygen and light penetration in the ecosystem. Consequently, changes will tend to move the reservoir water towards a more euthrophic condition. However, the magnitude of this trend, if at all present, cannot be anticipated at this time.
- An effect associated with the above described changes could be a shift towards and even more detritus dominated food chain in the ecosystem, favoring the harvesting of freshwater shrimp and mollusks over fish. The net flow of oxygen from and to the atmosphere and the net reduction in light penetration, if any, will play a very important role in the magnitude of that shift.
- Small salinity changes may negatively affect the relative abundance of rotifers and cladocerans, while increasing the relative abundance of calanoids and cyclopoids copepods. The impact of this switch on species dominance in the entire ecosystem is unpredictable at this time.
- The changes in other biological components of the ecosystem are even less predictable.
- A research and monitoring program could fill the information for more precise evaluations in the future.
- The use of ecosystem simulation techniques, as the ones described in this memo, could greatly enhance the efficiency of the research program by focusing on those gaps that are more critical for understanding the reservoir's metabolism.

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Annex 1.
Description of forcing functions, state variables and flows and pathways coefficients in the Lake Gatun salinity model

Label	Name	Units	Quantity	Turn-overtime	Pathway coefficients	Saliniy effect	Salinity level mg/L
Outside Forcing Functions							
E	Sunlight (mean daily)	cal/cm^2	variable				**50**
W	Wind speed (monthly mean)	m/sec	1.82				
R_1	Rainfall (monthly)	m/m^2	variable				
N,P_1	Phosphorus in rain(mean concentration ppm)	mg/l	0.01				
R_2	Runin (mean monthly)	m/m^2	variable				
$N.P_2$	Phosphorus in runin (mean monthly ppm)	mg/l	0.0083				
OM_1	Organic matter in runin (mean monthly concentration)	mg/l	186.3				
S_1	Salt in runin (mean monthly concentration)	Ppm	239				
L	Lockage water	m/m^2	0.57				
S_2	Salt water inflow from locks	ppm	variable				
GS	Goods and services (treated as a constant)	constant	1				
B	Bird feeding (treated as a constant)	constant	1				
F	Fishing	percent	variable				
Q_1 - Diatoms		g C * m^{-3}	**9.36**	**11.4**		0.00%	
J_{1p}	Production	gC*m^{-3}*day^{-1}	0.82		10.8099		
J_{1r}	Active Respiration	g C*m^{-3}*day^{-1}	0.363		4.7853		
J_{112}	Death	g C*m^{-3}*day^{-1}	0.087		0.0093		
J_{14}	Consumption by Cladocera	g C*m^{-3}*day^{-1}	0.23		0.0177		
J_{15}	Consumption by Copepods	g C*m^{-3}*day^{-1}	0.11		0.0175		
J_{17}	Consumption by Benthic Organisms	g C*m^{-3}*day^{-1}	0.039		0.0194		
J_{1s}	Salinity Respiration	g C*m^{-3}*day^{-1}	0		0.000000		
Q_2 – Green Algae		g C * m^{-3}	**0.71**	**10.3**		0.00%	
J_{2p}	Production	g C*m^{-3}*day^{-1}	0.068		10.6772		
J_{2r}	Active Respiration	g C*m^{-3}*day^{-1}	0.025		3.9254		
J_{212}	Death	g C*m^{-3}*day^{-1}	0.0059		0.0083		
J_{24}	Consumption by cladocera	g C*m^{-3}*day^{-1}	0.0232		0.0235		
J_{25}	Consumption by copepods	g C*m^{-3}*day^{-1}	0.012		0.0252		
J_{26}	Consumption by 1° Consumers	g C*m^{-3}*day^{-1}	0.0039		0.0280		
J_{2s}	Salinity Respiration	g C*m^{-3}*day^{-1}	0		0.000000		

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Q_3 – Blue-green Algae		g C * m^{-3}	**3.6**	**17.1**		0.00%
J_{3p}	Production	g C*m^{-3}*day^{-1}	0.21		3.4354	
J_{3r}	Active Respiration	g C*m^{-3}*day^{-1}	0.146		2.3884	
J_{312}	Death	g C*m^{-3}*day^{-1}	0.064		0.0178	
J_{35}	Consumption by Copepods	g C*m^{-3}*day^{-1}	0.001		0.0004	
J_{3s}	Salinity Respiration	g C*m^{-3}*day^{-1}	0		0.000000	
Q_4 - Cladocerans		g C * m^{-3}	**1.39**	**10.8**		0.00%
J_{4i}	Ingestion	g C*m^{-3}*day^{-1}	0.13		0.0093	
J_{4r}	Active Respiration	g C*m^{-3}*day^{-1}	0.048		0.0034	
J_{412}	Death	g C*m^{-3}*day^{-1}	0.01		0.0052	
J_{46}	Consumption by 1° Consumers	g C*m^{-3}*day^{-1}	0.04		0.1468	
J_{47}	Consumption by benthic organisms	g C*m^{-3}*day^{-1}	0.03		0.1004	
J_{4s}	Salinity Respiration	g C*m^{-3}*day^{-1}	0		0.000000	
Q_5 - Copepods		g C * m^{-3}	**0.67**	**5.2**		0.00%
J_{5i}	Ingestion	g C*m^{-3}*day^{-1}	0.13		0.0193	
J_{5r}	Active Respiration	g C*m^{-3}*day^{-1}	0.04		0.0059	
J_{512}	Death	g C*m^{-3}*day^{-1}	0.003		0.0067	
J_{56}	Consumption by 1° Consumers	g C*m^{-3}*day^{-1}	0.041		0.3122	
J_{57}	Consumption by benthic organisms	g C*m^{-3}*day^{-1}	0.038		0.2638	
J_{5b}	Consumption by Birds	g C*m^{-3}*day^{-1}	0.004		0.0060	
J_{5s}	Salinity Respiration	g C*m^{-3}*day^{-1}	0		0.000000	
Q_6 - Primary Consumers		g C * m^{-3}	**0.196**	**183.2**		0.00%
J_{6i}	Ingestion	g C*m^{-3}*day^{-1}	0.00109		0.0005	
J_{6r}	Active Respiration	g C*m^{-3}*day^{-1}	0.00054		0.0002	
J_{612}	Death	g C*m^{-3}*day^{-1}	0.00007		0.0018	
J_{68}	Consumption by 2° Consumers	g C*m^{-3}*day^{-1}	0.00014		0.0125	
J_{69}	Consumption by 3° Consumers	g C*m^{-3}*day^{-1}	0.00015		0.1093	
J_{6b}	Consumption by Birds	g C*m^{-3}*day^{-1}	0.00015		0.0008	
J_{6s}	Salinity Respiration	g C*m^{-3}*day^{-1}	0		0.0000	
Q_7 - Benthic Organisms		g C * m^{-3}	**0.215**	**33.2**		0.00%
J_{7i}	Ingestion	g C*m^{-3}*day^{-1}	0.0065		0.00265	
J_{7r}	Active Respiration	g C*m^{-3}*day^{-1}	0.00275		0.00112	
J_{712}	Death	g C*m^{-3}*day^{-1}	0.0013		0.0281	

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J_{78}	Consumption by 2° Consumers	g C*m^{-3}*day^{-1}	0.0012		0.0979
J_{79}	Consumption by 3° Consumers	g C*m^{-3}*day^{-1}	0.0012		0.7973
J_{7s}	Salinity Respiration	g C*m^{-3}*day^{-1}	0		0.000000
Q_8 - Secondary Consumers		g C * m^{-3}	**0.057**	**363.1**	
J_{8i}	Ingestion	g C*m^{-3}*day^{-1}	0.00016		0.0068
J_{8r}	Active Respiration	g C*m^{-3}*day^{-1}	0.00008		0.0034
J_{812}	Death	g C*m^{-3}*day^{-1}	1.4E-05		0.0043
J_{89}	Consumption by 3° Consumers	g C*m^{-3}*day^{-1}	0.00002		0.0501
J_{8b}	Consumption by Birds	g C*m^{-3}*day^{-1}	0.00002		0.0004
J_{8h}	Consumption by Humans	g C*m^{-3}*day^{-1}	0.00002		0.0004
Q_9 - Tertiary Consumers		g C * m^{-3}	**0.007**	**736.8**	
J_{9i}	Ingestion	g C*m^{-3}*day^{-1}	9.5E-06		0.0029
J_{9r}	Active Respiration	g C*m^{-3}*day^{-1}	5E-06		0.0015
J_{912}	Death	g C*m^{-3}*day^{-1}	1E-06		0.0204
J_{9b}	Consumption by Birds	g C*m^{-3}*day^{-1}	1.5E-06		0.0002
J_{9h}	Consumption by Humans	g C*m^{-3}*day^{-1}	2E-06		0.0003
Q_{10} - Water Column Nutrients (phosphorus)		mg P * m^{-3}	**0.03**	**1.0**	
J_{10i}	Inflow of nutrients in runoff	mg * l^{-1}	0.00219		1.0000
J_{1310}	Resuspended nutrients from benthos	mg * day^{-1}	0.05		0.0125
J_{1013}	Phos settling to benthos	mg * day^{-1}	0.0082		0.2733
J_{101}	Uptake by diatoms	mg * day^{-1}	0.00073		0.0026
J_{102}	Uptake by green algae	mg * day^{-1}	0.0003		0.0141
J_{103}	Uptake by blue-green algae	mg * day^{-1}	0.00135		0.0125
Q_{11} - Water Column Organic Matter		mg OM * m^{-3}	**2.4**	**10.7**	
J_{11i}	Inflow of OM in runoff	mg * day^{-1}	0.1863		1.0000
J_{1112}	OM settling to benthos	mg * day^{-1}	0.22356		0.0932
J_{1211}	Resuspension of OM	mg * day^{-1}	0.03726		0.001863
Q_{12} - Benthic Organic Matter		600*(mg OM * m^{-2})	**20**	**76.2**	
J_{1112}	Inflow of Organic matter from water column	mg * day^{-1}	0.22356		0.0932
J_{12d}	Inflow of OM from death of organisms	mg * day^{-1}	0.17129		1.0000
J_{1211}	Resuspension of OM to water column	mg * day^{-1}	0.03726		0.001863
J_{1213}	Microbial decomposition	mg * day^{-1}	0.09315		0.0047

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J_{13x}	Sequestration	mg * day-1	0.25794		0.0129
Q_{13} - Benthic Nutrients (phosphorus)		4*(mg P * m^{-2})	**4**	**268.5**	
J_{1013}	Inflow of nutrients from water column	mg * day^{-1}	0.0082		0.2733
J_{1213}	Inflow from microbial decomposition of OM	mg * day^{-1}	0.0116		0.000580
J_{1310}	Resuspension of nutrients	mg * day^{-1}	0.01		0.002500
J_{13x}	Adsorption (sequestration)	mg * day-1	0.0107		0.00268