1　**The Panama Canal after a century of human impacts**

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Abstract

Large tropical river dam projects are set to accelerate over the forthcoming decades to satisfy growing demand for energy, irrigation and flood control. When tropical rivers are dammed, the immediate impacts are well studied, but the long-term (decades-centuries) consequences of impoundment remain poorly known. Here, we gather historical and paleoecological data from Gatun Lake, formed by the building of the Gatun Dam (Panama Canal, Panamá) over 100 years ago, to reconstruct the limnological evolution of the system in response to individual and linked stressors (river damming, forest flooding, deforestation, invasive species, pollution and hydro-climate). We found that after a century of dam construction parallels associated with the natural hydrological functioning of river floodplains persist. Hence, hydrology remains the most important temporal structural factor positively stimulating primary productivity, deposition of new minerals, and reduction of water transparency during wet periods. During dry periods, clear water and aerobic conditions prevail and nutrients transform into available forms in the detrital-rich reductive sediments. We highlight the importance of climate change as an ultimate rather than proximate anthropogenic factor for sustainable management options of tropical dams.

Introduction

The tropics contain more than 4 million bodies of freshwater[1] and many large tropical rivers have been dammed for water management, commerce and energy production[2]. Projections show a three-fold increase over the forthcoming decades in the number of large dammed (>15 m high) tropical river projects[3-5]. When rivers are dammed, the immediate impacts are well studied[3]. For instance, dams transform carbon cycling[6,7], alter river networks by creating artificial reservoirs[3,8], alter natural patterns of sediment transport[8], impede upstream-downstream movement of fish[3] and modify water quality and productivity[3,8]. Yet almost nothing is known about the long-term impacts and limnological evolution of impoundment of highly diverse, tropical rivers. Rivers in the neotropics (the tropical areas of North, Central and South America) are, in particular, poorly studied[8,9] with almost no long-term continuous time-series of data for multiple variables[10]. This constrains our understanding on how these aquatic systems can be sustainably managed in the long-term. In this study we combined exemplary historical and paleoecological approaches to provide a continuous long-term record of lake hydrology and geochemistry and the responses of different aquatic biological groups associated with the iconic Panama Canal.

In 1913 the Chagres River was dammed, forming Gatun Lake on which the Panama Canal is located (Fig. 1). At the time, Gatun Lake was the first neotropical large dam and was the largest man-made lake in the world with a surface area of 425 km^2. In contrast, most neotropical dams are no older than a quarter of century[8,10] making Gatun Lake a unique opportunity to reveal long term

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63   dynamics in a tropical dam system. Moreover, Gatun Lake has extensive

64   environmental and ecological records thanks to monitoring and research

65   programs established by the Panama Canal Authority (ACP for its acronym in

66   Spanish) and the longstanding presence of the Smithsonian Tropical Research

67   Institute (STRI) in Panama. Combining these records that are unavailable for

68   other old dams, with paleoecological data offer therefore an unrivalled

69   opportunity to explore the impacts of damming on a tropical river over a period of

70   more than 100 years.

71   In this study, we present sedimentary data of Gatun Lake to build a biological

72   and environmental chronological sequence of changes and combined it with

73   historical water quality records (secchi depths, pH, conductivity and dissolved

74   oxygen) available from 1969 to 2013, and on river annual flow and climate

75   (precipitation) records available from 1930 to 2013. The aim was to: (1)

76   reconstruct the limnological evolution of the Chagres River landscape (including

77   pre-impoundment times); and (2) assess individual and linked effects of river

78   damming, forest clearance and flooding, the introduction of invasive species,

79   water quality variation and climate on this aquatic landscape.

80

81   **Results**

82   **Environmental history of Gatun Lake:** The canal region experiences a

83   seasonal tropical monsoonal climate. Mean annual temperature across the canal

84   area is 26 °C and mean monthly temperature varies by just 1°C annually[11].

85   Rainfall ranges from around 1750 mm year^{-1} mean annual precipitation on the

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86   Pacific coast, to 4000 mm year[1] on the Caribbean coast[12]. Records beginning in

87   the late-1920s on the Smithsonian's Barro Colorado Island (BCI) in the canal

88   show that annual rainfall has varied considerably between years, apparently

89   related to ENSO conditions[13].

90   Gatun Dam led to flooding of large areas of tropical forest[14], an increase in

91   sediment accumulation[15] and, watershed deforestation[16,17] for agriculture, in

92   addition to the operation of the canal and urban expansion[17]. Almost 20 years

93   later, another portion of rainforest was flooded across the river headwaters by the

94   construction of a second dam, Lake Alajuela, built to regulate the stochastic

95   hydrology of the Chagres River[15] (Fig. 1). The consequences of forest flooding

96   have yet to be quantitatively assessed, but is likely that the expansive areas of

97   flooded allochthonous organic material would have contributed considerable

98   quantities of DOC into the newly formed lake[6,7] facilitating large emissions of

99   greenhouse gases to the atmosphere, even decades after construction of the

100   dam, as has been shown in other tropical dams[7,18].

101   Salinity of Gatun Lake has been historically below 0.2 ppt[19]. However,

102   increases in salinity above the United States Environmental Protection Agency

103   (EPA) drinking water standards (>3.0 ppt) have been reported in the Miraflores

104   locks during the dry season since the completion of the Canal[20]. Furthermore,

105   recent (2004-2015) expansion of the canal has resulted in higher water demands

106   to operate a new set of larger locks resulting in more salt water penetrating the

107   lake, especially during the dry season[20]. The consequences of this emergent

108   salinization of Gatun Lake continue to be debated but observations of brackish

109   water fauna, such as the non-native North American Harris mud crab

110   (*Rhithropanopeus harrisii*)[21] and the Iraqi crab (*Elamenopsis kempi*)[22], and

111   increases in observations of marine fish have already been reported in the lake[23].

112   Gatun Lake has also been subjected to introductions of several nuisance

113   aquatic species. The Asian macrophyte *Hydrilla verticillata* was first recorded in

114   the lake around the 1930s, which rapidly dominated the lake after it was filled[24].

115   Introduction of the peacock bass (*Cichla ocellaris*) to the lake in the late-1960s

116   caused a major ecological reorganization associated with dramatic declines in

117   native littoral planktivorous fish species[25], and these impacts endure 45 years

118   later[23]. Other known introductions have included the Asian bryozoan *Asajirella*

119   *gelatinosa*[26], the Asian *Melanoides* (Thiara) *tuberculata* and, the South American

120   apple (*Pomacea bridgesii*) snail[27]. There are likely myriad other introductions that

121   have been undocumented or that are projected to occur under the new canal

122   expansion[28].

123   **Paleoecological data:** We focused our paleoecological analysis on three

124   biological groups from which fossil remains are commonly well preserved in lake

125   sediments: macrophytes, invertebrates (bryozoans, chironomids, cladocerans

126   and mollusks) and diatoms. As a measure of temporal environmental change we

127   combined information on the variation of single trace elements (potassium [K]–

128   river erosion; calcium [Ca]–salinity; lead [Pb], copper [Cu] and zinc [Zn]–

129   pollution)[29] and elemental ratios (iron/magnesium [Fe/Mn]–reductive conditions;

130   titanium/calcium [Ti/Ca–detrital inputs])[29]. The carbon contribution of terrestrial

131   plants, macrophytes, and bacteria-algae was assessed through *n*-alkanes $C_{15}-$

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132 C_{31} biomarkers[30]. The *n*-alkanes information was also used to calculate the

133 terrigenous aquatic ratio (TAR) and the submerged/floating aquatic macrophyte

134 inputs vs. emergent/ terrestrial plant input ratio (Pmar-aq)[31]. A methane index

135 (MI) [32] was obtained via archaea-glycerol dialkyl glycerol tetraethers [GDGTs]).

136 Major zones of temporal change were assessed through clustering analysis and

137 the links between biological and environmental variation were tested via multiple

138 factor analysis–MFA[33].

139 **Core chronology and sedimentation rates:** A sediment core (87 cm long;

140 LGAT1) was retrieved from a littoral area (9°2'49.58"N, 79°50'6.33"W) at a water

141 depth of approximately 1 m (Fig. 1). Sediments were dated using the constant

142 rate of ^{210}Pb supply (CRS) model[34] resulting in a chronology spanning the last

143 c.150 years (Fig. 2). The pre-canal riverine conditions were contained within the

144 87-50 cm of the core and the post-canal lake conditions within the top 50 cm. The

145 age model showed that sedimentation rates at post-canal times remained

146 relatively uniform (each cm representing c. 8-15 years) until the early-2000s

147 when rates almost doubled (Fig. 2).

148 **Long-term shifts in paleoecological proxies:** Temporal variation on the

149 selected geochemical and biomarker data is presented in Fig. 2. Sixteen

150 macrophytes, 19 invertebrates and 81 diatom taxa (Figs. S1-S3) were identified

151 throughout the sediment core and summarized into functional groups according

152 to growth type (macrophytes), habitat preference (diatoms) and feeding mode

153 (invertebrates) as follows (Fig. 3): *macrophytes* submerged; anchored-floating;

154   free-floating and emergent; *invertebrates* filter-feeders (bryozoans),

155   macrophyte/detrital (chironomids), shredders (Trichoptera cadis case larvae),

156   benthic (chironomids), and grazers (mollusks and cladocerans); *diatoms*

157   planktonic, benthic, littoral, aerophilous, and salinity-tolerant[35,36]. Diatom benthic

158   species were further sub-grouped into acidic, oligotrophic, benthic-mobile and

159   eutrophic species[37-39].

160   Results uncover a dynamic aquatic history from before the formation of

161   Gatun Dam by the Panama Canal to the present day. As expected, results

162   describe over four main temporal zones of biological and environmental change a

163   gradual transition from a river-governed system to a lake system (Figs. 2,3).

164   During pre-canal times (Zone 1 c. pre-1870), the geochemical and biomarker

165   data reflected swamp-like alluvial conditions characterized by reductive

166   sediments (high MI index and Fe/Mn ratio respectively), low nutrient and acidic

167   waters, and high detrital (Ti/Ca) inputs (Figs. 2,4). Before the creation of the

168   Panama Canal, the Chagres River meandered through an alluvial floodplain of

169   vast areas of swampy conditions[13,40]. In agreement with those records, we found

170   a prevalence of rushes and sedges, free-floating plant species *(e.g. Ludwigia*

171   *sedoides, L. helminthorrhiza, Pistia stratiotes*, *Salvinia rotundifolia;* Fig. S1) and

172   high occurrence of littoral and benthic diatoms (e.g. *Eunotia, Encyonema* and

173   *Pinnularia;* Fig. S3b) and charophyte macro algae (*Chara* spp. and *Nitella* spp.

174   Fig. S1), all of which commonly occur in low turbulence and low nutrient waters[37-

175   39,41]. The occurrence of planktonic diatoms (e.g. *Aulacoseira* spp., Fig. S3a)

176   further indicates an environment hydrologically connected to a main river

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177 channel[37-39]. Abundant Trichoptera shredders and macrophyte/detrital-associated

178 invertebrates (e.g. *Cladopelma* spp*., Zavreliella* spp*.,* and *Stenochironomus* spp.;

179 Fig. S2) along with anaerobic bacteria-archaea all suggest a highly reductive

180 environment. In particular, the latter suggests that carbon cycling at the time

181 might have mainly occurred through methanogenesis and sulphate reduction

182 pathways[42].

183   Construction of the Panama Canal led to a clear anthropogenic signal (Fig.

184 2). From 1870-1913 (Zone 2) pollutants such as Cu, Zn, and Pb, previously

185 associated with mining activity, coal burning and gasoline combustion[43],

186 increased considerably. These activities were most likely linked to the coal

187 combustion by large machinery used for the dredging and excavation of the

188 canal[40]. Submerged (e.g. *Najas guadalupensis, Najas marina*, and

189 *Ceratophyllum demersum;* Fig. S1) and anchored-floating plants (likely

190 *Nymphaea ampla*), benthic-mobile diatoms (e.g. *Navicula radiosa* and *Navicula*

191 *recens;* Fig. S3c), caddisfly larvae (Trichoptera) shredders and bryozoan filter-

192 feeders (*L. carteri,* and *Plumatella* spp.) responded positively to these novel

193 conditions while diatoms shifted from littoral to benthic-planktonic associations

194 (Fig. 4). Increases in the bryozoans *L. carteri* and the colonizing *A. gelatinosa* in

195 particular, were likely responding to an expansion of macrophyte cover[26,44]. The

196 observed proliferation of caddisfly larvae may also have ultimately been driven by

197 increased detrital inputs and food availability as they prey on bryozoans[44].

198   As the lake infilled after formation of the dam in 1913 (Zone 3), littoral detrital

199 (Ti/Ca) and river-fed elements (e.g. K) declined (Fig. 2). Declining erosion after

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200   dam construction likely continued following construction of the Alajuela Dam in

201   1935 in the headwaters of the Chagres, reducing the supply of river material into

202   Gatun Lake[15]. However, contributions of allochthonous organic carbon (high TAR

203   index) increased up until the mid-1980s (Fig. 2). Possible sources of this

204   terrestrial carbon include the flooded forest areas[13] and particulate material

205   derived from watershed deforestation, which peaked during the mid-1970s[16].

206   These patterns of increasing terrestrial organic matter inputs from early-1920s to

207   the mid-1980s partially supports recent findings showing that the degradation of

208   flooded forest material in tropical impoundment projects may endure for decades

209   after reservoir infilling, a period when CO_2 and CH_4 production is commonly

210   facilitated[7,18]. Yet, our data suggest that such carbon pathways may take even

211   longer to develop (four-five decades) than previously suggested for tropical dam

212   projects[7,18].

213   In general, our findings show that macrophyte growth was encouraged as the

214   lake infilled, promoting aerobic conditions (Fig. 4). This trend matches the

215   historical macrophyte records from Gatun Lake[24], and other similar tropical

216   impoundment projects[8,45]. For instance, the invasion of *H. verticillata* that resulted

217   in many hectares of the lake becoming choked with this submerged species was

218   accompanied by increases in other submerged plants like *Najas* and

219   *Ceratophyllum* (Fi. S1). Free-floating plants, such as *Eichhornia spp.*, and *P.*

220   *stratiotes*, also disseminated rapidly, while anchored plants (*N. alba* in particular),

221   invertebrate shredders, filter-feeders and macrophyte/detrital associated taxa

222   declined (Fig. 3, Figs. S1,2.).

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223   Diatom and invertebrate assemblages mirrored the trends in macrophytes

224   following impoundment (Fig. 4). Over time, invertebrate communities shifted from

225   detrital to benthic associations, while bryozoan filter-feeders declined (Fig. 4),

226   which could have been a response to the gradual decline of anchored-floating

227   plants[26,44]. Diatoms shift to a benthic-aerophilous-saline diatom assemblage

228   characterized by increases *Cocconeis placentula* and *N. amphibia,* by

229   aerophilous genera such as *Diadesmis, Luticola* and *Orthoseira* and by the

230   salinity-tolerant species *Terpsinoe musica,* and *Tabularia fasciculate*[35-37](Fig.

231   S3). This shifts in diatom composition suggest that the progressive macrophyte

232   expansion provided an increase in habitat availability for benthic-mobile species

233   and suitable macrophyte littoral habitats for aerophilous species[38,39] while

234   increases in saline-tolerant taxa were most likely driven by salt-water intrusions

235   from the passage of ships through the dam locks[20] and ion runoff resulting from

236   deforestation[16].

237   As the lake aged (post-1995; Zone 4) submerged and free-floating

238   macrophytes increased and carbon cycling shifted in concordance to within-lake

239   production (high Pmar-aq index value)[31] (Fig. 2, 3). This shift in habitat structure

240   marked an upsurge in the abundance of grazing invertebrates and benthic diatom

241   species that prefer productive environments (fig. 2).

242   **Impoundment and natural river floodplain dynamics:** We found that after a

243   century of the dam construction, there are still remarkable parallels associated

244   with the natural hydrological functioning of a river floodplain system. In particular,

245   precipitation and annual river flow emerged as the most important factor driving

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246 most of both abiotic and biotic compartments (Fig. 4) in agreement with floods

247 and droughts being major drivers of river abiotic change and community

248 reorganization[46]. Shifts in hydro-climatic variables were suggested to alter a

249 series of interconnected processes such as sedimentation dynamics, water

250 quality, productivity, and sediment reductive/oxygenated conditions. During drier

251 periods for instance, sedimentation was relatively low due to lower physical

252 erosion while detrital inputs where high (Fig. 4). There was also a prevalence of

253 reductive sediments and relatively higher secchi depths (> 3m), oxygenated

254 surface waters (> 6 ppm), higher conductance (>60 µS/cm) and higher nutrient

255 availability (Table 1; Fig. 4). Similar increases in conductance resulting from

256 reduced dilution of salt ions concentrations during the dry season have been

257 observed in the Amazon River, where conductance values in oxbow lakes can

258 increase up to 200 times the value of the main river[46]. Accumulation of organic

259 matter and debris in the lakebed causing reductive soil conditions have been also

260 described in the Paraná River system and attributable to low rates of water

261 circulation during drier phases[47]. The observed anoxic sediment conditions (high

262 Fe/Mn ratio) in Gatun, would have transformed nutrients (phosphorus in

263 particular) into more available forms[42] that along with clearer and less variable

264 water levels would have favored planktonic diatoms[37-39] and submerged and free

265 floating macrophytes[45,47]. As submerged plants grow in clearer waters they would

266 have also photosynthesized more increasing surface DO levels in the water[48].

267   Wet periods positively stimulated sedimentation, deposition of new minerals

268 (e.g. Ca and K) and reduced water transparency (Fig. 4). Lower secchi depths

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269   were strongly linked to reductions in pH, conductance and dissolved oxygen (Fig.

270   4), which likely reflects the storage of organic matter during the dry phase,

271   coming from both autochthonous production and allochthonous inputs from the

272   lavish riparian vegetation surrounding the lake catchment[47]. A positive long-term

273   relationship between macrophyte productivity and wet periods also existed (Fig.

274   4). We attribute this increase in productivity to a decadal macrophytes

275   succession that was accompanied by increases in abundances and

276   representation of different plant taxonomic groups (Fig. S1). Furthermore, high

277   rates of river water exchange during high floods can act as a significant source of

278   propagules, especially for submerged and floating plants in neotropical rivers[47].

279   The action of water transporting sediments and nutrient (TP and TN) additions

280   from surrounding soils, may promote further spatial heterogeneity in the lake[46,47]

281   opening up additional ecological niches for macrophytes and co-associated

282   benthic diatoms. Light attenuation in the water column coupled with fluctuation in

283   water levels may further stress the submerged vegetation while favoring

284   increases in floating macrophytes through enhanced nutrient input from the

285   flooded land[45,47]. The weak negative relationship between macrophyte

286   abundance and nutrient concentration (Fig. 4), suggests that primary productivity

287   in the lake may not yet be limited by nutrients. Moreover, changes in habitat

288   structures (anchored floating plants) rather than nutrient availability are

289   suggested to favor the variation of nutrient-rich associated benthic diatoms.

290   We are aware that the use of paleoecological data to infer past communities

291   and ecological responses has limitations as they can suffer from bias due to the

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292 differential production, transport and preservation of organismal remains[49].

293 Nevertheless, our paleoecological data was in agreement with the historical

294 changes previously described for the lake. Uncertainties in the age model and

295 use of different historical environmental records might have also introduced some

296 discrepancies in our MFA model. Nevertheless, the observed limnological

297 changes agree with the literature of river floodplain dynamics[46,47]. This thesis is

298 further supported by the geochemical data that showed a coherent signal with

299 increases in precipitation over 2010-2011. We observed a drastic decline in Ca

300 coupled with increases in sedimentation rates, Fe/Mn, and Ti/Ca (Fig. 2), which

301 resemble the historical riverine pre-damming conditions and that are in

302 agreement with "La Purísima" rainstorm, which flooded the whole lake system

303 and increased sedimentation rates by almost 100-fold[50].

304 **Is the Gatun Lake becoming more saline?** Our data are concordant with a

305 gradual increase in salinity in some parts of Gatun Lake after the early-2000s as

306 observed by increases in saline-tolerant diatom species and Ca concentrations.

307 Seawater likely intrudes into the lake through the locks of the Panama Canal and

308 the deposit of ballast water into the lake, which was only forbidden after 1996.

309 The locks may not be the only reason for increasing salinity. Runoff associated

310 with the enclosed drainage basin and land-use change may have led to an

311 increase in ion input and hence increased water salinity. These two processes

312 are often governed not only by greater runoff but also by evaporation; a pattern

313 that is consistent with the peak in salinity-tolerant diatom species and increases

314 in emergent macrophytes during the drier period of the mid-1960s to mid-1980s

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315   (Figs. 3, 5b). The more recent increases in salinity-tolerant diatom species

316   (including two marine morphtypes; Fig. S3f) in the Gatun Lake after the early-

317   2000s implies an increase in the rate of salinization of the lake. This coincides

318   with the canal expansion work, which began in 2005 and the use of new locks

319   built to permit the transport of larger vessels (Post-Panamax) through the canal[20].

320   These new locks use a tiered water sharing system that can more easily move

321   salt water up into the lake easier. Recent STRI salinity monitoring data supports

322   this inference (Steve Paton, pers. comm.). As deforestation in the lake catchment

323   has declined in the last two decades[17,24], it is likely that runoff patterns might not

324   have been playing such an important role in salt intrusions in comparison to the

325   locks.

326   If the predicted drying of the canal area due to global climate change is

327   correct[12], and global shipping traffic increases[28], it is likely that salinity will

328   continue to increase in the lake with major implications for drinking water[17]. The

329   ecological consequences of increased salinity has yet to be properly explored but

330   the recent increase we observe in *n*-alkane bacteria and both the MI and Pmar-

331   aq indices could be a warning that the halocline will render surface sediments

332   anoxic[51].

333   **Ecological responses to fish invasion:** The invasion of the apex predator

334   *Cichla* (peacock bass) into Gatun Lake in 1969 had a profound impact on the

335   native littoral planktonic fish community[25], which resonate today with

336   marginalized native populations[23]. Zaret and Paine[24] predicted that predation by

337   *Cichla* would also lead to cascading effects through the lake's food web,

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338 particularly on zooplankton (e.g. *Ceriodaphnia*), aquatic insects (e.g.

339 mosquitos/chironomids) and primary producers. Our results however do not

340 support the latter, as cladoceran ephippia only became apparent after the late

341 1990s, a period that instead coincides with increasing *n*-alkane algae

342 contribution. We found no evidence of increasing abundances or shifts in specific

343 functional groups (e.g. planktonic taxa) during or post-*Cichla* times that would

344 support evidence for a long-term cascading effect of predation down the food

345 web. Instead, evidence during this period points towards a bottom-up flow of

346 energy and nutrients coupled with asymmetric benthic–littoral production likely

347 associated with the development of macrophytes[52].

348

349 **Remarks and management options**

350 Our data help reconstruct the biotic and abiotic dynamics of the Chagres River

351 landscape over the last ~150 years, providing a unique insight into the natural

352 and anthropogenic impacts of impoundment on tropical rivers. Species invasions,

353 land-use changes and ship traffic have impacted the lake's ecosystem. Yet, our

354 multiple lines of evidence emphasize that the system still retains some of the

355 natural riverine functions on a decadal scale. It is however anticipated that

356 climate change will modify precipitation, evapotranspiration, and runoff in the

357 tropics[12]. Thus, increasing drier and wetter periods could fundamentally modify

358 the functioning of Gatun Lake. Drier periods will likely encourage the on-going

359 spread of *Hydrilla* and *Eichhornia* and increases in salinity via reduced dilution.

360 Wetter periods in turn, may stimulate sedimentation rates, nutrient inputs, salt

361   intrusions from storm surges and floating plant dominance. Many neotropical

362   impoundment projects have become highly eutrophic within a few decades,

363   rapidly overriding the importance of hydrology[8,10,45]. However, Gatun Lake stands

364   apart, by having high precipitation rates (annual mean > 2.200 mm), a unique

365   occurrence of large extensions of protected forest areas (e.g. Barro Colorado

366   Natural Monument and Soberanía) in the lake catchment, and large quantities of

367   water leaving the system (> 1 million m^3/year)[53] every time a ship pass through

368   the lake locks. These factors may provide some buffering, helping to reduce

369   shifts in runoff, water pollution and maintaining the natural hydrological balance

370   under a changing climate. Our study emphasizes that to preserve natural riverine

371   system functioning in tropical impoundment projects, management activities must

372   not only include better design and management of flow releases[3] but also the

373   understanding of key long-term natural ecosystem structural drivers such as river

374   flow, runoff patterns and water exchange rates.

375

376   **Materials and Methods**

377   **Study area**: Gatun Lake is situated in the valley of the Chagres River to the

378   south of Colón, Panama ($9^o11´N$ 79° $53`W$) (Fig. 1). It is an artificial large lake

379   (425 km^2) with a maximum water depth of 30 m and extensive areas of shallow

380   water (<5 m). The lake waters are well mixed throughout much of the dry (mid-

381   December to mid-April) and wet (mid-April to mid-December) season[53]. The lake

382   level is 26 m above sea level storing 5.2 km^3 of water[53]. It serves a dual purpose,

383   as a channel facilitating global trade and cross-oceanic travel, and as a

384   freshwater reservoir (Gatun Lake) providing a water supply to Panamá City and

385   other towns[17].

386   **Sampling**: A sediment core (87 cm long; LGAT1) was retrieved in 2013 from

387   near "La Represa" village in the southeast area of the lake (Fig. 1). The basin

388   offered an ideal coring site given that it lies outside the dredging zone of the

389   canal and is located in one of the most deforested areas of the lake watershed.

390   The core (LGAT1) was retrieved from a littoral area (9° 2'49.58"N, 79°50'6.33"W;

391   Fig. 1) at a water depth of approx. 1 m. We used a modified Livingstone Piston

392   Sampler of 4 cm diameter. Sediment samples were extruded in the field at 1 cm

393   intervals.

394   **Core dating:** Fourteen dried sediment samples from core LGAT1 were analyzed

395   for ^{210}Pb, ^{226}Ra, ^{137}Cs and ^{241}Am by direct gamma assay in the Environmental

396   Radiometric Facility at University College London, using ORTEC HPGe GWL

397   series well-type coaxial low background intrinsic germanium detector. The

398   sedimentary chronology was determined using the Constant Rate of Supply

399   model (CRS)[34].

400   **Geochemical elements**: Elemental composition on 1cm-thick discrete samples

401   was measured via X-Ray Fluorescence (XRF) on a handheld XRF analyzer

402   spectrometer, XMET 7500. Dry sediment samples were ground and

403   homogenized using a mortar and pestle. Three g of sediment sample were used

404   and covered with a Chemplex thin-film sample support. The handheld XRF

405   analyzer spectrometer was calibrated against certified material prior to analysis

406   and mean values for each element were determined from duplicate

407   measurements. Sampling resolution was at 2-cm intervals for the top 50 cm of

408   the core and at 4-cm for the remainder. A total of 34 samples were analyzed.

409   Calcium (Ca), potassium (K), iron (Fe), manganese (Mn), titanium (Ti), lead (Pb),

410   copper (Cu) and zinc (Zn) data were selected for this study. The elements Pb, Cu

411   and Zn were used as proxies for human-derived pollution events, Ca as a proxy

412   of marine influence, and K as a proxy of physical erosion[56]. We calculated

413   complementary index ratios to investigate changes in reduction conditions

414   (Fe/Mn) and detrital input (Ti/Ca.)[29].

415   **Biomarkers**: We analyzed *n*-alkanes composition in 10 sediment samples[30]. We

416   used *n*-alkanes C_{15}–C_{31}, as indicators of terrestrial plants, macrophytes, and

417   bacteria-algae[30]. Compounds were measured with a Shimazu GC-2010 gas

418   chromatograph interfaced to a Shimazu GCMS-QP2010 (see ref–58 for detailed

419   methodology).

420   Besides relative *n*-alkane contribution, we also calculated the terrigenous

421   aquatic ratio (TAR), which quantifies the *in situ* algal vs. terrestrial organic

422   matter[31] and the submerged/floating aquatic macrophyte inputs *vs*. emergent/

423   terrestrial plant input ratio (Pmar-aq)[31]. The Pmar-aq quantifies the non-emergent

424   aquatic macrophyte input to lake sediments relative to that from the emergent

425   aquatic and terrestrial plants[31]. Values of Pmar-aq <0.1 corresponds to terrestrial

426   plants, of 0.1-0.5 to emergent macrophytes and of >0.5-1 to submerged/floating

427   macrophytes[31].

428   The methane index (MI) that quantifies the relative contribution of

429   methanotrophic Euryarchaeota against ammonia oxidizing Thaumarchaeota was

430   also calculated[32]. MI values close to 1.0 indicate anaerobic environments,

431   whereas values close to zero indicate aerobic conditions[32]. To calculate the MI

432   index we measured glycerol dialkyl glycerol tetraethers (GDGTs) using an Agilent

433   1260 UHPLC coupled to a 6130 quadrupole MSD high performance liquid

434   chromatography-atmospheric pressure chemical ionization-mass spectrometry

435   (HPLC-APCI-MS).

436   **Plant and invertebrate macrofossil:** We analyzed 23 sediment samples for

437   plant and invertebrate remains. Between 2-4 g of dried sediment material per

438   sample were used and all samples were disaggregated in 10% potassium

439   hydroxide (KOH) before sieving. Macrophyte fossils were retrieved from the

440   residues of sieved core material (using mesh sizes of 355 µm and 125 µm)

441   following standard methods[54]. Plant macrofossil data were standardized as the

442   number of fossils per 100 cm^3 and identified by comparison with reference

443   material and by using relevant taxonomic keys[54]. Due to poor preservation of

444   *Hydrilla* remains, we estimated temporal abundances through its well-

445   documented historical records[23] and expressed in a 0-3 scale, where 0 is absent

446   and 3 highly abundant. All macrophyte taxa were then classed based on

447   preferred growth-type as submerged; anchored-floating; free-floating and

448   emergent. Invertebrate taxa were classed according to feeding behavior or

449   preferred habitat as: filter-feeders (bryozoans); macrophyte/detritus

20

450   (chironomids), shredders (Trichoptera larvae); benthic (chironomids), and grazers

451   (mollusks and cladocerans).

452   **Diatoms**: Twenty-three samples were analyzed for diatoms following standard

453   procedures by Battarbee et al.[55]. The diatom suspension was mounted on slides

454   with Naphrax® after the removal of carbonates by HCl and organic matter by

455   H_2O_2. Diatom taxonomy and ecology mainly followed Diatoms of North America

456   (https://diatoms.org). Diatom species were classed based on preferred habitat

457   type as planktonic, benthic, littoral and aerophilous, and as salinity-tolerant.

458   Benthic species were sub grouped into acidic-oligotrophic, eutrophic, and mobile

459   species. For each sediment sample, we counted a minimum of 400 valves.

460   **Historical environmental archives**: Historical data on water quality and hydro-

461   climatic variables are presented in Table 1. Long-term hydro-climatic, i.e.

462   precipitation (three and five years average) and river annual discharge data, from

463   1930 to 2013 were obtained from the monitoring division of STRI (Steve Paton,

464   pers. comm.) and the Panama Canal Authority (23). Long-term physical and

465   chemical variables from 1969-2013 (pH, conductivity, dissolved oxygen [DO],

466   total nitrogen [TN], total phosphorous [TP], chlorophyll a [Chl-a] and secchi

467   depth) were obtained from literature[56, 57] and from the ACP Water Quality

468   Monitoring Division reports[57]. For the ACP data we used the average annual

469   values of each selected variable recorded at two sampling stations (Laguna Alta–

470   LAT and Toma de Agua Represa–TAR) located near our coring site area.

471   **Data analysis**: A stratigraphic plots of the study biological functional groups were

472   achieved using the ''Rioja'' Package in R[58]. Major zones of change were

473   achieved through clustering analysis. To summarize and visualize the most

474   important gradients of temporal change in the different biological functional

475   groups, environmental variables, and historical data we used multiple factor

476   analysis (MFA)[33] in R (*Factoextra* and *FactoMiner* packages in R). This analysis

477   is a multivariate technique in which individuals (core depths) are described by

478   several sets of variables (quantitative in our case) structured into groups. The

479   analysis takes into account the contribution of all groups of variables to define the

480   distance between core depth samples. Variables within a group were normalized

481   by applying a weight equal to the inverse of the first eigenvalue of the analysis of

482   the group[33].

483   We ran two separate MFA analyses according to data availability. The first

484   analysis focused on the historical hydro-climatic variables (river flow and

485   precipitation; n=15 data points) and all paleoecological data spanning since pre-

486   canal times and clustered into five major groups: macrophytes (submerged,

487   anchored-floating, free-floating and emergent; n=23 data points for each group),

488   diatoms (littoral, benthic, planktonic, salinity-tolerant, and aerophil; n=23 data

489   points for each group), invertebrates (filter-feeders, shredders, benthic,

490   macrophyte/detritus and grazers; n=23 data points for each group), geochemical

491   elements and ratios (n=23 data points for each element or ratio), and biomarkers;

492   (n=10 data points for each parameter). Missing information at given time-periods

493   for biomarkers (10 samples analyzed) and hydro-climatic data (spanning from

22

494   1930-2013), was replaced in the MFA by the mean of each variable[33]. The

495   second MFA focused on the time-period 1969-2013 from which historical water

496   quality data (pH, conductivity, phosphorous, chlorophyll-a, and secchi depths;

497   n=13 data points) was available (Table 1). For this analysis we included the

498   historical hydro-climatic data (n=13 data points) and the paleoecological groups

499   data (n=13 data points for each biological and geoechemical group), excepting

500   biomarkers (too limited number of samples), from analysis 1. To quantify the

501   contribution of each variable in the MFA maps we used the argument col.var =

502   "contrib" (*Factoextra* package, R). Prior to MFAs we run exploratory principal

503   component analyses (PCA) to detect uninformative or redundant historical water

504   quality variables (see Fig. S4 for details). As a first step we discarded nitrates

505   due to low variation (Fig. S4b) and subsequently, we discarded phosphates and

506   chl-a as these two variables showed a strong correlation with DO at the water

507   surface (positive) and with DO in the water column (negative) respectively (Fig.

508   S4c). We left both DO measurements instead of nitrates and chl-a due to a better

509   historical record (see Table 1).

510   **Data Availability:** all relevant data are available from the authors and the data

511   will be deposit in a public repository.

512

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23

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528   Hanyang, South Korea. The collection and exporting of sediment material was

529   assessed under the ARAP collecting permit No. 25.

530   **Author Contributions:** JS designed the study and collected the sediment

531   material. JS produced and analyzed the plant and invertebrate macrofossil data,

532   CH and JC produced and analyzed the biomarker data, and MV produced and

533   analyzed the diatom data. NR and HY produced and analyzed the

534   lithostratigraphic and radiometric data. JS wrote the first manuscript and all

535   authors contributed substantially for the final version.

536   **Competing interests:** The authors declare no competing financial interests.

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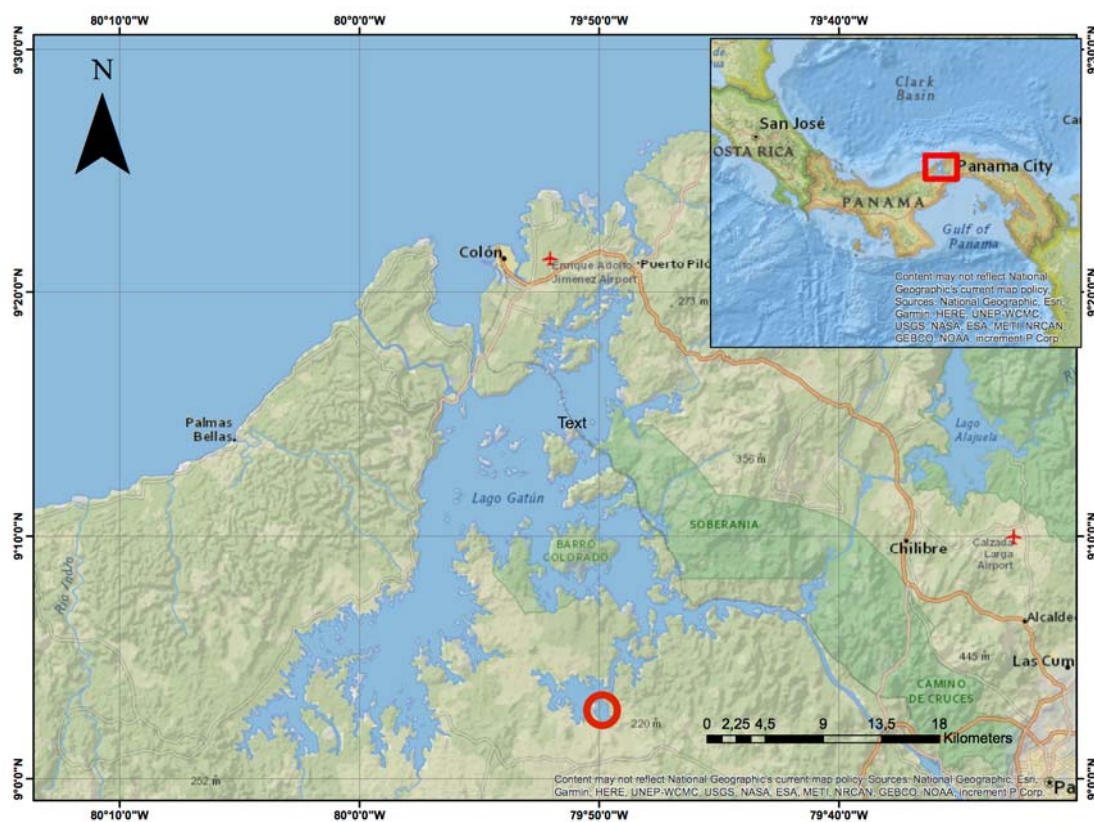
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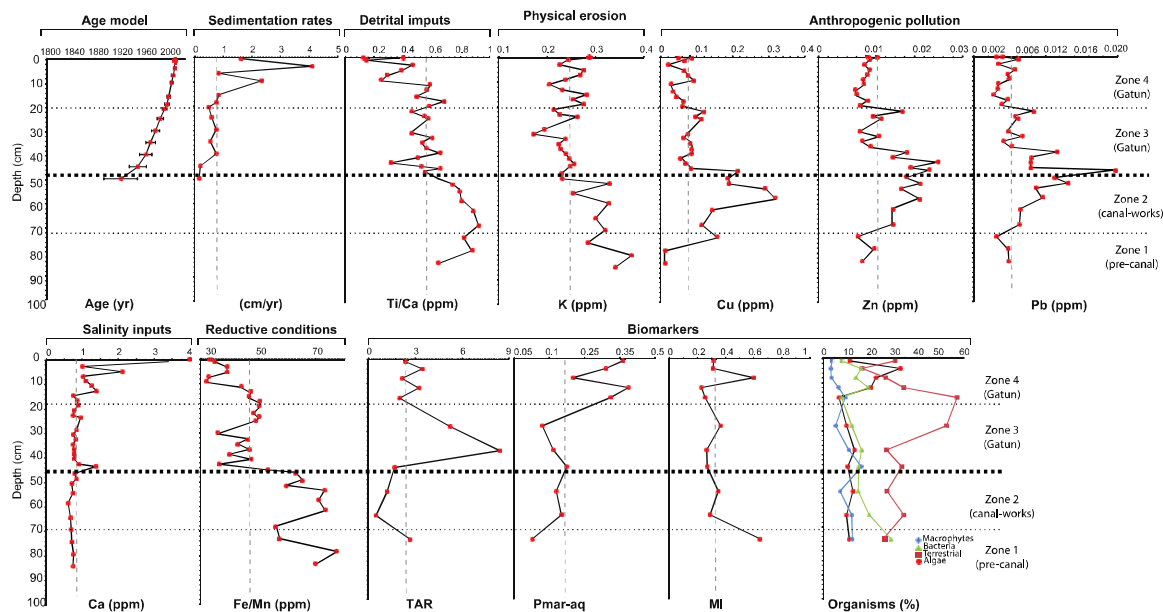
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710   **Figures and Tables**

711

712   **Figure 1. Map of the River Chagres watershed**. The artificial Gatun and

713   Alajuela lakes and the connecting River Chagres are indicated in blue. A red

714   circle shows the coring location of LGAT1 core. Natural protected areas are

715   shown in dark-green.

716

717

718

Figure 2. Sedimentary profile of the ^{210}Pb age model (dates and ages and

standard deviations are presented), sedimentation rates, selected

geochemical elements and ratios, and biomarkers indices in LGAT1

sedimentary core. Terrigenous aquatic ratio–TAR; Methane Index –MI; the

submerged/floating aquatic macrophyte inputs vs. emergent/ terrestrial plant

input ratio–Pmar-aq. Major temporal zones of change determined by clustering

analysis, corresponding to Zone 1 c. pre-1870, Zone 2 c.1870-1914, Zone 3

1923-1990, and Zone 4 1991-2013. A vertical grey dotted line indicates the mean

value of each parameter.

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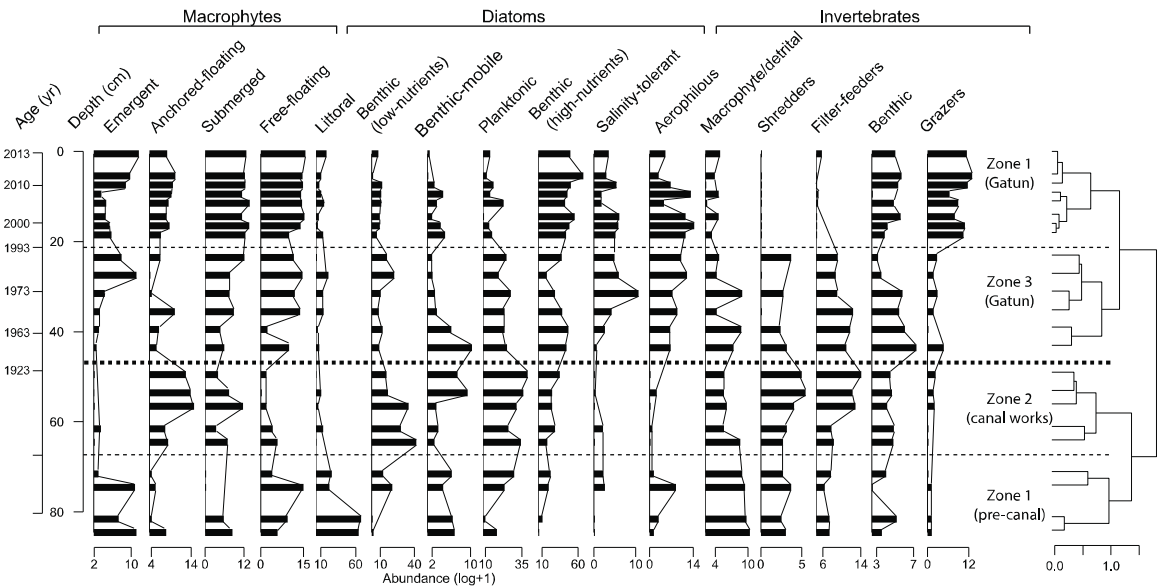
Figure 3. Sedimentary profile of the study biological functional groups in LGAT1 sedimentary core. Major temporal zones of change determined by clustering analysis are shown by dotted lines, corresponding to Zone1 *c.* pre-1870, Zone 2 *c.*1870-1914, Zone 3 1923-1990, and Zone 4 1991-2013.
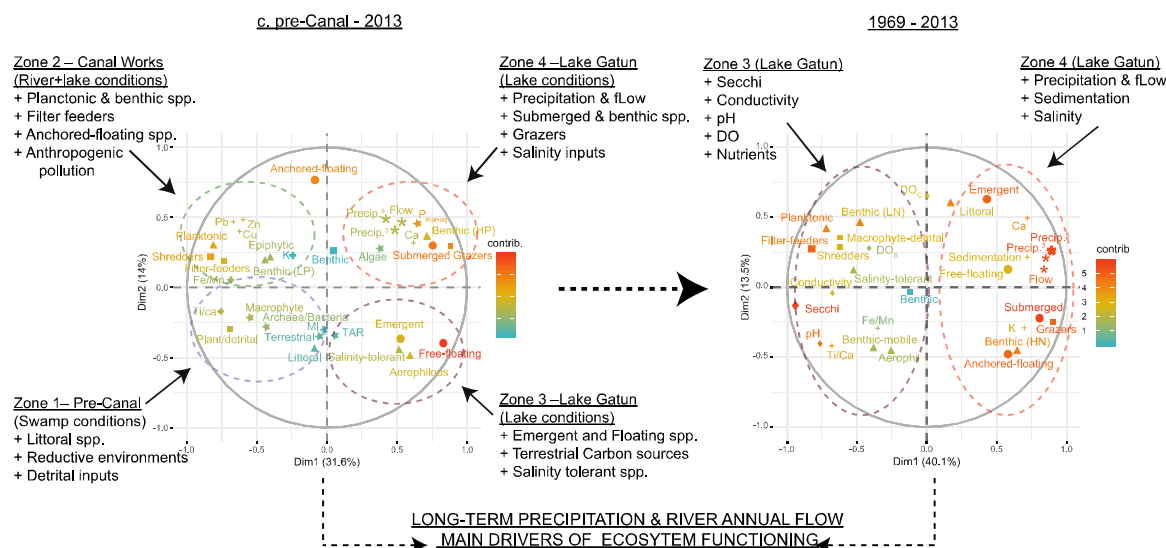
Figure 4. Multiple factor analysis (MFA) results for the time periods *c.* pre-canal-2013 and 1969-2013. The analysis was run on hydro-climatic data (precipitation and river flow–hash), biological data (macrophytes–circle, diatoms–triangle, invertebrates–square), geochemical data (cross), biomarker data (star) and water quality data (period 1969-2013–diamond). The contribution of each variable in the analysis is indicated according to a color scale. Low nutrients (LN), high nutrients (HN), three years average precipitation data (Precip.[3]), five ars average precipitation data (Precip.[5]), river annual flow (Flow). Sediments samples within each major temporal zone of compositional change are encircled according to Zone 1 c. pre-1870, Zone 2 c.1870-1914, Zone 3 1923-1990, and Zone 4 1991-2013.

748 **Table 1. Historical environmental records of Lake Gatun.** Historical data on

749 three years average precipitation data (Precip.[3]), five years average precipitation

750 data (Precip.[5]), and annual river flow in Gatun Lake for the periods 1930-2013,

751 and historical data on nitrates (NO_3), phosphates (PO_4), secchi depth,

752 conductivity, pH, dissolved oxygen at the water surface (DO_s) and at the water

753 column ($DO_c < 1m$ depth), and chlorophyll a (Chl-a) for the period 1969-2013.

Time (yrs.)	Precip. 5 (mm)	Precip. 3 (mm)	Annual flow (m3/s)	pH	DO_S (mg/L)	DO_C (mg/L)	NO_3 (mg/L)	PO_4 (mg/L)	Cond. (µS/cm)	Chl-a (µl/L)	Secchi (cm)
2013†	2964	3381	41	6.41	6.44	5.25	0.04	0.01	42.34	2.31	146
2011†	2841	2778	38	6.35	6.60	5.12	0.07	0.01	47.86	3.22	150
2009†	2664	2640	31	6.50	6.48	5.01	0.03	0.00	49.38	4.18	167
2008†	2769	2741	31	6.59	6.28	4.23	0.03	0.01	55.62	5.09	177
2006†	2569	2685	29	6.56	6.25	3.51	0.04	0.02	55.62	2.89	212
2005†	2620	2689	27	6.53	6.23	2.52	0.03	0.01	45.21	4.72	192
2003†	2593	2802	30	7.13	6.61	2.90	0.03	0.02	50.33		
2000†	2688	2644	37	6.76	6.48	3.02	0.05		49.92		
1993§	2589	2669	28	7.39	6.22	1.94		0.04	54.00		
1989§	2517	2524	26		8.66	4.94	0.03	0.04	44.88	2.05	393
1978*	2508	2332	25	7.20	7.78		0.06		90.00	4.10	700
1972*	2331	2371	26	7.56	8.00		0.05	0.02	98.00		
1969*	2497	2444	27	7.21	5.59	5.12					530
1955	2663	2859	29								
1930	2679	2488	27								

754 *ref-53; §ref-56; † ref-57; precipitation data were obtained from (Steve Paton,

755 pers. comm.) and annual flow data from ref–23.

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