AN ASSESSMENT OF THE EFFECT OF THE CLOSED SEASONS ON ABUNDANCE OF THE SILVER CYPRINID, RASTRINEOBOLA ARGENTEA, IN LAKE VICTORIA

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ABSTRACT

Lake Victoria is currently dominated by the introduced Nile perch, \textit{(Lates niloticus)}, Nile tilapia \textit{(Oreochromis niloticus)} and the endemic cyprinid \textit{Rastrineobola argentea}. \textit{R. argentea} is second only to Nile perch in terms of commercial importance. With the recent declining trends in the catches of Nile perch and most other fish species in the lake, interest has gradually been shifting to the exploitation of \textit{R. argentea}. From time to time Lake Victoria partner states have been implementing management measures aimed at ensuring sustainable utilization of the fisheries. One such measure was to implement a yearly closed season for fishing of \textit{R. argentea} for four months period, starting in 2001. However this ban was only implemented by Kenya. The objective of this study is to assess the effect of the closed seasons in the Kenyan part of the lake on the abundance of \textit{R. argentea}. Catch, CPUE and biomass data were analysed to establish trends between 1999 and 2011, for the Kenyan and Ugandan portions as well as the entire lake. The results indicated an increased biomass not only on the Kenyan side, where closed seasons are implemented, but also in the entire lake. This indicates that factors other than fishing, such as environmental and ecological changes play a crucial role in the fluctuations of \textit{R. argentea} abundance in the lake. This study highlights the need for more information on the biology of \textit{R. argentea} in order to develop management strategies. Furthermore, since this is a short-lived species, a total ban should be replaced with a more focused restriction targeting critical breeding areas and nursery grounds in cooperation with fishers.

This paper should be cited as:
http://www.unuftp.is/static/fellows/document/robert12prf.pdf
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1. INTRODUCTION

1.1. Background information

Lake Victoria is the world’s second largest fresh water body, after U.S.A’s Lake Superior, (Prado et al. 1991). It is one of the African Great Lakes, covering approximately 68 000 km². The lake is shared by Kenya (6% by area), Uganda (43%) and Tanzania (51%) (Figure 1). It has a mean depth of 40 m, maximum depth of 84 m, shoreline of 3 450 km, a water retention time of 140 years and a catchment area of 193 000 km², which extends into Rwanda and Burundi (Cowx et al. 2003).

The population in the Lake Victoria basin that depend directly or indirectly on the lake’s resources is approximately 30 million. Fisheries contribute around 3% to the gross domestic product of the riparian states and they are major sources of income, food, employment and foreign exchange earnings. Lake Victoria is the most important source of affordable animal protein, in the form of fish, in East Africa. It is also the most important source of freshwater fish on the African continent. The fishery is diverse, highly dispersed, and fragmented with about 1 500 landing sites and more than 120 000 fishers. The lake is also important in conservation terms because of the great diversity of endemic fish species (Cowx et al. 2003).

![Figure 1: Map of Lake Victoria showing the international boundaries (Cowx et al. 2003).](image)

The Lake Victoria ecosystem once hosted a diverse fish community dominated by hundreds of fish species. Today this fish assemblage is highly altered by the effects of anthropogenic activities, with at least half of the indigenous species either extinct or very rare. The fish community in the lake has changed radically to a current dominance by the introduced Nile perch, the endemic cyprinid R. argentea and the introduced Nile tilapia. A few relic populations of indigenous fish species are also present (Ogutu-Ohwayo 1990 a). The intriguing species dynamics in Lake Victoria was observed by Witte et al. (1992), citing a
fourfold increase in the biomass of a pelagic cyprinid, *R. argentea*; a rapid increase that was attributed then to the disappearance of most of the zooplanktivorous haplochromines which were thought to compete with *R. argentea* for food. The group of haplochromines consists of more than 300 species inhabiting almost all types of habitats and trophic niches. They were known to co-exist in such great numbers of closely related species in relatively small areas as noted by Kigongo (2002).

Over the past decades, Lake Victoria has undergone dramatic ecological changes associated with physical, chemical and biological processes (Witte *et al*. 1992, Lung’ayia *et al*. 2000, Mugidde *et al*. 2005). The introduction of new species, degrading environment and ever increasing fishing effort have led to a decline in fish catches (Cowx *et al*. 2003). Changes in the lake’s biodiversity, threaten the sustenance of the lake fishery upon which millions depend on for their livelihoods (Njiru *et al*. 2008). According to Gichuki *et al*. (2010), secchi disc visibility has decreased by about 75% in the last four decades. Oxycline depth decreased by 50% indicating that a large body of the deeper waters cannot support life as it did before. Primary productivity has doubled over the period and there has been an 8-10 fold increase in algal biomass. Changes in ecological interactions due to species introduction, predation accelerated by the environmental changes and increased fishing pressure have disrupted the ecosystem dynamics of Lake Victoria and pose serious uncertainties on the lakes future stability and sustainability of the fisheries resources (Gichuki *et al*. 2010).

*R. argentea* (Figure 2), the silver cyprinid, is a species of ray-finned fish in the Cyprinidae family, and is the only member of the genus *Rastrineobola* and is endemic to Lake Victoria. It’s local names are Omena in Kenya, dagaa in Tanzania and mukene in Uganda. It is widely distributed throughout the pelagic zone of Lake Victoria, with a variation in the size distribution between different locations around the lake (Marshall & Cowx, 2003). According to Kigongo (2002) the highest abundance of *R. argentea* is found at shallower and near the bottom zone during the day (5 to 9m from the bottom), and is homogeneously distributed throughout the whole water column at dusk. During the night the highest abundance occurs near the surface, between 2 to 4m, and at dawn a homogeneous distribution over the whole water column can be observed again.

Figure 2: *R. argentea* from Lake Victoria.
*R. argentea* is more or less an obligate zooplantivore and as such has a crucial role in the ecosystem of the lake as a link between the zooplankton and the higher predators such as Nile perch (Figure 3).

Figure 3: Food chain of some of the main species affecting the *R. argentea* ecology, based on published feeding studies discussed in the text.

*R. argentea* feeds on a wide range of zooplankton taxa in the lake especially copepod and cladocera. Wanink (1998) and Wandera (1992) reported the diet of *R. argentea* to predominantly consist of copepods, with relatively little contribution from cladocerans and rotifers. Studies done in much shallower areas found *R. argentea* to select cladocerans as their prey of choice but copepods were also taken. Other studies using stable isotopes showed incorporation of other prey items into their diet including insects (Ojwang *et al.*
R. argentea compete to some extent with the zooplanktivorous haplochromines, for the same food. In the 1970s, haplochromine cichlids used to be the main prey of the introduced Nile perch in Lake Victoria. After depletion of the haplochromine stocks at the end of the 1980s, Nile perch shifted to the shrimp, Caridina nilotica, and to a lesser degree to its own young and R. argentea. A dramatic increase of the Nile perch in the 1980s (Ogutu-Ohwayo 1990b, Goudswaard et al. 2008) coincided with the disappearance of about 40% of the almost 500 endemic haplochromine cichlid species (Witte et al. 1992). Concomitant with the disappearance of haplochromine species, increases of R. argentea and of the shrimp C. nilotica were noted (Wanink 1999). About a decade later Nile perch yields declined due to intense fishing and resurgence of some haplochromine species was observed in the lake (Seehausen et al. 1997, Balirwa et al. 2003, Witte et al. 2007).

R. argentea is one of the most important commercial fisheries of Lake Victoria. In the early 1990s the fishery contributed between 30-40% of the total catch of Lake Victoria (Othina and Osewe-Odera 1997). In 2011, the catch was 54% of the total weight of fish landed on the Kenyan side of the lake (GoK 2011).

Generally, R. argentea is harvested from V-shaped bottom Sesse boats, pointed at both ends and powered by sails and/or paddles (Figure 4), or rarely motorised Sesse boats flat at one end. The total numbers of boats, whose length measures 9 metres on average, are approximately 3000 in Kenya, 2700 in Uganda and 8000 in Tanzania (LVFO 2010). Fishing is performed with small seine nets (commonly called mosquito seines) and attraction lamps (paraffin or solar).

Figure 4: Sesse boat (pointed at both ends) on the shore of Lake Victoria, used for fishing R. argentea.

This technology defines the monthly pattern of harvesting the fish in most parts of the lake. Peak harvesting occurs during dark nights, when the effect of artificial attraction to light is maximised. In the shallower waters of the lake, however, the low depths and high turbidity reduce the benefits of using lamps. Therefore; fishing in the shallower waters takes place without any lamps for attraction. Because of the lunar cycles, deep water fishing of R. argentea usually only takes place for 18-24 days in a month. Most R. argentea fishers use the remaining days of the month to mend and prepare their gear or attend to other non-fishery engagements. It has sometimes been argued that this natural one-week ‘R. argentea closure’ provides a natural replenishment period for this fish (GoK 2004).

Price trend analysis of R. argentea in Kenya (adjusted for inflationary changes) indicates that the prices tripled between 1990 and 2000. This is attributable to an increase in demand
for the fish, particularly due to the expansion in the fishmeal processing industry, which started using *R. argentea* in the mid-1980s (Bokea and Ikiara 2000, Abila and Jansen 1997). About 50% of all landings are utilized as fishmeal in the animal feed industry (Baer 2001).

### 1.2. Problem statement

A closed period for fishing *R. argentea* in the Kenyan waters was established as management measure in 2001 through a Gazette notice (GoK 2001). By this notice, it is illegal to fish and display for sale *R. argentea* between 1st April and 31st July each year. This measure was taken after an outcry by the fishermen that the catches per unit of effort for this species were going down, demanding action from the governments sharing the lake. A baseline survey on *R. argentea* breeding areas and seasons was carried out and its findings, coupled with indigenous knowledge on Lake Victoria fisheries informed the decision by the Ministry of Fisheries to implement closed seasons for the fishing of *R. argentea*. The decision was also supported with scientific information obtained from earlier studies done in Lake Victoria when alarm was raised concerning the decreasing catches of the species (Manyala *et al.* 2001).

Closed season for the *R. argentea* has never been implemented in the Ugandan or Tanzanian parts of the lake. Research carried out so far shows biomass of the species has been increasing and the catch per unit of effort has been stable during the last three years (GoK 2011). There have been complaints by stakeholders in the fisheries sector who question the necessity of the closed season especially as it is only implemented by one of the three fishing nations. Therefore the question to be answered is whether it is necessary to continue implementing seasonal closures in the Kenyan part of the lake.

### 1.3. Objectives of the study

The objective of the study was to assess the effect of closed seasons on the abundance of *R. argentea* in Lake Victoria. More specifically the study;

1. Reviewed trends in the biomass of *R. argentea* in the Kenyan, Ugandan and Tanzanian portions of Lake Victoria, before and after introduction of closed seasons in the Kenyan portion of the lake.
2. Compared the biomass, yield and exploitation ratio of *R. argentea* in the Kenyan and Ugandan portions of Lake Victoria before and after introduction of closed seasons in Kenyan portion of the lake
3. Explored whether the environmental changes in the lake could have had an effect on the abundance of *R. argentea*
4. Makes recommendations based on the results of the study.
2. MATERIALS AND METHODS

2.1. Data sources

Biomass estimates of *R. argentea* based on acoustic surveys in Kenyan, Ugandan and Tanzanian portion of the lake, collected twice a year from 1999 to 2011, were used as an input in a dynamic production model for calculation of trends in biomass in individual countries and the entire lake (Table 1). A team collected the acoustic data from the Fisheries Research Institutes of the three riparian countries. Official landing statistics of Kenya and Uganda were used to assess the total annual catch in the commercial light fishery for *R. argentea* from the two countries from 1997-2011 (Table 2). These data together with effort data gathered in frame surveys were used to obtain the catch per unit of effort (CPUE) for these two countries. The landings data were collected by the respective ministries in-charge of fisheries activities in the partner states while the effort data was collected by the Lake Victoria Fisheries Organization (LVFO), Frame Survey Regional Working Group. Landings data of *R. argentea* for Tanzania were found to be inconsistent and were therefore not used in this study.

Table 1: Biomass (metric tons) of *R. argentea* in Lake Victoria based on acoustic surveys performed February and August from 1999 to 2011.

<table>
<thead>
<tr>
<th>Year</th>
<th>February</th>
<th></th>
<th></th>
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<th>August</th>
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<td>Uganda</td>
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<td>Uganda</td>
<td>Kenya</td>
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<td></td>
<td></td>
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<td></td>
<td>Lake</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td>46 970</td>
<td>25 098</td>
<td>227 723</td>
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<tr>
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<td>345 240</td>
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<td>2001</td>
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<td>51 464</td>
<td>806 758</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td>582 440</td>
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<td></td>
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<tr>
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<td>2004</td>
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<td>2005</td>
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<td>78 551</td>
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<td>918 653</td>
<td></td>
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</table>
Table 2: Kenya and Uganda catches, effort and CPUE for *R. argentea* in Lake Victoria from 1997-2011.

<table>
<thead>
<tr>
<th>Year</th>
<th>Uganda catches (Metric tons)</th>
<th>Uganda Effort No. of Boats</th>
<th>Uganda CPUE (Tons/boat/yr)</th>
<th>Kenya Catches (Metric tons)</th>
<th>Kenya Effort No. of Boats</th>
<th>Kenya CPUE (Tons/boat/yr)</th>
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<td>2845</td>
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Environmental data on: dissolved oxygen, chlorophyll, secchi-depth, pH-value and temperature in the Nyanza gulf, from 1997 to 2011, were collected by the Kenyan Marine and Fisheries Research Institute, during the day (average taken for morning and evening readings) at an average depth of 7 metres (Table 3). These data were compared to the estimated biomass for the Kenya portion of the lake generated by the dynamic production model.

### 2.2. Data analysis

#### Dynamic production model.

Dynamic biomass models also known as surplus production models are often used by fisheries scientists in cases of limited data. They require less data and are appropriate for limited datasets, for stock assessment. They are based on the principle of time series fitting using maximum likelihood or non-linear least squares minimization. Estimates of the initial biomass and model parameters are generated and catch data are then fitted in the production model to predict the whole biomass series. A measure of difference between observed and predicted values is identified and then the differences are minimized to fit the models (Hilborn and Walters 1992, Prager 1994, Punt and Hilborn 1996).

The statistical program R was used to model biomass, recruitment, yield, exploitation ratio and Index of biomass of *R. argentea* between 1999 and 2011, for Kenya and Uganda
portions of the lake. The input into the model was catch, CPUE and biomass data for the two countries (Tables 1 and 2). The outputs showed trends of observed and predicted biomass, recruitment, yield, exploitation ratios and Index of abundance for Kenya and Ugandan waters.

Table 3: Environmental parameters and biomass of *R. argentea* in the Lake Victoria's Nyanza gulf, Kenya, Biomass is based on the results of the dynamic production model.

<table>
<thead>
<tr>
<th>Year</th>
<th>Biomass (metric tons)</th>
<th>Secchi-depth (metres)</th>
<th>Dissolved oxygen (ppm)</th>
<th>Temperature (°C)</th>
<th>pH</th>
<th>Chlorophyll (Mg/l⁻¹)</th>
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<td>6.13</td>
<td>26.8</td>
<td>8.45</td>
<td>-</td>
</tr>
<tr>
<td>2006</td>
<td>360 321</td>
<td>0.71</td>
<td>5.74</td>
<td>26.8</td>
<td>8.56</td>
<td>14.8</td>
</tr>
<tr>
<td>2007</td>
<td>361 467</td>
<td>0.69</td>
<td>5.36</td>
<td>26.9</td>
<td>8.59</td>
<td>15.7</td>
</tr>
<tr>
<td>2008</td>
<td>332 610</td>
<td>0.66</td>
<td>4.81</td>
<td>26.9</td>
<td>8.64</td>
<td>16.8</td>
</tr>
<tr>
<td>2009</td>
<td>325 940</td>
<td>0.51</td>
<td>3.71</td>
<td>26.9</td>
<td>8.84</td>
<td>12.7</td>
</tr>
<tr>
<td>2010</td>
<td>343 744</td>
<td>0.45</td>
<td>2.98</td>
<td>26.9</td>
<td>9.03</td>
<td>-</td>
</tr>
<tr>
<td>2011</td>
<td>332 681</td>
<td>0.25</td>
<td>2.05</td>
<td>26.9</td>
<td>9.11</td>
<td>-</td>
</tr>
</tbody>
</table>

The model incorporates, stock size, recruitment, natural mortality and weighting correction factors which are explained below.

- Stock size

The estimation of *R. argentea* biomass of each year was based on a model of population number:

\[ N_{y+1} = N_y + R_y - C_y \]

Where \( R_y \) is the recruitment in year \( y \), \( N_y \) is the number that survive in year \( y \), while \( C_y \) is the catch in the year. Biomass was then calculated by:

\[ B_y = \sum (N_{ay} \times w_a) \]

Where \( N_{ay} \) is the number of a particular age that survive during the year and \( w_a \) is average weight.

- Recruitment
The spawning stock per recruit in the fishery was estimated by using the Beverton and Holt equation:

\[ R = \frac{as}{1 + \frac{s}{k}} \]

Where \( R \) = recruitment, \( s \) = spawning stock, \( a \) = coefficient used as a multiplier for prospective recruitment, \( k \) = size of the spawning stock that produces half maximum recruitment.

- Natural mortality

Natural mortality, \( M \), was also required as one of the inputs in the model. Since there was no sufficient data to compute, it was assumed to be 0.9. This value was acquired from literature of (Manyala et al., 1995), who obtained it by computing from the empirical formula of Pauly (1980). Estimates of \( L_\infty \) and \( K \) were used as inputs for a mean annual temperature of 22°C for Lake Victoria.

\[ \log M = -0.0152 - \log L_\infty + 0.6543 \log K + 0.0643 \log T \]

- Fitting the dynamic production model

The model was fitted by first using initial parameters stated above and followed by defining the functions in R, which utilizes a non-linear minimization. The model was evaluated by comparing the model output to the data and this is done by computing the sums of squares between each data set and the fitted values they correspond to (Stefansson 2007).

Coefficients of variation, CVs for different parameters were used as weighting factors assigned to the sums of squares which were then minimized in order to estimate the parameters in the model. Assuming that all terms are log transformed data. Each term is then of the form:

\[ \lambda \sum (\ln(x_j) - \ln(\bar{x}_j))^2 \]

where \( x_j \)'s were annual landings, biomass index, recruitment factor, fishing mortality and \( \lambda \) is the weighting factor.

Statistically, the “correct” weighting factor is the inverse of the variance, \( \lambda = 1/\sigma_{\ln(x)}^2 \).

But in the case of a low dispersion, the standard deviations of the log-transformed quantities and the coefficient of variation of the original numbers are similar. Thus, CV(x) is used as \( \sigma_{\ln(x)} \).

The CV for catch, CV(Y) was assumed to equal 0.01 since catch data are quite precise. The CV(Y) used here thus assumes that 95% of annual catch estimates lie within 20% (two standard deviations) of their true values (we assume here again that the errors are symmetrical). The coefficient of variation for biomass index, CV(I), was set to 0.01, coefficient of variation of fishing mortality, CV(F), was similarly set at 0.01 and coefficient of variation of recruitment, CV(R), was set to 10000000. During the iteration process, these values were allowed to deviate freely until better CVs were obtained to fit the model. The model is fitted by first using the initial parameters stated above, followed by defining the functions in R, which utilizes a non-linear minimization.
The model was evaluated by comparing the model output to the data and this is done by computing the sums of squares (SSE) between each data set and the fitted values they correspond to. Coefficients of variation, CVs for different parameters are used as weighting factors assigned to the sums of squares which will then be minimized in order to estimate the parameters in the model (Stefansson 2007).

The statistical program R was also used to run a linear regression model to determine if there was a significant relationship between the biomass of *R. argentea* in the Kenya part of the lake and each of the environmental parameters.

Excel program was used to draw scatterplots for visual comparisons of the estimated biomass in the Kenyan part of Lake Victoria (outputs from the dynamic production model) and data on temperature, pH, dissolved oxygen and secchi-depth in 1997-2011.

3. RESULTS

3.1 Review of the status of biomass of *R. argentea* in Lake Victoria

The information covers the period from 1999-2011, no data were collected in 2003 and 2004. In addition no acoustic surveys were carried out in August 2002 and 2010 and February 2005 and 2010 (Table 1). However when the acoustic estimates for the whole lake were plotted (august-survey), it shows a steady increase in the biomass from 1999-2007 and a rather stable period from 2007-2011 (Figure 5).

![Figure 5: Trend of biomass in entire Lake Victoria estimated in acoustic survey in August, 1999-2011.](image-url)
3.2 Biomass, exploitation ratio, Index of abundance, Yield and Recruitment of *R. argentea* in the Kenya and Uganda portions from 1997 to 2011

The outputs from the dynamic production model for the Kenyan part of Lake Victoria are shown in Figure 6. Figures 6(a) and 6(b) show annual catch and biomass index, with small circles for actual data and lines fitted by the model. Figures 6c, 6d, and 6e are recruitment, biomass and exploitation ratio respectively.

The yield was rather stable from 1997 to 2004, followed by a sharp increase in 2005 and a stable period of high yield after that. The same patterns were evident for the biomass index, the recruitment pattern and the calculated biomass. The exploitation has fluctuated over the period.

The results from the dynamic production model for the Uganda part of Lake Victoria are shown in Figure 7. According to the model outputs, the yield in the Ugandan portion of the Lake were rather stable from 1998 to 2003 but have been rising steadily since. The same patterns were evident for the biomass index, the recruitment pattern and the calculated biomass. The exploitation ratio (Figure 7e) has been fluctuating through the period, without a clear trend.

Values of CPUE in the *R. argentea* fisheries in the Ugandan and Kenyan part of the lake from 1997-2011 are rather stable and the fluctuations similar in the two regions (Table 2 and Figure 8). However the CPUE did not show any correlation with biomass and is not useable as a less expensive substitute for the biomass survey. The CPUE from the fishing boats was therefore not used in further analysis.
3.3 Relationship between environmental changes in Lake Victoria on the abundance of *R. argentea*

There was a gradual increase in pH from 1997 to 2011 (Figure 9a), while the biomass of *R. argentea* dropped from 1997 to 2000, increased gradually until 2007 and has been relatively stable since then. Figure 9b indicates a positive correlation between biomass and pH in the lake. Figure 10a shows a steady drop in secchi disc visibility and biomass while figure 10b indicates negative correlation between the two parameters. The temperature gradually increased from 1997 to 2008 and thereafter remained more or less steady (Figure 11a). Figure 11b indicates a positive relationship between the biomass and the temperature. Figure 12a shows a gradual decrease in dissolved oxygen from 1997 to 2011 and figure 12b indicates a negative relationship between dissolved oxygen and biomass of *R. argentea* in the Kenyan part of Lake Victoria.
Figure 7: Yield (Tons) (a), Index of biomass (b), recruitment (Numbers in millions) (c), trends of biomass (Tons) (d) and, the exploitation ratio (e) of *R. argentea* in the Ugandan part of Lake Victoria, vertical line shows when the seasonal ban was first implemented on the Kenyan part of the lake.

Figure 8: CPUE for the fisheries of *R. argentea* in the Ugandan and Kenyan part of Lake Victoria from 1997-2011.
Figure 9: Trends of biomass and pH (a) and the relationship between biomass of *R. argentea* and pH (b), in the Lake Victoria's Nyanza gulf, Kenya from 1997-2011.
Figure 10: Trends of biomass of *R. argentea* and Secchi-depth (a) and the relationship between biomass and secchi-depth (b) in the Lake Victoria's Nyanza gulf, Kenya from 1997-2011.
Figure 11: Trends of biomass of *R. argentea* and Temperature (a) and the relationship between biomass and temperature (b) in the Lake Victoria's Nyanza gulf, Kenya from 1997-2011.
Figure 12: Trends of biomass of *R. argentea* and dissolved oxygen (a) and the relationship between biomass and dissolved oxygen (b), in Lake Victoria's Nyanza gulf, Kenya from 1997-2011.
Outputs of P-values for environmental parameters from the R-statistical Program

When tested whether there was a significant correlation between the environmental parameters and the biomass, the biomass was significantly correlated to all parameters except the amount of chlorophyll (a) (Table 4).

Table 4: Results of linear regressions between the biomass of *R. argentea* and environmental parameters in the Lake Victoria’s Nyanza gulf, Kenya from 1997-2011, significant codes: 0'***'0.001'**'0.01'*'0.05.

<table>
<thead>
<tr>
<th>Environmental Parameter</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature</td>
<td>0.001423**</td>
</tr>
<tr>
<td>Chlorophyll a</td>
<td>0.09573</td>
</tr>
<tr>
<td>PH</td>
<td>8.913e-06***</td>
</tr>
<tr>
<td>DO</td>
<td>0.001557**</td>
</tr>
<tr>
<td>Secci disc</td>
<td>0.001484**</td>
</tr>
</tbody>
</table>

4. DISCUSSION

This study reviewed the trend of biomass of *R. argentea* in the entire Lake Victoria for the period before and after the implementation of closed fishing-seasons in the Kenyan part of the lake, which commenced in 2001. The biomass of *R. argentea* in the entire Lake Victoria was low between 1999 and 2001 compared to later values (Figure 3). This low level might be a result of ecological and environmental changes and/or possibly of increased fishing effort for the then newly commercialized species. Gichuki *et al.* (2010) and Njiru *et al.* (2008) argued that changes in ecological interactions due to species introduction, predation accelerated by the environmental changes and increased fishing pressure continue to cause complicated ecosystem dynamics in Lake Victoria and pose uncertainties on the lakes future stability and sustainability of the fisheries resources.

Then there is a major increase in the biomass of *R. argentea* in the entire lake from 2005 to 2011, with the peak in 2007, six years after enforcement of a seasonal ban on fishing in the Kenyan portion of the lake. This study agrees with Kayanda *et al.* (2009) about the increase in *R. argentea* biomass from 1999-2008. He reported the biomass of *R. argentea* in 1999 to be about 245 000 tons (10% of the total fish biomass in the lake), 477 000 tons (23%) during 2000- 2001, and just over million tons in 2005-2008 or 50% of the total fish biomass. The increase in the biomass of *R. argentea* in the entire lake can be a result of various interacting factors. One such important factor, which could affect the biomass of *R. argentea*, is a decrease in the biomass of zooplanktivorous haplochromines in the lake, which compete with *R. argentea* for food and space (Kishe *et al.* 2012). Increasing predation of Nile perch on the endemic haplochromines, the preferred prey of Nile perch, may therefore have led to an increase in abundance of *R. argentea*. (Wanink 1999, Ogutu-Ohwayo 1990b, Goudswaard *et al.* 2008, Witte *et al.* 1992).
The decreasing yield from 1997 to 2000 in the Kenyan part of the lake may have justified the authorization of a closed fishing-season for *R. argentea* in 2001. The question is though, what factors were responsible for this decrease? (Figure 6a). Based on figure 6e the exploitation ratio was high in the period before the closure (1998-2000), which could have resulted in reduced spawning stock and consequently low recruitment of *R. argentea*. The yield and biomass in Kenyan waters was highest in 2007 (Figure 6a) at the same time when the biomass of the entire lake peaked (Figure 5). The yield on the Uganda part was also low from 1997 to 2001 (Figure 7a), but after 2003 it increased steadily to date. However the yield in the Ugandan part of the lake has been much lower than on the Kenya side although the biomass in the Ugandan part has been twice as high. Like in the Kenyan part of the lake, the biomass began increasing in Ugandan waters from 2003. While the biomass in Kenyan waters rose from 2003-2005 and then levelled off, the biomass in Ugandan water have been rising steadily to date. This poses the question of whether this increase resulted from the closed season in the Kenyan portion of the lake or if some other changes e.g. the environment played a bigger role.

If the closed season in the Kenyan portion of the lake were supposed to lead to an overall increase in biomass in the entire lake, then it must be assumed that the main spawning takes place during the closed season and that the most important spawning areas are within the Kenyan part of the lake. If so the ban may have helped in increasing the spawning population and recruitment of the species. However very little information about breeding seasons of this species is available and what is available is inconsistent. According to Wandera (1992), *R. argentea* breeds throughout the year with peaks occurring just after the rain seasons in April-May and August-September. Wandera (1999) later notes based on a research carried out in Ugandan waters in 1996-1997, that the species breeds throughout the year and two breeding peaks were observed during the drier months of August and December-January. Minimal breeding was observed in the rainy months of April-May and October-November. According to a report on fish breeding areas and seasons in Lake Victoria- Kenya (Manyala et al. 2001) there are two peaks in the rainy seasons in March to August and October to December, which are found to be the major fish breeding seasons for most species of fishes of Lake Victoria. Njiru (1995) noted that breeding seasons are May to November for Nyanza Gulf and May to October for open waters. The information above about the breeding season of *R. argentea* contradicts the conclusions of Okedi (1973) who noted that *R. argentea* breeds in the months of June, July and August.

Many things seem to support the idea that the increasing biomass of *R. argentea* in the whole lake resulted from favourable climatic or environmental conditions, since fluctuations in the biomass of pelagic fish stocks of short lived species are often climate driven (Marie and Allison 2000, Jeppe et al. 2008). A comparison of changes in environmental parameters in the lake (dissolved oxygen, temperature, turbidity, chlorophyll and pH) and biomass of *R. argentea* indicate a significant correlation between the biomass of *R. argentea* and changes in environmental parameters except chlorophyll-a concentration, which had fewer measurement points than the others (Table 4). Biomass of *R. argentea* can be related to environmental factors in many ways. Factors such as dissolved oxygen, temperature, transparency (secchi-disk depth), and pH-value can be an indicator of water quality which can influence some of the changes in fish biodiversity.
(Manyala et al. 2003). E.g. the decline in transparency of the water may be partly because of the algal blooms and silt carried in by the rivers may be implicated in the decline of the haplochromines by disrupting their mating behaviour, which relies heavily on visual cues (Seehausen et al. 1997). Oxygen is necessary to sustain life of fishes. Availability of dissolved oxygen (DO) is one abiotic factor that can limit distribution, growth, reproduction, and survival of fishes (Kramer 1987). Currently, a hypoxia (condition of low oxygen) is evident in Lake Victoria (Table 3). Studies have found 3 mgL$^{-1}$ to be the critical DO concentration below, which most fish in Lake Victoria will not survive (Kaufman 1992, Wanink et al. 2001). However, the effects of hypoxia could be positive for some species as competition and predation by other species might decline.

Increasing pH and condition of low oxygen in the lake points to the process of eutrophication in the lake as a result of increased primary production, expressed in increased zooplankton production and in tertiary production in form of *R. argentea*. However at some stage this may lead to oxygen depletion stage reaching the entire lake, a case which impact negatively on all the fisheries productivity in the lake. (Jeppe et al. 2008).

Inter-annual and seasonal variability in rainfall and temperature can also affect primary productivity equilibrium at higher trophic levels, which will then be reflected in the fluctuating biomass and catch rates of *R. argentea* with no unpredictable pattern (Johnson 2009, Kayanda et al. 2009).

However, since all the environmental parameters’ measurements were from Nyanza gulf, this case may not necessary be representative of the whole lake but gives a likely scenario of what could be going on within gulfs of the entire lake thus having impacts on fish populations as gulfs are fish breeding areas.

Relatively little information has been published on small pelagic species in fresh water lakes (Marie and Allison 2000). However, available information on ecosystems, environmental studies and government fishery statistics all point to the fact that small pelagic clupeids and cyprinids in fresh water lakes fluctuate extensively from year to year, most likely, as a response to climate driven variations in primary and secondary biological productivity (Tweddle and Lewis 1990, Allison et al. 1995, Plisnier 1997). The management strategies employed to manage the fisheries in African inland lakes often focuses too much on optimal catch rates, while ignoring the fact that the inherent fluctuations in many fish stocks, especially short lived pelagics, are closely linked to climate which keeps changing (Marie and Allison 2000).
5. CONCLUSIONS AND RECOMMENDATIONS

5.1 Conclusions

*R. argentea* biomass increased considerably after implementation of closed seasons on the Kenyan side of the lake. However, it did so as well in the entire lake, without closed season being implemented in Uganda and Tanzania portions of the lake. At the same time considerable environmental changes have been occurring in the lake. The yield in Kenya and Uganda portions of the lake improved from 2003 and has been fairly stable or increased since 2007 to 2011.

There is no consensus on the peak breeding seasons of *R. argentea* in Lake Victoria, although it was one of the key assumptions when the ban was implemented, that it would enhance breeding success. It is not clear why closed seasons for fishing in Kenya are from April to July, not any other period of the year and why it had to be exactly four months and not more or less (Wandera 1992, Wandera 1999, Manyala *et al.* 2001, Okedi 1973).

The *R. argentea* fishery in Lake Victoria might be influenced by the fishing pressure but probably more so environmental changes as reflected in the fluctuations in the yield and biomass (Gichuki *et al.* 2010) in synchrony with fluctuations in environmental parameters.

5.2 Recommendations

*R. argentea* is an important fish to the livelihood of riparian communities (Othina and Osewe-Odera (1996). Management interventions should take into account the socioeconomic wellbeing of the communities. The following are therefore recommended:

- More information of the general biology of *R. argentea* are necessary to be able to manage the fishing responsibly.
- If seasonal bans are thought to be necessary, it should be focused restriction targeting a few critical breeding areas and nursery grounds as there is not strong evidence that the current seasonal closures are working.
- A consistent collection of catch and hydro acoustic data are necessary, to enable continuous monitoring of stocks and catches.
- Management measures to be employed should consider the facts that *R. argentea* is a short-lived species and the stock dynamics are closely linked to environmental factors.
- Fisheries management approaches should be reviewed from time to time based on research findings.
ACKNOWLEDGEMENTS

My sincere and heartfelt gratitude goes to my supervisors Hreidar Thor Valtýsson and Hlynur Ármannsson for their support and patient guidance during the course of the project work. I am highly indebted to the United Nations University Fisheries Training Programme for offering me the fellowship. I would also like to extend my sincere thanks to the Programme coordinators, Tumi Tómasson, Thor Asgeirsson, Mary Francis Davidson and Sigríður Ingvarsdóttir for their support. Special thanks go to the staff of Kenya Marine and Fisheries Research Institute, and in particular Chrisphine Nyamweya, for making available the required data. Can’t forget the senior staff of the Ministry of Fisheries Development, Kenya for nominating and allowing me to attend this course. Last but not least, I thank the Marine Research Institute and the year 2012 fellows of the Fisheries Training Programme for their resourcefulness.
Glory to God!
LIST OF REFERENCES


APPENDICES

R-SCRIPTS

R-script for Uganda Waters

# Set up data - R. argentea specific
yrs<-1997:2011 # actual data years
ages<-1 # actual ages

# Annual catch data
Y<-c(13454,15685,17572,12162,12163,11981,8248,22902,25672,22618,30800,33000,47000,63560,NA)

# Annual abundance index
I<-c(NA,NA,46970,168219,83833,NA,NA,NA,255221,360262,469553,352566,369045,369045,NA,404583)
Wts<-rep (1.6, length (yrs))/1000 # Wt ages repeated to the length of years

# Number of ages and years
g<-length(ages) # Number of true age groups
totyrs<-length(Y) # Number of years

# Initialize values of all parameters
# Some will later be estimated - others simply fixed at assumed values
M<-2 # Natural mortality
aveRecr<-100000000
selpat<-rep(0.9,15) # Selection pattern - might estimate - probably not
q<-1 # Initial value of catchability
Fvec<-rep(0.5,totyrs) # Annual fishing mortality

# now set up an appropriate mean weight at age for age grps 1:g and plus grp
#Zplus<-1.08 # cumZ values in the plus group
#Nplus<-aveRecr*exp(-Zplus) # age structure in plus group
#wtplus<-3.9/1000 # mean wt in plus grp
w<-wts # Weight at age 1 from from (Manyala,1995)

# Initial stock size: Assume equilibrium
Ninit<-aveRecr*exp(-cumsum(c(0,M))[1:g]) # only true ages
# alternatively, sum up instead of using a formula:
#
# Ninit<-aveRecr*exp (-cumsum(c(0,rep(0,3,100))))
# Ninit<-c(Ninit[1:g],sum(Ninit[(g+1):100]))
Rvec<-rep (aveRecr, totyrs) # Initial values of annual recruitment

# Put the initial values of parameters to be estimated into a vector
Parameters<-c(log(Fvec), log(Rvec),log(q))  # Initial values of all parameters  
# aspm.r  
# aspm: Performs forward simulation of populations, given values of parameters  
aspm<-function(Fvec,Rvec,totyrs,M,w){  
  Yhat<-NULL  
  Bhat<-NULL  
  Rtemp<-Rvec[1]  
  #N0<-Ninit # First start-of-year stock size - fixed  
  #N0<-Rtemp*exp(-cumsum(c(0,M[1:(length(M)-1)]))) # initial start-of-year stock size - equil.  
  N0<-aveRecr*exp(-cumsum(c(0,M))[1:g]) # better: first only true ages  
  for (year in 1:totyrs){  
    baseF<-Fvec              # Base fishing mortality  
    F0<-baseF*selpat       # Fishing mortality during the year  
    C<-F0/(F0+M)*(1-exp(-(F0+M)))*N0  
    Ytemp<-sum(C*w)                    # Total landings  
    Ntemp<-N0*exp(-F0-M)           # Forw proj - gives ages 2:(g+1)  
    Noldest<-Ntemp[g]+Ntemp[g+1]   # Allow for plus-group  
    #print(Ytemp)  
    Yhat<-c(Yhat,Ytemp)  
    Bhat<-c(Bhat,sum(N0*w))  
    Rtemp<-Rvec[year]  
    N1<-c(Rtemp,Ntemp[1:(g-1)],Noldest)# Set up stock at end of year  
    N0<-N1                         # Prepare for next round  
  }  
  return(list(Yhat=Yhat,Bhat=Bhat))  
}  
#ssefcn.r  
ssefcn<-function(parameters,Y,I,M,w){  
  totyrs<-length(Y)  
  Fvec<-exp(parameters[1:totyrs])  
  Rvec<-exp(parameters[(totyrs+1):(2*totyrs)])  
  q<-exp(parameters[2*totyrs+1])  
  #alpha<-parameters[2*totyrs+2]  
  #K<-parameters[2*totyrs+3]  
  proj<-aspm(Fvec,Rvec,totyrs,M,w)  
  Yhat<-proj$Yhat  
  Bhat<-proj$Bhat  
  #print(Bhat)  
  Ihat<-q*Bhat  
  CVR <-0.01  
  CVF <-0.01  
  CVY <-0.01  
  CVI <-0.01  
  SSEY<-sum(na.omit((log(Y)-log(Yhat)))^2)  
  SSEI<-sum(na.omit((log(I)-log(Ihat)))^2)  
}
```r
# SSE = SSEI + SSEY + SSER
SSER <- sum((log(Rvec[2:totyrs]) - log(Rvec[1:(totyrs - 1)]))^2)
SSEF <- sum((log(Fvec[2:totyrs]) - log(Fvec[1:(totyrs - 1)]))^2)
# SSE = SSEI + SSEY + SSER
SSE <- (1/CVI^2)*SSEI + (1/CVY^2)*SSEY + (1/CVF^2)*SSEF + (1/CVR^2)*SSER
return(SSE)
}
# Get a better initial value of q...
fit0 <- aspm(Fvec, Rvec, totyrs, M, w)
q <- mean(na.omit(I))/mean(fit0$Bhat)
parameters.0 <- c(log(Fvec), log(Rvec), log(q))  # Initial values of all parameters
fm <- nlm(ssefcn, parameters.0, iterlim=500, Y=Y, I=I, M=M, w=w)
parameters <- fm$estimate
Fvec <- exp(parameters[1:totyrs])
Rvec <- exp(parameters[(totyrs + 1):(2*totyrs)])
q <- exp(parameters[2*totyrs + 1])
fmopt <- aspm(Fvec, Rvec, totyrs, M, w)
Yhat <- fmopt$Yhat
Bhat <- fmopt$Bhat
Ihat <- q*Bhat

Time <- 1:totyrs
par(mfrow=c(2,3), mar=c(4,4,2,1))
plot(yrs, Y, xlab="Year", main='Yield')
lines(yrs, Yhat)
plot(yrs, I, xlab="Year", ylim=c(0, max(na.omit(I))), main='Index')
lines(yrs, Ihat)
plot(yrs, Rvec, xlab="Year", ylab="Recruitment", ylim=c(0, max(Rvec)),
    type='h', main='Recruitment', lwd=3)
# plot(yrs, Fvec, xlab="Year", ylab="F", ylim=c(0, max(Fvec)), main='Fishing mortality')
plot(yrs, Bhat, xlab="Year", ylab="Biomass",
    type='l', lwd=2, main='Biomass')
plot(yrs, Y/Bhat, xlab="Year", ylab="Exploitation ratio", type='l', lwd=2)

R-script for Kenya waters
yrs <- 1997:2011        # actual data years
ages <- 1            # actual ages
# Annual catch data
Y <- c(40315, 42336, 40168, 38968, 49165, 35455, 31659, 34679, 54019, 57929, 49472, 46966, 49326, 70000, 72314)
# Annual abundance index
I <- c(21.42, 14.65, 20.05, 19.37, 23.00, 16.91, 12.34, 11.38, 18.44, 18.21, 16.45, 15.41, 17.07, 25.93, 25.42)
```

UNU – Fisheries Training Programme
wts<-rep(1.6,length(yrs))/1000 # Wt ages repeated to the length of years
# Number of ages and years
g<-length(ages) # Number of true age groups
totyrs<-length(Y) # Number of years
# Initialize values of all parameters
# Some will later be estimated - others simply fixed at assumed values
M<-2 # Natural mortality
aveRecr<-10000000
selpat<-rep(0.9,15) # Selection pattern-might estimate-probably not
q<-1 # Initial value of catchability
Fvec<-rep(0.5,totyrs) # Annual fishing mortality
# now set up an appropriate mean weight at age for age grps 1:g and plus grp
#Zplus<-1.08 # cumZ values in the plus group
#Nplus<-aveRecr*exp(-Zplus) # age structure in plus group
#wtplus<-3.9/1000 # mean wt in plus grp
w<-wts # Weight at age 3-6 from MRI 2011 report
# Initial stock size: Assume equilibrium
Ninit<-aveRecr*exp(-cumsum(c(0,M))[1:g]) # only true ages
# Alternatively, sum up instead of using a formula:
#
# Ninit<-aveRecr*exp(-cumsum(c(0,rep(0.3,100))))
# Ninit<-c(Ninit[1:g],sum(Ninit[(g+1):100]))
Rvec<-rep(aveRecr,totyrs) # Initial values of annual recruitment

# Put the initial values of parameters to be estimated into a vector
parameters<-c(log(Fvec),log(Rvec),log(q)) # Initial values of all parameters

# aspm.r
# aspm: Performs forward simulation of populations, given values of parameters
aspm<-function(Fvec,Rvec,totyrs,M,w){
  Yhat<-NULL
  Bhat<-NULL
  Rtemp<-Rvec[1]
  #N0<-Ninit # First start-of-year stock size - fixed
  #N0<-Rtemp*exp(-cumsum(c(0,M[1:(length(M)-1)]))) # initial start-of-year stock size - equil.
  N0<-aveRecr*exp(-cumsum(c(0,M))[1:g]) # better: first only true ages

  for(year in 1:totyrs){
    baseF<-Fvec # Base fishing mortality
    F0<-baseF*selpat # Fishing mortality during the year
    C<-((F0/(F0+M))*(1-exp(-(F0+M))))*N0
  }
}
Ytemp<-sum(C*w)           # Total landings
Ntemp<-N0*exp(-F0-M)      # Forw proj - gives ages 2:(g+1)
Noldest<-Ntemp[g]+Ntemp[g+1]   # Allow for plus-group
# print(Ytemp)
Yhat<-c(Yhat,Ytemp)
Bhat<-c(Bhat,sum(N0*w))
Rtemp<-Rvec[year]
N1<-c(Rtemp,Ntemp[1:(g-1)],Noldest)# Set up stock at end of year
N0<-N1                     # Prepare for next round
}
return(list(Yhat=Yhat,Bhat=Bhat))
}
ssefcn<-function(parameters,Y,I,M,w){
totyrs<-length(Y)
Fvec<-exp(parameters[1:totyrs])
Rvec<-exp(parameters[(totyrs+1):(2*totyrs)])
q<-exp(parameters[2*totyrs+1])
# alpha<-parameters[2*totyrs+2]
# K<-parameters[2*totyrs+3]
proj<-aspm(Fvec,Rvec,totyrs,M,w)
Yhat<-proj$Yhat
Bhat<-proj$Bhat
# print(Bhat)
Ihat<-q*Bhat
CVR <-0.01
CVF <-0.01
CVY <-0.01
CVI <-0.01
SSEY<-sum(na.omit((log(Y)-log(Yhat)))^2)
SSEI<-sum(na.omit((log(I)-log(Ihat)))^2)
cat('n
n')
cat(SSEI,'n')
cat('n
n')
SSER<-sum((log(Rvec[2:totyrs])-log(Rvec[1:(totyrs-1)]))^2)
SSEF<-sum((log(Fvec[2:totyrs])-log(Fvec[1:(totyrs-1)]))^2)
# SSE<-SSEI+SSEY+SSER
SSE<- (1/CVI^2)*SSEI +(1/CVY^2)*SSEY +(1/CVF^2)*SSEF +(1/CVR^2)*SSER
return(SSE)
}
# Get a better initial value of q...
fit0<-aspm(Fvec,Rvec,totyrs,M,w)
q<-mean(na.omit(I))/mean(fit0$Bhat)
parameters.0<-c(log(Fvec),log(Rvec),log(q))     # Initial values of all parameters
fm<-nlm(ssefcn,parameters.0,iterlim=500,Y=Y,I=I,M=M,w=w)
parameters<-fm$estimate
Fvec<\exp\{parameters[1:totyrs]\})
Rvec<\exp\{parameters[(totyrs+1):(2*totyrs)]\}
qu<\exp\{parameters[2*totyrs+1]\})
fnopt<\text{aspm}(Fvec,Rvec,totyrs,M,w)
Yhat<\text{fnopt}\text{\$Yhat}
Bhat<\text{fnopt}\text{\$Bhat}
Ihat<q\ast\text{Bhat}
time<-1:totyrs
par(mfrow=c(2,3), mar=c(4,4,2,1))
plot(yrs,Y,xlab="Year",ylab="Yield",ylim=c(0,max(Y)), main='Yield')
lines(yrs,Yhat)
plot(yrs,I,xlab="Year",ylab="Recruitment",ylim=c(0,max(na.omit(I))), main='Index')
lines(yrs,Ihat)
plot(yrs,Rvec,xlab="Year",ylab="Recruitment",ylim=c(0,max(Rvec)),
type='h', main='Recruitment', lwd=3)
#plot(yrs,Fvec,xlab="Year",ylab="F",ylim=c(0,max(Fvec)), main='Fishing mortality')
plot(yrs,Bhat,xlab="Year",ylab="Biomass",ylim=c(0,max(Bhat)),
type='l', lwd=2,main='Biomass')
plot(yrs,Y/Bhat,xlab="Year",ylab="Exploitation ratio", type='l', lwd=2)

\textbf{Outputs for Temperature, Secchi disc, Dissolved oxygen, PH and chlorophyll from R-statistical programme.}

\textbf{Summary (lm (Bhat~Temp, env.data))}
Call:
\texttt{lm(formula = Bhat ~ Temp, data = env.data)}
Residuals:
\begin{tabular}{cccc}
\text{Min} & 1Q & Median & \text{Max} \\
-65174 & -45991 & 3013 & 29679 & 97177 \\
\end{tabular}
Coefficients:
\begin{tabular}{cccc}
\text{Estimate} & \text{Std. Error} & \text{t value} & \text{Pr(>|t|)} \\
\text{(Intercept)} & -7751680 & 1989652 & -3.896 & 0.00184 ** \\
\text{Temp} & 300171 & 74443 & 4.032 & 0.00142 ** \\
\end{tabular}
Signif. codes: \texttt{0 \textbf{****} 0.001 \textbf{**} 0.01 \textbf{*} 0.05 \texttt{.} 0.1 \texttt{ ' } 1}
Residual standard error: 51000 on 13 degrees of freedom
Multiple R-squared: 0.5557, Adjusted R-squared: 0.5215
F-statistic: 16.26 on 1 and 13 DF, \texttt{p-value: 0.001423}

\textbf{Summary (lm (Bhat~ Chl, env.data))}
Call:
\texttt{lm(formula = Bhat ~ Chl, data = env.data)}
Residuals:
\begin{tabular}{cccc}
3 & 4 & 10 & 11 \\
-89323 & -20835 & 48920 & 22420 & -40224 & 79043 \\
\end{tabular}
Coefficients:
\begin{tabular}{cccc}
\text{Estimate} & \text{Std. Error} & \text{t value} & \text{Pr(>|t|)} \\
\end{tabular}
> summary(lm(Bhat ~ PH, env.data))

Call:
  lm(formula = Bhat ~ PH, data = env.data)

Residuals:
   Min     1Q   Median     3Q    Max
-45693 -23739  -8230  28750  50680

Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept) -750514     145542  -5.157 0.000185 ***
PH            123917      17623   7.031 8.91e-06 ***

Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 1

Residual standard error: 34910 on 13 degrees of freedom
Multiple R-squared: 0.7918, Adjusted R-squared: 0.7758
F-statistic: 49.44 on 1 and 13 DF,  p-value: 8.913e-06

> summary(lm(Bhat ~ Do, env.data))

Call:
  lm(formula = Bhat ~ Do, data = env.data)

Residuals:
   Min     1Q   Median     3Q    Max
-58051 -29502 -17254  26193  85931

Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   454510      47925   9.484 3.32e-07 ***
Do           -31380       7871  -3.987  0.00155 **

Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 1

Residual standard error: 51320 on 13 degrees of freedom
Multiple R-squared: 0.5501, Adjusted R-squared: 0.5155
F-statistic: 15.89 on 1 and 13 DF,  p-value: 0.001551

> summary(lm(Bhat ~ Secci, env.data))

Call:
  lm(formula = Bhat ~ Secci, data = env.data)

Residuals:
   Min     1Q   Median     3Q    Max
-67788 -38382   2688  44681  71091

Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  400424      34899  11.478 3.57e-08 ***
Secci       -151317      37736  -4.011  0.00148 **

Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 1

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Residual standard error: 51160 on 13 degrees of freedom
Multiple R-squared: 0.5529,  Adjusted R-squared: 0.5185
F-statistic: 16.08 on 1 and 13 DF,  p-value: 0.001484