Some aspects of the ecology and reproduction of the small pelagic cyprinid, *Rastrineobola argentea* in Lake Victoria.
The conclusions and recommendations given in this and other reports in the LVFRP series are those considered appropriate at the time of preparation. They may be modified in the light of further knowledge gained at subsequent stages of the Project. The designation employed and the presentation of the material in this publication do not imply the expression of any opinion on the part of the EU, the EDF, the LVFRP, FIRRI, KMFRI nor TAFIRI concerning the legal status of countries, territories, cities or areas or concerning the determination of their frontiers and boundaries.
Some aspects of the ecology and reproduction of the small pelagic cyprinid, *Rastrineobola argentea* in Lake Victoria.

by

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6. REFERENCES
It is now well established that the fisheries of Lake Victoria are under considerable stress due to many factors. This has been recognised in the implementation of the Lake Victoria Fisheries Research Project (LVFRP), a regional programme supported by the European Development Fund. LVFRP is striving to assess the status of the fish stocks, to reveal the exploitation patterns and socio-economic issues relating to the ever changing fisheries and their management as a sustainable resource.

As part of this programme, The University of Hull International Fisheries Institute (HIFI) in the UK is collaborating with fisheries institutes in East Africa to investigate the status of the fish stocks. This research involves assessment of the three major commercial fisheries, namely the Nile perch *Lates niloticus*, the dagaa *Rastrineobola argentea* and the Nile tilapia *Oreochromis niloticus*. A diverse range of methodologies is in use, from experimental trawling through hydroacoustic surveys to data collection on the landing beaches for catch assessment purposes. The scale of the work is vast. It requires considerable manpower and other resources. To assist in the collection and analysis of the data, HIFI has co-opted several MSc students from its postgraduate programme. The contribution of these young energetic researchers is greatly appreciated by myself and other staff directly involved in the activities of LVFRP.

The thesis presented in the following pages, written by James Roy Marshall as his MSc dissertation, represents an important output from this collaboration. The research attempts to identify changing patterns in the ecology of *R. argentea* in Lake Victoria, based mainly on samples collected by trawling during the biennial lake-wide hydroacoustic surveys. The work has also identified a potentially important issue relating to the parasitisation of *R. argentea*. This problem could well have profound effects on the future of the fishery in the long term.

Finally, in addition to the acknowledgements mentioned in the thesis, we wish to thank the Director and staff at FIRRI, Uganda, for their help and encouragement of this research, especially Dr. R. Ogutu-Ohwayo and S.B. Wandera. Thanks also go to Rhoda Tumwebaze for supplying the basic material, to Martin van der Knaap for his logistical support and to David MacLennan who edited and prepared the text for this publication.

Dr. Ian Cowx  
Director HIFI
ABSTRACT

This study concentrated on the reproductive biology of the small pelagic cyprinid *Rastrineobola argentea*. The results indicate that this fish is an inshore spawning species, which agrees with other recent studies. It was also found that in areas where fishing intensity was likely to be relatively high, the size at first maturity of *R. argentea* was reduced, which is likely to be an effect of the fish altering its reproductive strategy according to life history theory. The CPUE results showed a general trend of decreasing with distance from shore, however areas less than one kilometre from the shore were not sampled. Evidence was also found suggesting that the cestode parasite, *Ligula intestinalis* had an adverse effect on the maturation and fecundity of *R. argentea*. Some management options concerning the findings in this study are also briefly discussed.
I would like to take this opportunity to thank a number of people for their help during the course of this study.

Firstly, I must thank Dr. Ian Cowx for his patience and assistance, and everyone else from the HIFI freshwater fisheries laboratory, who include Dr. John Harvey, Andy Nunn and Richard Noble.

During my trip to Uganda, I met a large number of friendly, helpful people, too numerous to mention here, but special thanks must be extended to Mr. S.B. Wandera for his help with maturity identification and for the contribution of the samples which I worked on.

I would also like to thank Mr. Martin van der Knaap for his advice, and for letting me watch the World Cup at his house!

Lastly, I would like to extend the most heartfelt gratitude to George Passiotis and Sheila Maclennan for their gracious hospitality during my stay in Uganda.
1. INTRODUCTION

Lake Victoria, at 68800 km², is the largest tropical lake in the world (Lowe-McConnell, 1993) and the third largest lake in the world (Wanink, 1998a). The lake has a maximum length of 400 km and width of 240 km (Tumwebaze, 1997). Despite its size, the lake is only approximately 80 m deep, with a mean depth of 40 m (Lowe-McConnell, 1993), so is relatively shallow in comparison to other large lakes in Africa, such as Lake Tanganyika and Malawi (Tumwebaze, 1997). Lake Victoria straddles the equator between latitudes 0 ° 30" N and 3 ° 00" S and longitudes 31 ° 40" E to 34 ° 50" E, and is therefore shared by Tanzania (51%), Uganda (43%) and Kenya (6%) (Tumwebaze, 1997) (Fig. 1.1).

In the last three decades the ecosystems of Lake Victoria have undergone dramatic changes (Bugenyi and Magumba, 1996) that have irreversibly altered the habitat of the lake (Goldschmidt, Witte and Wanink, 1993). For example, to boost fisheries the Nile perch (*Lates niloticus*) was introduced into the lake in the late 1950s (Goldschmidt, Witte and Wanink, 1993) and early 1960s (Ogutu-Ohwayo, 1988). However, in the 1980s the numbers of this predator dramatically increased so that by 1990 it was making up 90% of the total catch (Ligtvoet and Mkumbo, 1991). Although the Nile perch became a predator of numerous species (Mkumbo, unpublished), the haplochromines became its chief prey. It was due to this increased predation that the haplochromine populations were decimated (Witte, Goldschmidt, Goudswaard, Ligtvoet, Oijen and Wanink, 1992) with an estimated two-thirds of the haplochromine cichlid taxa having now disappeared (Lowe-McConnell, 1993). The diminishing haplochromine populations, combined with the presence of a new large predator, obviously disrupted food chains within the lake. Various predators switched from a haplochromine diet to feed on the *R. argentea* populations, as these actually increased with the introduction of the Nile perch (Witte, Goldschmidt, Goudswaard, Ligtvoet, Oijen and Wanink, 1992). *R. argentea* has become the diet of both the adult siluroid catfish (*Bagrus docmac*) (Olowo and Chapman, 1999; Manyala, Nyawade and Rabuor, 1992), and the avian piscivore, the pied kingfisher (Wanink and Goudswaard, 1994; Wanink, Berger and Witte, 1993), both of which previously fed on the haplochromines.

The decline of the haplochromines also affected the lower trophic levels within the lake, for with their demise the consumption of phytoplankton and detritus was reduced (Gophen, Ochumba and Kaufman, 1995). Therefore the disappearance of the haplochromines was detrimental to the water quality of the lake. Consequently, the deeper sections of the lake have become deoxygenated (Hecky, 1993; Lowe-McConnell, 1993; Tumwebaze, 1997). These anoxic conditions, which have created less space for the fish to inhabit, has therefore exposed them to an increased pressure from predation (Wandera, unpublished (b)) which has compounded the demise of certain species as opposed to others. As some species, such as the ‘small pelagics’ (*R. argentea, Yssichromis, Y. laparogramma* and *Y. fusiformis*), are able to use the water below the oxycline as a refugia from predators (Wandera, unpublished(b)).
Fig. 1.1 Geographic location of Lake Victoria, East Africa (Tumwebaze 1997).
The invasion of water hyacinth (*Eichhornia crassipes*) into the lake was an auxiliary in sustaining the anoxic conditions under its mat (Bugenyi and Magumba, 1996). However, more recently water hyacinth has disappeared, again illustrating how temporary changes can effect the ecosystems within the lake. These factors can be beyond human control, for example the average lake water temperature has risen in by 0.5 °C as the regional climate has increased (Bugenyi and Magumba, 1996). The increased temperature raises the water height (Bugenyi and Magumba, 1996), which in turn affects lake habitats.

The problem of the water quality, which altered the lake’s ecosystems, was compounded by the external, man-made environment surrounding the lake. In fact, Bugenyi and Magumba (1996) directly blame the burgeoning human population growth, which was recorded at the rate of 3 - 4 % annually, in 1996 (Bugenyi and Magumba, 1996). The increasing growth and urbanisation effects the lake, as waste, both organic and chemical, is disposed of directly into the water (Bugenyi and Magumba, 1996). The modifications which have been made to enable these agricultural and industrial changes have included the reduction of the forests which were essential in filtering the nutrients and silt which enter the lake (Tumwebaze, 1997). This increase of nutrients, combined with the 0.5 °C increase in the lake water temperature, explains the increased primary production which has increased 2 to 3 - fold in the last thirty years (Bugenyi and Magumba, 1996).

Finally, the system of the lake has shifted due to human error. It has been recognised that the fishery of Lake Victoria was consistently mismanaged (Okaronon, 1994), so that overfishing, unregulated gill net mesh sizes and exploitive fishing techniques have contributed to the decline of certain species, including the haplochromines (Bugenyi and Magumba, 1996). Although the fishing effort in the Ugandan section of the lake increased by 78% from 1972 to 1990, the yield decreased from 132, 000 tonnes in 1989 to 103, 000 tonnes in 1994 (Okaronon, 1994).

Both the trophic levels and the water quality in Lake Victoria have been altered (Bugenyi and Magumba, 1996) and the ecosystem has become highly simplified, as it is focused on less than six species of great importance (Kaufman and Cohen, 1993). Indeed, many believe that Lake Victoria has become dominated by three species: the Nile perch, an introduced tilapian cichlid, *Oreochromis niloticus*, and the native cyprinid *Rastrineobola argentea* (Branstrator, Lehman and Ndawula, 1996; Tumwebaze, 1997; Witt, Goldschmidt, Goudswaard, Ligtvoet, Oijen and Wanink, 1992). Unlike many species, the *R. argentea* (Pellegrin, 1904) population increased with the introduction of Nile perch (Wanink, 1991), and is believed to have increased tenfold between 1970-1990 (Wandera, unpublished(b)), which makes it one of the most important fish in Lake Victoria.

Wanink (1998b) has suggested that the reason this species has been neglected by fishermen and biologists until recently is due to its small size, for it rarely exceeds 8 cm standard length. Although a light fishery started in the 1960s for this species (Wanink, 1998b), it was not until the 1980s, when the haplochromine demise was recognised, that both this fishery and the academic interest in *R. argentea* started in earnest (Wanink, 1998b; Mannini et al., 1992). Today, *R. argentea* is regarded as the second most important fish in Lake Victoria, after the Nile Perch (Wanink,
which is reflected in the contribution of *R. argentea* in the commercial catches. For it has risen from less than 1% before 1987 to 13% in 1995 (Tumwebaze, 1997). The main methods for fishing *R. argentea* in the lake is by beach seines or boat seines, which both use kerosene lamps to attract the fish to the surface (Katunzi, 1992; Chitamwebwa, 1992; Wandera, 1993).

The importance of this small endemic species is twofold. It is commercially important as it is a relatively cheap source of food for humans and livestock including cattle and poultry (Mannini *et al*., 1992; Manyala, Vandenberghe and Dadzie, 1995). Secondly, due to the demise of the haplochromines, *R. argentea* plays a crucial role within the ecosystem as it provides the link between lower and higher trophic levels. *R. argentea* transfers the energy it gains from eating zooplankton, which in turn consumes primary producers, to higher trophic levels, including the Nile perch (Wandera, 1992; Katunzi, 1992; Wanink, Goudswaard and Berger, 1998). This is important as the Nile perch are commercially valuable.

1.1 Study aims

The basic study aim of this research is to attempt to gain an understanding of some aspects of the reproductive biology of *R. argentea* within Lake Victoria. These aspects will include whether they are an inshore or an offshore spawning species, and hence where the juvenile section of the population may be found. It is hoped this information may be combined with data on spawning times, so that sound management decisions can be made on protecting both breeding adults, and new recruits to the fishery, which may be invaluable in maintaining a sustainable fishery.

This study will also attempt to look into the distribution and catch per unit effort (CPUE) of *R. argentea* around the lake. This will give information on where the most abundant stocks are found, and hence where the most important fishing areas are. This information may also be combined with data on the reproductive biology of *R. argentea*, so that the ‘correct’ part of the population lake-wide is exploited, again to ensure a sustainable fishery in the future.

Lastly, it has been noted in recent studies that the cestode parasite *Ligula intestinalis* (Linnaeus) infests some populations of *R. argentea*. This study aims to assess the effect of *L. intestinalis* on *R. argentea* with respect to the fishes maturation and breeding, and what size range of the fish is most susceptible to the parasite.
2. MATERIALS AND METHODS

2.1 Study areas

Samples of *Rastrineobola argentea* (Pellegrin 1904) were collected during August 1999 and February 2000 by the research vessel MV Ibis, which is 17.1m long and fully rigged (Tumwebaze, 1997). The 1999 survey began in Jinja, Uganda and terminated in Mwanza, Tanzania (Fig. 2.1), whereas in 2000 the survey began in Mwanza and terminated in Jinja (Fig. 2.2).

Samples were collected from all over the lake at intervals along the vessels cruise track, including open waters, coastal waters, deep and shallow trawls in waters of all the riparian states. In 1999 a total of 21 sites were sampled, compared to 23 in 2000. The 2000 survey included more sites from the centre of the lake (Fig. 2.2). The sampling sites for both the 1999 and 2000 surveys are shown in (Fig. 2.1) and (Fig. 2.2) respectively.

The depth of each site was recorded, and the distance from the shore was calculated using a scale map of Lake Victoria (Table 2.1). A graphical relationship between depth and distance from the shore is given in Figure 2.3. The exact position of each site was determined using a hand held Global Positioning System (GPS).

It was predicted that some sites in each year could be loosely grouped according to their proximity to each other and location as they may show some common characteristic such as size distribution and breeding status of the fish populations. The exact groupings are discussed further in Section 3 where the population dynamics of *R. argentea* are examined.

2.2 Fisheries data collection

Fisheries data were collected using a frame trawl. This method is easier to operate than a conventional pelagic trawl as it requires less experience and less specialised equipment, saving both money and time during the course of the Lake Victoria Research Project LVFRP (Ridgeway, pers. comm.). The frame trawl consisted of a funnel of graded mesh of 152 mm to 51 mm, leading to a cod-end of polyamide twine of 5mm mesh net. Attached to the open end of the netting was a steel frame of 3.5 m × 3.5 m, which was towed by the vessel at the required water depth. The depth of the net was set at the position of greatest density of fish in the water column, and controlled by a netsonde detector. The duration of each trawl varied from 10 min to 30 min, and in 1999 the time of trawl ranged between 7.50 am and 17.25 pm, and in 2000 between 8.19 am and 6.46 pm.

Catches were weighed initially to determine total catch, after which individual species were separated and weighed again to evaluate CPUE per species. Sub-samples of approximately 200-400 g of *R. argentea* were taken if the samples were large enough to do so (greater than 500 g), and preserved in 4% formalin solution. These samples were retained for analysis in the laboratory.
Fig. 2.1 Sample sites for *R. argentea* during August 1999 (Vessel course from Jinja to Mwanza)
Fig. 2.2 Sample sites for *R. argentea* February 2000 (Vessel course from Mwanza to Jinja)
Table 2.1 Information on the depth and distance from the shore for each site sampled in 1999 and 2000.

<table>
<thead>
<tr>
<th>Site</th>
<th>Depth (m)</th>
<th>Distance from the shore (km)</th>
<th>Site</th>
<th>Depth (m)</th>
<th>Distance from the shore (km)</th>
</tr>
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<tbody>
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<td>U1</td>
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<td>1.9</td>
<td>U1</td>
<td>20</td>
<td>3.4</td>
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<tr>
<td>U2</td>
<td>37</td>
<td>6.4</td>
<td>U2</td>
<td>25</td>
<td>2.5</td>
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<td>62</td>
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<td>U3a</td>
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<tr>
<td>U3b</td>
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<td>4.4</td>
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<tr>
<td>K2</td>
<td>14</td>
<td>2.9</td>
<td>K3</td>
<td>45</td>
<td>2.2</td>
</tr>
</tbody>
</table>
Fig. 2.3. Relationship between the distance away from the shore and the depth of Lake Victoria.

\[ y = 2.356x + 24.638 \]
\[ R^2 = 0.5668 \]
2.3 Laboratory examination

Samples were soaked overnight in 70 % alcohol to remove excess formalin, and washed with water before examination to remove excess alcohol.

2.3.1 Fish length

Fish were measured using standard length (SL) to the nearest mm, and sorted into 1 mm length intervals. Standard length was chosen to measure the fish for the tail’s were frequently damaged, making fork length or total length difficult to obtain. Standard length involves a measurement from the most anterior extremity (mouth closed) to the insertion of the median tail fin rays (Lagler, 1978).

2.3.2 Fish weight

Individual fish weights could not be determined accurately owing to the imprecise weighing equipment available during the course of this study. Only fish above approximately 40 mm in length could be weighed individually, and for this reason a group of fish of each length class was weighed to the nearest tenth of a gram. An average weight per fish was then calculated.

2.3.3 Sex and maturity

If possible, ten random specimens were taken from each 1 mm length class. These were then dissected in order to establish the sex and maturity of each individual. Maturity was based on the status of the gonad following the criteria of Wandera (1999), who in turn cited the subjective methods of Bagenal and Braum (1978). The sex and maturity of R. argentea was established by close examination of the gonads using a dissecting microscope. The females had flat ovaries when immature or resting (Table 2.2), and eggs are easily discernible when mature and/or breeding (Table 2.2). The male on the other hand has tubular testes, which are thin and small when immature, and smooth and plump with milt when breeding (Bagenal and Braum, 1978). The gonads of both the males and females lie on either side of the ventral cavity, and can be removed by careful dissection. A more detailed account a generalised fish maturity analysis is given in table 2.2, which closely matches the criteria upon which maturity analysis was based.

2.3.4 Fecundity

While analysing the sex and maturity of the fish, females which were found to be carrying mature eggs had their ovaries removed and flattened on a glass slide to a one egg thick surface layer, and manipulated to form a square. Sub-samples were counted based on the grid and multiplied up to obtain an estimate of the total number of eggs for each individual. Generally, only females of maturity stages five and six had eggs which could be separated sufficiently to count them.

2.3.5 Ligula intestinalis infestation
Every fish from all of the samples were checked for *L. intestinalis*. Fish that were not already dissected to determine their sex and stage of maturity were cut open along their ventral surface and inspected for the presence of the parasite. *L. intestinalis* is found in the ventral cavity of its intermediate fish host, and can be distinguished with ease from the fish’s internal organs due to differences in texture and colour. When *L. intestinalis* was found, the length of the fish host was noted, as well as its maturity and sex. The lengths of the parasite were noted, and as many fish harboured more than one parasite, the number of *L. intestinalis* in each fish was recorded.

2.4 Data analysis

2.4.1 CPUE analysis

CPUE data for *R. argentea* populations around the lake were analysed for each site, taking into account the location of the site with respect to depth, distance from the shore, and in which of the riparian states they were located. A general relationship between both depth and distance from the shore was then determined for populations sampled in 1999 and 2000, to establish if any disparities existed between population densities in inshore and offshore locations.

2.4.2 Length analysis

From the length data, Petersen length-frequency histograms were constructed to assess the population size structure at the time of sampling for each sample site. Mean lengths were also calculated for each site so that the relationship between mean population length and depth and distance from the shore could be determined. Table 2.3 gives the mean population lengths used for this analysis. The modes for each population were identified using Battacharya’s method on FISAT, and the mean for each mode established.

2.4.3 Weight analysis

For each site, a log length-log weight relationship was determined, upon which regression analysis was performed. The output from this analysis was in the form of the following equation:

\[ \log \text{ weight} = \log a + b \log \text{ length} \]

Where \( b \) is the regression coefficient, normally a number between two and four, and \( \log a \) is the intercept on the y axis (Bagenal and Tesch, 1978). A comparison between the percent of fish infected with *L. intestinalis* (prevalence) in each *R. argentea* population, and the regression coefficient of the log weight – log length relationship was then made. This was carried out to establish whether *L. intestinalis* had an effect on the regression coefficient for the log weight - log length relationship of *R. argentea* populations. A coefficient less than three may indicate a reduced body condition if growth of the species is isometric, which is assumed to be the case with *R. argentea* (Wanink, 1989).
Table 2.2 Method used to classify fish into maturity stages (Adapted from Kesteven, 1960).

<table>
<thead>
<tr>
<th>Stage</th>
<th>Description</th>
<th>Descriptive name</th>
<th>Maturity level</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Very small sexual organs close to the vertebral column. Testes and ovaries transparent, colourless to grey. Eggs invisible to the naked eye.</td>
<td>Virgin</td>
<td>Immature</td>
</tr>
<tr>
<td>2</td>
<td>Testes and ovaries translucent, grey-red. Length half or slightly more than half the length of the ventral cavity. Single eggs can be seen with magnifying glass.</td>
<td>Maturing virgin</td>
<td>Immature</td>
</tr>
<tr>
<td>3</td>
<td>Testes and ovaries opaque, reddish with blood capillaries. Occupy about half the ventral cavity. Eggs visible to the naked eye with a whitish granular appearance.</td>
<td>Developing/Resting</td>
<td>Mature – not breeding</td>
</tr>
<tr>
<td>4</td>
<td>Sexual organs filling ventral cavity. Testes white. Eggs completely round, some already translucent and ripe.</td>
<td>Developing/Resting</td>
<td>Mature – not breeding</td>
</tr>
<tr>
<td>5</td>
<td>Roe and milt drop with slight pressure. Most eggs translucent with few opaque eggs remaining in ovary.</td>
<td>Gravid</td>
<td>Mature - breeding</td>
</tr>
<tr>
<td>6</td>
<td>All eggs are fully translucent, with no opaque eggs left. Eggs are easy to separate with little interstitial tissue binding them together.</td>
<td>Spawning</td>
<td>Mature - breeding</td>
</tr>
<tr>
<td>7</td>
<td>Testes and ovaries empty (perhaps one or two large eggs remaining, in a state of reabsorption).</td>
<td>Spent</td>
<td>Mature - spent</td>
</tr>
<tr>
<td>3</td>
<td>Ovary / testes return to resting at stage 3.</td>
<td>Developed/Resting</td>
<td>Mature – not breeding</td>
</tr>
</tbody>
</table>

2.4.4 Sex and maturity analysis

Sexing and establishing the maturity stage of the fish was used to give a number of useful parameters relating to the *R. argentea* populations around the lake. The length at first maturity (LM50) was estimated by examining the proportion of mature fish (stages five and six) in each length class. LM50 was determined by Solver, an Excel program which fits a sigmoid curve through a data set ranging from no mature fish to all mature fish. LM50 is point on the curve where 50 % of fish are mature. This
parameter gives an insight into the length of the fish that are mature at the various sites, and comparisons between the sites can therefore be made.

Mean $LM_{50}$ (males and females) for all the *R. argentea* populations in 1999 and 2000 were then compared to the depth and the distance from the shore to determine if any relationship was present.

The data were also used to examine the proportion of length class at each maturity stage, at all of the sites to establish any relationships which could be a result of external factors, both natural and unnatural. The proportion of the *R. argentea* population exhibiting maturity stages five or six was then compared to the depth and distance from the shore to gain an indication of where the highly mature *R. argentea* were found, and thus perhaps where they were breeding.

2.4.5 Fecundity analysis

The fecundity of individual *R. argentea* was determined to establish the relationship between fish length and fecundity. A comparison was then made between the fecundity of *L. intestinalis* parasatised fish and that of the fish not infected with *L. intestinalis*.

2.4.6 *Ligula intestinalis* infestation analysis

The prevalence (% of fish in each population with *L. intestinalis*) of *L. intestinalis* was established. This data were analysed to give an indication of its effect on the fish populations with respect to their maturity at the various sites. This was achieved by comparing the patterns of maturity for whole populations of *R. argentea*, with those obtained for fish (within the same population) only parasatised by *L. intestinalis*. It would have been more appropriate to compare the maturity stages of fish regardless of their *L. intestinalis* status. However during the analysis of their maturity stages, no distinction was made between infected and non-infected fish for the population as a whole. The effect of *L. intestinalis* on the maturity of *R. argentea* was only analysed for sites which had a high enough prevalence of *L. intestinalis* to make the findings viable (above 10% prevalence).

Numerous relationships were established between *L. intestinalis* and the length of individual *R. argentea*, including the prevalence, length and number of the parasite, in order to ascertain which part of the *R. argentea* population was most prone to *L. intestinalis* infection. The relationship between fecundity and the presence of *L. intestinalis* was also examined (as mentioned previously).

The prevalence of *L. intestinalis* in fish over 40 mm in length was then compared to the depth and the distance from the shore. This was to establish whether a populations proximity to shore, and hence its accessibility to avian predators, (some of which are the definitive hosts of *L. intestinalis*), effects the prevalence of the parasite.
3. RESULTS

3.1 CPUE analysis

Data from both the 1999 and 2000 surveys gave a wide range of catch per unit effort (CPUE) estimates based on weight of fish caught per trawl hour. Where the sites were comparable in relation to location and bottom depth in the two years, the sites were given the same identification number for ease of comparison. It should be noted that trawls were rarely at the same GPS position so the comparisons were based on samples taken in the same general locations. For the actual locations of all the sites given below, refer to Figures 2.1 and 2.2 for 1999 and 2000 respectively.

Ugandan sites

In the north east corner of the Ugandan region of the lake, sites U1, U2 and U4 exhibited varying CPUE values between both the sites and the years. Site U1 had a *R. argentea* CPUE of 0 in 1999, yet in 2000 this rose to 8800 g trawl hr\(^{-1}\) (Table 3.1). The reverse occurred at site U2 for in 1999 the CPUE was 1091 g trawl hr\(^{-1}\) which decreased in 2000 to 520 g trawl hr\(^{-1}\) (Table 3.1). Overall the values obtained in both years were similar to other sites over the lake, with the exception of site U4 at Busiri-Bugai which experienced a low CPUE of 30 g trawl hr\(^{-1}\).

Towards the western side of the Ugandan section of the lake the sites situated south of the Sesse islands, namely U5 and U6, had lower *R. argentea* CPUE than U7 and U8, the sites north of the islands (Table 3.1). Regardless of whether these sites were north or south of the Sesse islands, the shallower locations at site U5 (due north) and U7 (due south) had higher CPUE's (Table 3.1) than their deeper water counterparts, U6 and U8 respectively (Table 3.1).

The remaining Ugandan sites were all sampled in the 2000 survey, bar U3 which was sampled in both years (Table 3.1) and were either located in open water (sites U9, U11a, U11b and U12) or in areas with little shelter (Site U10). All of these sites had a notably low CPUE. Indeed, site U9 had the highest CPUE of all the locations, yet this was only 480 g trawl hr\(^{-1}\) (Table 3.1).

Tanzanian sites

Site T1 in the 1999 survey had no comparable site in 2000, however, it had a similar depth and distance from shore profile to T2, which was sampled in both years. In 1999 sites T1 and T2 showed very similar CPUE's of 13 and 15 g trawl hr\(^{-1}\), (Table 3.1), whereas in the 2000 survey, site T2 gave a higher CPUE of 1760 g trawl hr\(^{-1}\). Site T3, which was sampled only in 1999, and is in the same general location as sites T1 and T2, supported a CPUE of 4488 g trawl hr\(^{-1}\), somewhat higher than the other two sites (Table 3.1). Site T3 is different to sites T1 and T2, as the water is shallower by about 10 m (Table 3.1).

At site T4, which was sampled in both 1999 and 2000, very different CPUE values were obtained; 20500 g trawl hr\(^{-1}\) in 1999 compared to zero in 2000. Again, this site
was effected by the water depth, for in 1999 it was shallower than its 2000 counterpart by 13 meters (Table 3.1).

Sites T5, T6 and T7, which range in depth from 45 m (T7, 2000) to 70 m (T5, 1999) (Table 3.1) were all open water sites. The CPUE for these sites was low, the highest being 72 g trawl hr\(^{-1}\) at site T6 in 1999 (Table 3.1). These three open water sites tended to give higher *R. argentea* CPUE in 1999 than their corresponding sites in 2000 (Table 3.1).

Site T8, which was only sampled during the 2000 survey had a depth of 40 m, and was considered to be in open water, although it gained some shelter from Nyabulu Island. It exhibited a low CPUE of 552 g trawl hr\(^{-1}\), and displayed similar characteristics to the open water sites described above.

The sites in the south west sector of the lake, namely T9, T10 and T11, showed an increasing CPUE trend in 1999 from west to east, even though the water depth increased (Table 3.1). In 2000 however, the trend was reversed with an increase from east to west, T11 to T10 (Table 3.1). A major difference between these two sites and sites T9, T10 and T11 from the 1999 survey was, that in 1999, the deepest site was T11 (Table 3.1), at 41 m, whereas in the 2000 survey, site T11 had a depth of 53 m (Table 3.1).

Sites T12a and T12b from the 1999 survey and T12 from the 2000 survey all gave reasonably high CPUE values, contributing to the trend along the southern coast of the lake of high CPUE values. There seemed to be a reduction in *R. argentea* CPUE from 1999 to 2000 at site T12 (Table 3.1). However, at site T13, which was further to the east, and shallower (Table 3.1), the trend from year to year was reversed.

**Kenyan sites**

Three of the four Kenyan sites were sampled in water less than 20 m (Table 3.1). In general, these sites gave high CPUE values. Site K1 showed a decrease in CPUE from 5760 g trawl hr\(^{-1}\) in 1999 to 3800 g trawl hr\(^{-1}\) in 2000 (Table 3.1). Site K2, which is situated in the heart of the Nyanza Gulf, in water only 14 m deep, gave an extremely high *R. argentea* CPUE of 86232 g trawl hr\(^{-1}\). This result is four times higher than at any other site. The final Kenyan site, K3, was sampled in deeper waters (Table 3.1), and gave a lower CPUE of 1750 g trawl hr\(^{-1}\).

**3.1.1 Analysis of CPUE with respect to depth and distance offshore**

The relationship between depth and CPUE suggests that as depth increases, the CPUE derived from the *R. argentea* populations decreased (Fig. 3.1). The correlation of this relationship is however weak, \(r^2\) values = 0.08 and 0.27 for 1999 and 2000 respectively, (Fig. 3.1). As expected, the relationship between the distance from the shore and CPUE exhibited similar characteristics, and again the correlation was weak (Fig. 3.2). The relationship between depth and distance from shore is shown in Figure 2.3.
Table 3.1 CPUE and water depth data for the 1999 and 2000 surveys.

<table>
<thead>
<tr>
<th>Uganda sites 1999</th>
<th>Uganda sites 2000</th>
</tr>
</thead>
<tbody>
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<td><strong>Site</strong></td>
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</tr>
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<table>
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<tr>
<td>T13</td>
<td>20</td>
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<td></td>
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<tr>
<td>Kenya sites 1999</td>
<td>Kenya sites 2000</td>
</tr>
<tr>
<td><strong>Site</strong></td>
<td><strong>Water depth (m)</strong></td>
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<td>K2</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td>K3</td>
<td>45</td>
</tr>
</tbody>
</table>
Fig. 3.1 Relationship between CPUE and depth in A - 1999, B - 2000 and C - combined 1999 and 2000 results.
Fig. 3.2 Relationship between CPUE and distance from the shore in A - 1999, B - 2000 and C - combined 1999 and 2000 results.
3.2 Length frequency analysis

Data used for the length frequency analysis did not include all the sites sampled in the surveys in 1999 and 2000, due to low, or no, *R. argentea* catches, or missing samples. Furthermore, it was only possible to compare three sites between the years, as the others were too far removed from each other with respect to habitat, water depth and proximity to shore to make any meaningful comparison.

From both surveys, it was possible to examine the fish size distributions in many different lake environments, including examples from the three riparian states, deep and shallow waters, and open and sheltered areas. The sites referred to in this analysis are given in (Fig 2.1 and 2.2) for the 1999 and 2000 surveys, respectively. During this analysis, the modal means for each site are given in Table 3.2.

**Ugandan waters**

The sites sampled in Ugandan waters showed a variety of population size distribution characteristics. The first major point is that there appears to be a tendency for larger fish to inhabit deeper, or less sheltered, open water environments. In the north east sector of the Ugandan part of the lake in 1999, site U4, at 30 m deep, was one of the shallowest sites (Table 3.1), and two modes were determined at 25 mm and 32 mm (Fig. 3.3). Site U2, with a depth of 37m is the next shallowest site (Table 3.1), and showed a marked increase in fish length in comparison to site U4 as the modal means were 47 mm and 53 mm (Fig. 3.3). Site U3 had a depth of 62 m (Table 3.1), and the population exhibited a single mode at 51 mm (Fig. 3.3). Although this value was lower than the larger of the two modal means for the population at site U2 (53 mm), the population as a whole consisted of larger fish at U3 than at U2 (Fig 3.3). The final two sites sampled in Ugandan waters in 1999 (U5 and U6 located south of the Sesse islands) contradicted this trend. Site U5 was the shallower of the two sites at 29 m, yet the population had a modal mean of 51 mm (Fig. 3.3), compared to the population found at site U6 which was 46 m deep (Table 3.1), and yet the modal mean was 48 mm (Fig 3.3). In the 2000 survey, the trend of increasing mean fish length with water depth was more pronounced. Sites U1, U7, U8 and U9 (Fig. 3.4), which have water depths of 20, 28, 39 and 55 m respectively (Table 3.1) exhibited a definite increase in mean population size as water depth increased.

When comparing sites U5 and U6 (Fig. 3.3) sampled in 1999 south of the Sesse Islands and sites U7 and U8 (Fig. 3.4) sampled in 2000 north of the Sesse Islands, sites U5 and U6 had no fish below 43 mm in length, suggesting an absence of juvenile fish. Sites U7 and U8, however, had a number of juveniles within the population, although site U7, which was closer to shore than U8, supported less juveniles in the population than site U8 (Fig. 3.4).

**Tanzanian waters**

The size distributions of *R. argentea* populations in the Tanzanian sector of the lake appeared to be more randomly structured in comparison to sites from Uganda. There seems to be little correlation between size distribution and water depth. Site T3 in 1999 was the closest to the shore and there were many juvenile fish present, the modal
means in this case being 22 and 31 mm (Fig. 3.3). Site T11 in 1999 displayed similar characteristics (Fig. 3.3), as there were many juvenile fish, with a few adult fish. The populations found at sites T12a and T12b (Fig. 3.3) also comprised a number of juvenile fish, even though the water depth was 44 m (Table 3.1). However, these sites were sheltered in comparison to many of the other sites. Sites T4, T9, and T13 from the 1999 survey were all located in water less than 30m (Table 3.1), but were characterised by populations which were comprised of larger fish. This was especially evident at sites T9 and T13 (Fig. 3.3).

The populations sampled in the 1999 survey illustrate that the open water sites (T5, T6, and T7) all contributed low catches comprising mainly large fish (Fig. 3.3).

In the 2000 survey, the sites in the south east of the Tanzanian sector of the lake (U12 and U13 (Fig. 3.4)) supported populations with larger individuals than site T10 (Fig. 3.4) located in the south east. Site T11 (Fig. 3.4) cannot be included in this comparison as too few fish were caught for a reliable length frequency analysis. Site T2 was the shallowest site in 2000, and harboured the *R. argentea* population with the lowest modal mean, 36 mm (Fig. 3.4).

**Kenyan waters**

All the sites sampled from Kenyan waters gave length frequency distributions comprising of juvenile and adult fish, apart from K3, where the majority of the population was juvenile (Fig. 3.3 for 1999 and 3.4 for 2000). This seems inconsistent with the majority of the other sites around the lake, as K3 is by far the deepest site in Kenyan waters, with a depth of 43 m (Table 3.1).

### 3.2.1 Length frequency comparisons between 1999 and 2000

The three sites that were compared in 1999 and 2000, were T12a and b (1999) and T12 (2000), T13 and K1. In 1999, the length frequency from site 12a was slightly different to site 12b (Fig. 3.4), in that the distribution from 12a was bimodal, whereas 12b only had one mode. The modal lengths of these two sites in 1999 were, however, basically the same. In comparison to site T12 in 2000, however, the modal length increased from around 35 mm in 1999 to 43 mm in 2000 (Table 3.2).

The length frequency distribution for site T13 situated in water 16-20 m in depth, in the south-east section of the lake (Table 3.1), showed a bimodal distribution in 1999 (Fig. 3.3). In 2000 this had almost become a single mode, however there were a few very small fish. Their presence may well indicate new recruits to the population (Fig. 3.4).

 Lastly, at site K1 the population in 1999 only had one mode with a mean length of 35.7 mm (Fig. 3.3). In 2000 this increased in mean length to 39 mm (Fig. 3.3), and another smaller peak with a mean length of 23 mm emerged. This could possibly indicate growth of the larger individuals along with recruitment of juvenile fish of a catchable size.
Fig. 3.3 Length frequency histograms for R. argentea - August 1969.
Fig. 3.3 (cont.) Length frequency histograms for *R. argentea* - August 1999.
Fig. 3.3 (cont.) Length frequency histograms for R. argentea - August 1999.
Fig 3.4 Length frequency histograms for *R. argentea* - February 2008.
Fig 3.4 (cont.) Length frequency histograms for A. argentea - February 2008.
Table 3.2 Modal means for the *R. argentea* populations in the 1999 and 2000 surveys. First, second and third modes are given where appropriate.

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<thead>
<tr>
<th>Site</th>
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</table>

3.2.2 *R. argentea* size distributions relative to depth and distance from the shore

Regression analysis performed on the relationship between depth and the mean population length of *R. argentea* suggested that as the depth increased, so did the mean population length. Although this trend was apparent in both 1999 and 2000 the correlation with respect to this relationship was weak. ($r^2 = 0.12$ and 0.07 for 1999 and 2000 respectively) (Fig. 3.5).

The relationship for the mean population length against distance of the population from the shore revealed that with the distance from the shore, the mean population length increased (Fig. 3.6). In the 1999 survey, this trend continued for a distance of around 10 to 12 km offshore, but then began to decline (Fig. 3.6). In the 2000 survey this decreases in the mean length past a certain point did not occur. Instead, the trend suggested a constant increase (Fig. 3.6). This may however be slightly misleading as there were not as many sites sampled in offshore waters in 2000 compared to 1999 (Fig. 3.6).
Fig. 3.6 Relationship between mean length of *R. argentea* populations, and depth, in A - 1999, B - 2000 and C combined.
Fig. 3.6 Relationship between mean length of P. argentea populations and distance from the shore, in A - 1999, B - 2000 and C combined.
3.3 Size at first maturity

The proportion of mature fish in each size group was established using maturity analysis. This was plotted against standard length, which helped establish whether size at first maturity analysis could be carried out (see Fig. 3.7 for example). The length at first maturity was determined using the SOLVER programme in Excel (Table 3.3).

![Graph](image)

**Fig. 3.7** Plot of the proportion of mature fish against standard length. The trendline was determined using the Excel program SOLVER.

**Ugandan waters**

As the Ugandan waters did not have any common sites, it was not possible for any comparisons to be made between the years. In 1999, it was not possible to calculate any LM50s for females in Ugandan waters, as all females were either mature, or immature (Table 3.3). Sites U2 and U3 in 1999 were both situated in open waters (Fig. 2.1) and exhibited, between them, very few immature fish. Only four males at site U2 were found to be immature, all of the other fish at these two sites were mature. Site U4 had far less mature fish overall than site U2, yet the LM50s of the male fish at these two sites was unexpected, for the males at site U2 matured at a smaller size than their counterparts at site U4 (Table 3.3). Sites U5 and U6 (Table 3.3) had no immature fish.

*R. argentea* populations in all of the Ugandan sites sampled in 2000 had similar LM50s of around 39 mm, although, the shallow site at U1 had a population which gave a lower LM50, especially for males (Table 3.3).
Tanzanian waters

The populations sampled in 1999 and 2000 gave similar values for \( L_{50} \) of around 39 mm, with the exceptions of T4 in 1999 (\( F = 41.5 \text{ mm}, M = 40.2 \text{ mm} \)), T12 in 2000 (\( F = 41.5 \text{ mm}, M = 40.5 \text{ mm} \)) and T13 in 2000 (\( F = 36.9 \text{ mm}, M = 37.4 \text{ mm} \)). The population at site T13 in 2000 gave a low \( L_{50} \) of 36.9 mm (Females) and 37.4 mm (Males) (Table 3.3), whereas in 1999, the \( L_{50} \) was 39.8 mm (Females) and 39 mm (Males) (Table 3.3), an average decrease of 2.3 mm. However at site T12, the \( L_{50} \) increased from 1999 to 2000 by about 2 mm (Table 3.3).

Kenyan waters

*R. argentea* within the Nyanza Gulf matured at a smaller size than populations sampled over the rest of the lake (Table 3.3). Site K2 situated well into the Nyanza Gulf, supported a population whose females had an \( L_{50} \) of 34.4 mm, while the males had an \( L_{50} \) of 34.9 mm (Table 3.3). A smaller than average \( L_{50} \) for both males and females was found at site K1 in both 1999 and 2000, however, there was a slight increase from 1999 to 2000. The other site sampled in Kenyan waters was site K3, which was not situated in the Gulf and in deeper water than the other two. The \( L_{50} \) for females at this site was 39 mm, and for males was 39.5 mm (Table 3.3).

3.3.1 Comparisons of \( L_{50} \)s between male and female *R. argentea*

In general, females matured at a larger size than males. For example, in 1999, where comparisons were possible, females matured at 38.8 mm \( \pm \) 5 mm, and males matured at 38.4 mm \( \pm \) 3.8 mm (Table 3.3). In 2000, females matured at 39.1 \( \pm \) 1.6 and males at 38.7 \( \pm \) 1.5 (Table 3.3).

3.3.2 How the depth and distance from shore are related to the size at first maturity of *R. argentea*

Generally, as depth increased, so did the \( L_{50} \) of the *R. argentea* population. In both the 1999 and 2000 surveys, this trend continued until a depth of around 40 m, and then the \( L_{50} \) decreased in deeper waters (Fig. 3.8). The fitted trendlines correlated relatively well with the data in both 1999 and 2000 (\( r^2 = 0.49 \) and 0.68 respectively).

The same trend was observed when the distance from the shore was compared to the size at first maturity rather than depth (Fig. 3.9). The trend was not clearly discernible from the 1999 data, however the 2000 and combined data (Fig. 3.9) showed a definite increase in \( L_{50} \)s until around 6.5 km offshore, which correlates with a depth of about 40 m, and then decreased.
Table 3.3 Size at first maturity for each site (1999 and 2000). Key NI = None immature, the number in brackets is the population mode, NM = none mature, the number in brackets is the population mode, ND = no data.

<table>
<thead>
<tr>
<th>Site</th>
<th>Female (LM50)</th>
<th>Male (LM50)</th>
<th>Site</th>
<th>Female (LM50)</th>
<th>Male (LM50)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Female (LM50)</td>
<td>Male (LM50)</td>
<td></td>
<td>Female (LM50)</td>
<td>Male (LM50)</td>
</tr>
<tr>
<td>U1</td>
<td>38.5</td>
<td>36.6</td>
<td>U7</td>
<td>38.9</td>
<td>39</td>
</tr>
<tr>
<td>U2</td>
<td>NI (46.7)</td>
<td>37.5</td>
<td>U8</td>
<td>39.5</td>
<td>39.5</td>
</tr>
<tr>
<td>U3</td>
<td>NI (50.8)</td>
<td>NI (50.8)</td>
<td>U9</td>
<td>39.1</td>
<td>39</td>
</tr>
<tr>
<td>U4</td>
<td>NM (28.2)</td>
<td>39.8</td>
<td></td>
<td>Variance</td>
<td></td>
</tr>
<tr>
<td>U5</td>
<td>NI (51.1)</td>
<td>NI (51.1)</td>
<td>U5</td>
<td>2.6</td>
<td>1.7</td>
</tr>
<tr>
<td>U6</td>
<td>NI (48.3)</td>
<td>NI (48.3)</td>
<td>U6</td>
<td>38.7</td>
<td>39</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td></td>
<td>T2</td>
<td>40.5</td>
<td>39.5</td>
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<td>Mean (Uganda)</td>
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<td></td>
<td></td>
<td>Variance</td>
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<td>Mean</td>
<td></td>
<td></td>
<td>Mean (Tanzania)</td>
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<td></td>
</tr>
<tr>
<td>Mean</td>
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<td>Mean (Kenya)</td>
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<td>MEAN</td>
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<td>Mean (Whole Site)</td>
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<tr>
<td>Mean</td>
<td>MEAN</td>
<td></td>
<td>Mean (Whole Lake)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Fig. 3.8 Relationship between the size at first maturity of R. argentea populations and depth in A - 1990, B - 2000 and C combined.
Fig. 3.9 Relationship between the size at first maturity for populations of R. argentea and distance from the shore, in A - 1999, B - 2000 and C - combined.
3.4 Maturity analysis

In general, if the population had a wide range of individual fish sizes present in the population, there was a gradual change in fish maturity from stage 1 to stage 6 as fish length increased, as in site T11 (Fig 3.10). The larger fish therefore seem to be carrying out most of the breeding within the population. In most of the populations sampled, fish tended to breed once they had reached about 43 or 44 mm in length. However, there was a small number of populations sampled which showed characteristics uncommon to the majority of the sites. For example, populations in the Nyanza Gulf, within Kenyan water (K1, K2), gave indications of individuals breeding at a small size (around 36 mm) (Fig. 3.10 – females, and Fig. 3.11 - males). The population sampled at K2 showed intense breeding from 35 mm, especially among females (Fig. 3.10 – females, and Fig. 3.11 - males).

Although the population from K1 (Fig. 3.10 – females, and Fig. 3.11 - males) did show some breeding at a small size, it was not as intense as was found at site K2. Furthermore, the males at site K1, in both the 1999 and 2000 surveys were mostly found to be at maturity stage three (resting) (Fig. 3.11, and 3.13 respectively).

Some further points to note, were that the populations at sites U5 and U6 in 1999 (Fig. 3.10 – females, and Fig. 3.11 – Males) were highly mature, especially site U6. Sites U9 and T8 in 2000 were also highly mature (Fig. 3.12 - females and 3.13 - males). Lastly, the populations at sites T12a and b in 1999 did not seem to show evidence of breeding, even though there were a large number of large fish present (Fig. 3.10 – females and Fig. 3.11 – males). In 2000 the situation at site T12 was slightly better in that more fish were breeding, but the incidence was still low (Fig. 3.12 - females and 3.13 - males).

3.4.1 The effect of depth and distance from the shore on the proportion of breeding R. argentea.

The main point to note about the effect of the depth on the proportion of R. argentea at maturity stages five or six in a population, is that there is no obvious trend. In both 1999 and 2000 there were large variations in the proportion of the population at maturity stage five or six, yet no trend was discernible (Fig. 3.14)

When the relationship between the proportion of R. argentea at maturity stages five or six and distance from the shore was examined, it was found that as distance from the shore increased, so did the proportion of the population ready to breed (Fig. 3.15). The data collected from the 1999 survey, suggested that after a distance of around 12 km offshore, the proportion at maturity stages five and six started to decrease, and the trendline correlated to the data relatively ($r^2 = 0.56$) (Fig. 3.15).
Fig. 3.10 Maturity stages of female *F. argentea* in the 1998 survey. Site identification numbers are given in the top right of each graph.
Fig. 3.10 (cont.) Maturity stages of female *F. argentea* in the 1989 survey. Site identification numbers are given in the top right of each graph.
Fig. 3.11 Maturity stages of male *R. argus* sampled in 1986. Site identification numbers are in the top right of each graph.
Fig. 3.11 (cont.) Maturity stages of male *R. argentea* sampled in 1999. Site identification numbers are in the top right of each graph.
Fig. 3.12 Maturity stages of female *R. argentea* sampled in 2006. Site identification numbers are given in the top right of each graph.
Fig. 3.12 (cont.) Maturity stages of female R. argentea sampled in 2000. Site identification numbers are given in the top right of each graph.
Fig. 3.13 Maturity stages of male *R. argentea* sampled in 2000. Site identification numbers are given in the top right of each graph.
Fig. 3.13 (cont.) Maturity stages of male R. argentea sampled in 2000. Site identification numbers are given in the top right of each graph.
Fig. 3.14 Relationship between the proportion of the *R. argentea* population at maturity stages 5 or 6, and depth, in A - 1993, B - 2000 and C - combined.
ig. 3.16 Relationship between the proportion of the R. argentea population at maturity stages 5 or 6 and distance from the shore, in A - 1990, B - 2000 and C - combined.
3.5 Fecundity

Data for fecundity were pooled with respect to year and site, as a comparison between sites would have proved difficult due to limited data for individual sites. The main point to note about the fecundity of R. argentea over the lake, was that it increased with fish length (Fig. 3.16). There is also a large variation in fecundity in each length class between populations of R. argentea (Fig. 3.16).

3.6 L. intestinalis analysis

3.6.1 L. intestinalis prevalence

The data collected for the infestation of L. intestinalis in R. argentea populations across the lake were pooled. In general as the as the fish got larger, so the prevalence of L. intestinalis increased, exponentially for fish greater than 40 mm (Fig 3.17).

When comparing the regression coefficient of the log weight, log length relationships of R. argentea populations with the prevalence of L. intestinalis, it was found that those populations where L. intestinalis was most prevalent showed the highest regression coefficients. This can be seen in Table 3.4, in that most of the populations gave a regression coefficient around three (isometric growth), but, sites U2, U5, T6 and T9, which all had L. intestinalis prevalence above 15%, gave regression coefficients above 3.6 (Table 3.4). Site U5, which had a L. intestinalis prevalence of 52.7% gave a regression coefficient of four, which normally implies that the weight of the fish is more than it should be for its length, often indicating a good condition factor. There were two anomalies to this trend, however, as sites T4 and T13 had L. intestinalis prevalence of 4.9% and 3% respectively, yet their regression coefficients were both 3.8, which is high in comparison to the majority of the other sites (Table 3.4). This again indicates a good condition factor.

3.6.2 The effect of depth and distance from the shore on the prevalence of L. intestinalis in R. argentea populations.

There was no clear relationship between the prevalence of L. intestinalis in fish greater than 40 mm in length, and either depth (Fig. 3.18) or distance from the shore (Fig. 3.19), in either 1999 or 2000. Linear regression was carried out to establish whether a trend was discernible, but none was found.

3.6.3 L. intestinalis intensity

L. intestinalis intensity is the number of parasites in each fish host. Below 40 mm, most fish infected with L. intestinalis harboured only one parasite (Fig. 3.20). In larger fish however, the intensity of L. intestinalis increased markedly, and fish above 58 mm in length harboured the greatest number of L. intestinalis (Fig. 3.20).
Fig. 3.16 Relationship between the length and fecundity of *R. argentea* in Lake Victoria.

\[ y = 38.306x + 0.11.89 \]
\[ R^2 = 0.2229 \]

Fig. 3.17 Relationship between *R. argentea* length and prevalence of *L. intestinale*.
Table 3.4 Length weight relationships from the 1999 survey, showing regression coefficient $b$, the intercept on the y axis $\log a$, the correlation $r^2$, and the prevalence of $L$. intestinalis.

<table>
<thead>
<tr>
<th>Site</th>
<th>Regression coefficient ($b$)</th>
<th>Intercept on y axis ($\log a$)</th>
<th>Correlation ($r^2$)</th>
<th>$L$. intestinalis prevalence (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>U2</td>
<td>3.8</td>
<td>-6.3</td>
<td>0.98</td>
<td>19.7</td>
</tr>
<tr>
<td>U3</td>
<td>3.3</td>
<td>-5.4</td>
<td>0.93</td>
<td>3.1</td>
</tr>
<tr>
<td>U4</td>
<td>2.8</td>
<td>-4.9</td>
<td>0.92</td>
<td>1.7</td>
</tr>
<tr>
<td>U5</td>
<td>4.0</td>
<td>-6.6</td>
<td>0.95</td>
<td>52.7</td>
</tr>
<tr>
<td>U6</td>
<td>2.9</td>
<td>-4.8</td>
<td>0.98</td>
<td>4.1</td>
</tr>
<tr>
<td>T4</td>
<td>3.8</td>
<td>-6.3</td>
<td>0.99</td>
<td>4.9</td>
</tr>
<tr>
<td>T6</td>
<td>3.7</td>
<td>-6.2</td>
<td>0.97</td>
<td>25.9</td>
</tr>
<tr>
<td>T9</td>
<td>3.6</td>
<td>-5.9</td>
<td>0.99</td>
<td>21.1</td>
</tr>
<tr>
<td>T11</td>
<td>3.3</td>
<td>-5.4</td>
<td>0.99</td>
<td>0.6</td>
</tr>
<tr>
<td>T12a</td>
<td>3.3</td>
<td>-5.5</td>
<td>0.99</td>
<td>0.0</td>
</tr>
<tr>
<td>T12b</td>
<td>3.2</td>
<td>-5.3</td>
<td>0.97</td>
<td>1.7</td>
</tr>
<tr>
<td>T13</td>
<td>3.8</td>
<td>-6.4</td>
<td>1</td>
<td>3.0</td>
</tr>
<tr>
<td>K1</td>
<td>3.1</td>
<td>-5.1</td>
<td>0.99</td>
<td>3.0</td>
</tr>
<tr>
<td>K2</td>
<td>3.1</td>
<td>-5.1</td>
<td>0.96</td>
<td>0.3</td>
</tr>
</tbody>
</table>

3.6.4 $L$. intestinalis size

It was apparent that the larger fish in the Lake Victoria $R$. argentea population harboured large $L$. intestinalis. In fact, it seemed that in fish below 40 mm in length, the length of the parasite was generally less than that of the host fish. However, as fish length increased, the proportion of the length of $L$. intestinalis in relation to fish length altered in favour of the parasite (Fig 3.21).

3.6.5 The effect of $L$. intestinalis parasitism on $R$. argentea fecundity

It was found that $L$. intestinalis parasitism reduced the fecundity of $R$. argentea (Fig. 3.22). The rate at which fecundity increases with size was also reduced by the presence of $L$. intestinalis, as was shown by a shallower trendline gradient (Fig. 3.22).

3.6.6 Effect of $L$. intestinalis on fish breeding

Four sites were chosen to examine the effect of $L$. intestinalis on the breeding of $R$. argentea. Only sites with an $L$. intestinalis prevalence of 10% or above, as well as a total sample number of over 100 fish. The sites which met these criteria were U2, U5 and T9 from the 1999 survey, and K1 from 2000. The data obtained were used to examine the proportion of the whole population breeding, including those parasatised by $L$. intestinalis, and compare these results to the proportion of the population breeding based solely on fish parasatised by $L$. intestinalis. The $LM_{50}$ was used as a starting length at each site, and was therefore site specific.
Fig. 3.18 The effect of depth on the prevalence of *L. intestinalis* in *R. argintae* populations, in A - 1999, B - 2000 and C - combined.

\[ y = 0.1007x + 12.055 \]
\[ R^2 = 0.0054 \]

\[ y = -0.1339x + 10.629 \]
\[ R^2 = 0.0333 \]

\[ y = 0.0142x + 10.943 \]
\[ R^2 = 0.0001 \]
Fig 3.10 The effect of distance from the shore on the prevalence of L. intestinalis in R. argenteus populations, in A - 1959, B - 2003 and C - combined.
Fig. 3.20 Relationship between the average number of *L. intestinalis* present in each fish and fish length

\[ y = 0.297e^{0.032x} \]

\[ R^2 = 0.6332 \]

Fig. 3.21 Relationship between fish length and average length of *L. intestinalis*

\[ y = 1.093x - 17.359 \]

\[ R^2 = 0.6929 \]
Table 3.5 Percent of the whole population breeding and the percent of those fish harbouring *L. intestinalis* breeding.

<table>
<thead>
<tr>
<th>Year</th>
<th>Site</th>
<th>Female</th>
<th>Male</th>
<th>Female</th>
<th>Male</th>
</tr>
</thead>
<tbody>
<tr>
<td>1999</td>
<td>U2</td>
<td>59</td>
<td>35</td>
<td>11</td>
<td>14</td>
</tr>
<tr>
<td>1999</td>
<td>U5</td>
<td>46</td>
<td>56</td>
<td>21</td>
<td>39</td>
</tr>
<tr>
<td>1999</td>
<td>T9</td>
<td>17</td>
<td>14</td>
<td>7</td>
<td>0</td>
</tr>
<tr>
<td>2000</td>
<td>K1</td>
<td>42</td>
<td>20</td>
<td>11</td>
<td>4</td>
</tr>
</tbody>
</table>

Fig. 3.22 Relationship between *R. argentea* length and fecundity. Equation 1 (corresponding to trendline 1) represents the fecundity of those fish with no *L. intestinalis* present. Equation 2 (corresponding to trendline 2) represents the fecundity of those fish parasitised by *L. intestinalis*.
It was found that when fish harbouring *L. intestinalis* were examined separately, in all cases the proportion of the percentage breeding was lower than when the population as a whole was examined (Table 3.5).

At site U2 (Fig. 3.23) the populations as a whole demonstrated a normal pattern of maturity stages. There seemed to be a number of fish at maturity stages five and six, as well as stage four, which is the development between resting and buried. In the sample from U2 which consisted entirely of *L. intestinalis* infected individuals, there was a dramatic difference, as the vast majority of the fish were at maturity stage three. Furthermore, there was no discernible pattern of progression through the maturity stages with an increase in length, as was found for the majority of the *R. argentea* populations throughout Lake Victoria (Figs. 3.10–3.13). This phenomena, where *L. intestinalis* infected fish remained at maturity stage three, was found throughout the sampled sites (Figs. 3.23 and 3.24). Indeed, at site K1 the infected males showed a higher proportion of fish at maturity stage two (Fig. 3.24), even up to a length of 46 mm, which is rare. Although not all the sites were compared directly for the effect of *L. intestinalis* on host maturity, it was noted from general observation that in the majority of cases, fish harbouring *L. intestinalis* did not progress past maturity stage three.
Fig. 3.23 Graphs on the left show the proportion of fish in each maturity stage in a whole \textit{R. argentea} population. Graphs on the right (corresponding to those on the left), are the maturity stages of only those fish found to be parasitised by \textit{L. intestinalis}. A - Site U2 (females), B - Site U2 (males) C - Site U6 (females), D - Site U6 (males)
Fig. 3.24 Graphs on the left show the proportion of fish in each maturity stage in a whole *R. argentea* population. Graphs on the right (corresponding to those on the left), are the maturity stages of only those fish found to be parasitized by *L. intestinalis*. A - Site T9 (female), B - Site T9 (male) C - Site K1 (female), D - Site K1 (male)
4. DISCUSSION

4.1 Trends in CPUE around Lake Victoria

The general trend for the catch per unit effort (CPUE) of *R. argentea* in Lake Victoria is a decrease with distance from the shore. Statistically, however, this trend, which is apparent in both 1999 and 2000 is weak: the highest $r^2$ value for the relationship between depth and CPUE is only 0.3. In theory, the amount of nutrients present in the water column will decrease as distance from the shore increases, as they are generally introduced to the lake system either by runoff from agricultural and urban sources (Kenyanya, 1999) or via rivers (Bootsma and Hecky, 1993). This ensures that areas in close proximity to the shoreline have a higher nutrient loading than offshore waters (Kenyanya, 1999). Furthermore, deep water is usually more resistant to mixing than the shallow littoral areas, especially when it is in a state of thermal stratification (Wetzel, 1983). Thus, when nutrients fall to the lakebed in the form of organic matter, they are recycled at a slower rate than they would be in shallow waters (Wetzel, 1983). The combined effect of both these factors is a nutrient concentration gradient, initially high in inshore waters, decreasing with distance from shore. The greatest primary production is therefore concentrated in inshore areas (Kenyanya, 1999), subsequently creating a basis upon which higher trophic levels can build, such as zooplankton communities, which in turn form a food source for fish populations like *R. argentea*. Furthermore, in offshore waters, primary production is not constant as the recycling of nutrients to the surface layers only occurs when the thermocline breaks down (Wetzel, 1983). This implies that even if there is no thermal stratification for most of the year (which is unlikely), there is likely to be some periods when there is little primary production, creating a less stable environment for fish populations. Inshore however, as nutrients are continually being introduced (Kenyanya, 1999), the problem of an unstable environment with respect to food availability is far less dramatic.

In the Mwanza Gulf region of Lake Victoria, the highest densities of adult *R. argentea*, and therefore the highest CPUE, were found 2 km offshore at a depth of around 14 m (Wanink, Goudswaard and Berger, 1998). These findings are comparable to the results in this study, as the CPUE seems to be high at around 2 km offshore in both 1999 and 2000. However, as the shallowest trawl in this study was 14 meters deep, a large component of the *R. argentea* population was missed, which means the trend in the CPUE of the species up to a depth of 14 m could not be established. These missing data would have been useful since it has been found that biomass increased from the shore to reach a peak at a depth of 14 m and then declined (Wanink, Goudswaard and Berger, 1998), which gives a far more holistic view of the situation.

The trend of decreasing CPUE with increasing distance from shore does not however continue indefinitely. At around 10 km offshore, around a water depth of 45 m, few *R. argentea* were caught, suggesting that the extreme open waters of Lake Victoria are not inhabited by *R. argentea*. Although *R. argentea* is considered a pelagic species (Mannini *et al.*, 1992), it has recently been recognised that its spawning areas lie inshore (Wanink, 1999). Perhaps this explains why the species was not caught in waters miles from shore, for it has a distinct life history strategy linked to its inshore breeding grounds. Furthermore, evidence suggests (Wetzel, 1983) that primary...
production in deeper waters is poor because the majority of the nutrients are locked in
the sediment, or else held below the thermocline which experiences little breakdown
in these deep, offshore waters (Kenyanya, 1999). Subsequently this lack of food
available to *R. argentea* makes the extreme offshore areas unable to sustain
populations of the fish.

Contrary to the overall trend, which asserts the decrease of the CPUE moving from
the shore, there are a number of anomalous populations associated with certain sites.
The first of these is site U4, sampled in 1999. Although it is located only 1 km
offshore it has an extremely low CPUE of 30 g trawl hr$^{-1}$. This may be due to the
location of the site as it is situated in a channel where the depth of the water is greater
than the predicted levels by about 10 m. Additionally, the channel’s profile may be
steep, which would ensure a lack in littoral breeding areas where *R. argentea* may
reproduce (Wanink, 1999), thus reducing the prospect of a viable population.
However, these explanations are academic for it is reasonable to assert that the frame
trawl may have missed *R. argentea* populations which were present.

Site U3, sampled in 1999, is another location where there is a notable anomaly
relating to the abundance of *R. argentea*. The site is 14.5 km offshore and has a water
depth of 62 m, yet the CPUE was 5870 g trawl hr$^{-1}$. This result is unusual both with
respect to depth and distance from shore, as it is much larger than predicted. The
unusually high catch could be explained if the trawl sampled just above the oxycline
where *R. argentea* feed during the daytime (Wanink, Kashindye, Goudswaard and
Witte, 1998; Wanink, 1992). It has recently been asserted that there is evidence which
suggests *R. argentea* school in response to emerging lakeflies (Wanink and Berger,
1998). Although this phenomenon is reported to occur at night, it could be argued that
the same idea could be applied to its feeding habits during the day. Shoals of *R.
argentea* could feed upon other prey, which may be concentrated by water currents in
the lake, thus intensifying their density, which would lead to unexpected high yields.

In most cases it was not possible to compare populations between years, as the sites
were not constant. The sampled sites were only situated in the same general locations,
and population dynamics can be altered by even the slightest inconsistencies in
environmental conditions. Nevertheless, the same basic trend was observed annually
as the CPUE decreased with distance from the shore. One site, however, is interesting
as it displayed a huge discrepancy between 1999 and 2000. In 1999 the CPUE at site
T4 was 20500 g trawl hr$^{-1}$, whereas in 2000 no fish were caught. This may be linked
to depth since the site was 13 m shallower in 1999 than in 2000, but this seems to be a
rather large discrepancy to be explained away by a change in the depth profile.
Alternatively, the depth may not be the defining feature, as the samples could have
been obtained at different times, with 1999 catch coinciding with a feeding shoal.
Nonetheless, these suggestions are only speculative as numerous explanations can
account for the difference. In order to form a reasonable conclusion more research is
necessary.

4.2 Length distribution of *R. argentea* over Lake Victoria

Both surveys demonstrate that as the distance from the shore, and hence the depth
increases, so does the mean length of the *R. argentea* populations. However, in both
surveys there was a wide variation between each site, even those with similar depth profiles. This is emphasised by the weak correlation when the data were pooled ($r^2 = 0.1$). Stronger correlations were found when the distance from the shore, as opposed to the depth, was used as the basis for comparisons of population mean lengths, with correlation coefficient of 0.61 and 0.42 for 1999 and 2000 respectively. This difference between the correlations may be explained by the depth fluctuations, as these occur naturally over the lakebed irrespective of the distance from the shore, and were found amongst the samples. Nevertheless, the trend observed was an increase in the mean length of *R. argentea* with depth and/or distance from the shore. This suggests that *R. argentea* is an inshore spawning species, as opposed to the earlier belief that the fish spawns in a pelagic environment (Graham, 1929; Greenwood, 1966; Wandera, 1993). This is supported by the lack of eggs in hundreds of samples of zooplankton from offshore waters (Wanink, 1999). Therefore, as *R. argentea* is now recognised as an inshore spawner, it is logical to expect the nursery areas for this species to be found along the shoreline, which would account for the higher proportion of smaller fish in the inshore zone in comparison to offshore areas.

Although the mean length of *R. argentea* increased with distance from the shore, this trend is not linear. Instead the results from 1999 suggest that the mean length of *R. argentea* reaches a plateau at approximately 10 km from the shore, then declines. This occurrence may be explained by the lack of nutrients in the deep open waters. Open waters generally support low levels of primary production, thus the food source available to the *R. argentea* populations is reduced. Just as this affects the CPUE, it also culminates in a diminished growth rate in *R. argentea* and hence a smaller overall size. This trend may also be explained by the horizontal migratory movements of *R. argentea*. As there seems to be growing evidence to suggest that *R. argentea* is an inshore spawning species, it means the young inhabit areas close to the shore, yet as its adult habitat is pelagic it must migrate as it grows. Therefore an apparent trend is established, where the mean population length increases with distance from the shore. The peak mean length at around 10 km offshore, may be because of a higher proportion of larger fish which may be present as they return from deeper waters to spawn. Thus a cycle is therefore where small fish inhabit inshore waters, migrate to their offshore grounds and return inshore to spawn.

From the length frequency information obtained from each site it possible to see that whilst there is a general trend, there are still large variations both with respect to mean length, as well as the modal distributions of fish at different ages within each population. In the 1999 survey, for example, site U3 had a single modal mean of 50.8 mm, site T3 had a bimodal distribution, with means of 21.7 mm and 30.8 mm, and site U2 displayed a trimodal distribution (means of 36 mm, 46.7 mm and 53.3 mm). The information regarding the depth and distance from shore of each site account for these differences. Site T3 is closest to the shore, which explains the populations small mean length, as juveniles contribute a high fraction of the catch. The smaller contribution of slightly bigger individuals (modal mean 30.8 mm) are probably *R. argentea* from the last but one spawning, which occur in August and December - January (Wandera, 1999), and have yet to move out into the lake. Site U2 which had the trimodal population distribution, is second furthest from the shore. The trimodal distribution probably represents the contribution from the spawning events. As these fish are different lengths it suggests that *R. argentea* do not move away from their nursery.
areas at uniform rates. This population may also include large buried females returning to the spawning areas to breed. Finally, site U3 that harbours the population with only one modal peak of large fish (50.8 mm) is furthest from the shore. Here the vast majority of the population are fish above 45 mm in length which supports the argument that *R. argentea* is an inshore spawning species which move into a more pelagic habitat to mature.

The results obtained for the length distribution for the population sampled at site U4 further supports the argument that small fish inhabit areas in close proximity to the shore for the distance from the shore of this site is 1 km. Although the small fish constitute the majority of the population (modal means are 25 mm and 32 mm), there are a number of larger fish, whose importance cannot be overlooked. Possibly, these larger fish are moving towards the shore to breed or returning to the deeper waters once they have spawned.

The most important point to note regarding the trend in length distributions of *R. argentea* populations, is that in general juveniles inhabit the inshore areas and as one moves away from shore, the fraction of adults constituting the population increases. As has been mentioned previously, (Wanink, Goudsward and Berger, 1998) it has been found that in the Mwanza Gulf region of the lake the highest fraction of adults were about 2 km offshore. This was not the case in this study, as the highest mean population lengths were about 10 km offshore. This discrepancy may be a result of experimental error, but a plausible explanation is that this study takes into account the whole lake, whereas the aforementioned study was solely concentrated on the Mwanza Gulf region. The theory that juvenile *R. argentea* inhabit inshore areas, which differs from the previously held view of *R. argentea* as a pelagic spawner (Graham, 1929; Wandera, 1993), has major implications with respect to management. For, if the inshore areas are overfished, especially with small mesh sized nets, such as mosquito seines which are being utilised more frequently, there is a very real danger of overfishing the juvenile fraction, and thus overexploiting the stock (Wanink, 1999). As the smaller *R. argentea* provide less protein for both man and animal, more are needed than if the larger ones were caught, which compounds the problem of exploitation. Therefore, in order to reduce the exploitation of juvenile fish, restrictions on fishing close to shore may need to be introduced, as well as regulations regarding the mesh sizes of the nets (Wanink, 1999; Wandera unpublished(a); Othina, 1999).

4.3 The maturity and breeding of *R. argentea*

Arguably, there are three major factors contributing to the survival of a species: growth, reproduction and mortality (Stearns, 1992). An organism must make tradeoffs between growth and reproduction to ensure the best chance of passing its genes on to the next generation before it dies (Wootton, 1990). This often leads to phenotypic changes in a fishes size at first maturity, fecundity, egg size, growth and life expectancy (Begon, Harper and Townsend, 1996). Over a longer time period, genes which are more favourable in certain environmental conditions, will be selected making the species as a whole better suited to its surroundings (Wootton, 1990). Indeed, under circumstances of increased mortality, resulting from stressful influences such as predation and overfishing, a fish invariably grows faster and reproduces earlier (Wootton, 1990). This strategy increases the chances of reproduction at a
younger age, rather than placing more effort into reproducing later when there is a higher chance of mortality, which would decrease the chance of any reproductive contribution to the population (Campbell, 1996).

In order to classify animals according to their life history tactics two terms are commonly used to signify opposing sides of a grey scale (Begon, Harper and Townsend, 1996), which are known as r and K strategies. A fish which is classed as r-selected is expected to show a higher degree of life history plasticity concerning factors such as age at first maturity and growth rate, and can therefore survive more effectively in a stressed environment (Wooton, 1990). Wanink (1998b) showed R. argentea to have a life history strategy which places it further towards being an r than a K strategist, especially when it is compared to its main competitors in the lake, the haplochromines (Wanink, 1991). This assumption has been drawn as R. argentea produces more and smaller eggs, exhibits less parental care, and feeds in a more generalist fashion than most haplochromines (Wanink, 1998b). Although it has been recently hypothesised that the haplochromines are becoming more r-selected (Kaufman and Ochumba, 1993), it would perhaps be more accurate to assert that in a stressful environment, their phenotypic plasticity is more likely to be apparent as they are forced to take the necessary steps to survive.

Life history theory predicts that as there is a trade-off between investing in reproduction and somatic growth (Stearns, 1992), earlier maturation may result in the reduction in fish length (Wanink, 1998a). Wanink continued by suggesting an alternative to this as he suggested that if the fish respond to increased stress by producing more eggs, the average size of the fish may expand, for as R. argentea's length increases so does its fecundity (Wanink, Witte and Hoogenboezem, 1998). Indeed, in a study in Kenyan waters, R. argentea with a length of 60 mm were found to have 1350 eggs, whilst fish of 41 mm only had 170 eggs (Manyala, Nyawade and Rabuor, 1992). Normally, an increase in fecundity correlates with a decrease in egg size (Wootton, 1990), yet it has been found that R. argentea do not conform to this phenomenon. Instead this species displays a positive correlation with respect to both egg size and fecundity, with fish size (Wanink, Witte and Hoogenboezem, 1998). However, the average fecundity for R. argentea has decreased by approximately 50 percent since the introduction of Nile perch (Wanink, 1991). Therefore, the initial statement where early maturation and a reduction in length will occur in response to a stressed environment, is the most likely outcome.

As information based upon temporal changes for R. argentea was not collected in this study, it was impossible to gain a detailed overview of the life history tactics adopted by R. argentea in response to a changing ecosystem. Nevertheless, it is possible to obtain a spatial comparison between sites over different parts of the Lake. The length at 50% maturity (LM50) found for the R. argentea populations over the whole lake was 38.7 mm ± 2.7 mm. LM50 for the Ugandan and Tanzanian sectors of the lake were 38.7 mm ± 0.1 mm and 39.4 mm ± 1.6 mm respectively, which correlates well with the whole lake population. However, the population in the Kenyan waters had a lower LM50 of 36.8 mm ± 3.5 mm. The Kenyan status may be due to a higher degree of fishing pressure, perhaps because of the high number of humans reliant on the fishery in the Kenyan waters. The sites within the Nyanza Gulf showed a much lower LM50 of only 36 mm in comparison to an LM50 of 39.3 mm at site K3, which is in Kenyan
open waters. Again, this may occur because of the increased pressure on the *R. argentea* populations within the Gulf due to fishing, which forces the fish to respond by altering their life history tactics and reproducing at a smaller size. Additionally, the trade-off between reproduction and somatic growth may result in a reduction in overall fish length and generation time (Wanink, 1998a).

A further explanation for the smaller LM50s of *R. argentea* populations in the Kenyan water is perhaps because this *R. argentea* fishery has been in existence for a relatively long period of time (over twenty years), as has the Tanzanian fishery. It has also been suggested that *R. argentea* in Kenyan waters is overexploited (Okaronon, 1994), and in the past the usual mesh size was 8-10 mm, whereas now mesh sizes of 5 mm are more common (Mannini et al., 1992). This combination of factors may have resulted in the selection of small fish, which can reproduce at a smaller size, and exhibit a shorter generation time (Wanink, 1991). This phenomenon is a classic case of growth overfishing, and arises when a fish stock becomes heavily exploited, and larger fish are removed from the population (King, 1996). This effect is compounded as the fishermen usually select the larger fish. As long as recruitment remains unaffected, and smaller fish are continually added to the exploitable section of the population, the mean length of fish in the population will decrease (King, 1996). A combination of fishing intensity and age of the fishery are likely to be the most important factors governing LM50 and mean generation time, which in turn is likely to be influenced by the accessibility of the fishing area, and the demand for fish in that region. Therefore, it is logical to assume that an area like the Mwanza or the Napoleon Gulf may exhibit many of the same characteristics as the Nyanza Gulf, however as the *R. argentea* fishery in the Napoleon Gulf is much younger, these effects have yet to be seen (Mannini et al., 1992). The only one of these areas which was sampled was the Nyanza Gulf which gave definite indications of low LM50 within the Gulf, highlighting the effect on *R. argentea* populations from fishing.

I have mentioned previously that as the sites were only grouped into the same general locations any comparison between years is difficult. Furthermore, the samples that constitute this study were taken at different times of the year and other factors may not have remained constant, such as fishing intensity or the Nile Perch density. Despite all of these shortcomings, in the 2000 survey, the *R. argentea* population in the Kenyan waters at site K1 appears to show an increase in LM50 of approximately 1.5mm. No conclusions can however, be drawn from this, as only six months had elapsed between surveys, so the most likely explanation is the capture of a different population of *R. argentea*. For any ecological conclusions to be developed this area would have to be re-tested in a way that ensures as many factors as possible are kept constant, and to sample at regular intervals over a longer time period.

It is not only the location which effects the LM50, as there is a relationship between the latter and water depth, and/or distance from the shore. Generally, as the water depth and/or distance from the shore increased so did the LM50, but it declined again in more open waters. The reason for the LM50 being lower at the inshore areas is probably due to the fishing pressure on *R. argentea*. The low LM50 would increase the individual's chance of reproduction under the circumstances of exaggerated mortality. As *R. argentea* migrates away from the shore, fishing pressure is reduced, as open water areas are more inaccessible to fishermen. Thus it becomes more beneficial for
the fish to put more effort into somatic growth, for at a larger size the female is able to produce a greater number of eggs (Wanink, Witte and Hoogenboezem, 1998). At around 40 metres deep, which is approximately 6.5 km from the shore (Fig. 2.3), the LM_{50} begins to decline. This trend is more difficult to explain. It may be a consequence of low food availability, which would indicate that the increased effort put into somatic growth instead of reproduction is wasted. Consequently, it would take longer to reach a length suitable for reproduction if the growth rate is slower, and hence increase the possibility of mortality before the reproductive act is completed. A more likely scenario however, would be the horizontal migration of large R. argentea as they return to the shore to breed. This would mean a higher proportion of larger fish would occupy waters close to the shore, thus increasing the LM_{50}.

4.4 Assessment of ripe R. argentea

In the majority of cases, the proportion of the R. argentea population which was sampled exhibiting stages five or six on the maturity scale, did not appear to show a strong relationship towards depth or distance from the shore, if indeed any relationship could be found. However, when the data for both years were pooled the proportion of males and females at maturity stages five or six was low in populations close to the shore, increasing offshore. The lower proportion of both ripe males and females found in shallow inshore waters contradicts the theory that R. argentea are inshore breeders, instead favouring the more traditional belief that the fish is a pelagic spawner (Graham, 1929). One explanation for this finding which would not negate the evidence of the species being an inshore breeder, would be to recognise how R. argentea mature for breeding in the offshore waters migrating inshore for spawning. In future research this behaviour will need further assessment as it is an important feature of R. argentea’s life cycle.

4.5 The effect of L. intestinalis on R. argentea

When comparing the log length, log weight relationships between populations of R. argentea, those which had a greater prevalence of L. intestinalis were heavier than expected for a given length, assuming that R. argentea exhibits isometric growth (Wanink, 1989). This is most probably due to the added weight of the parasite, as it has been found in previous studies that R. argentea infected with L. intestinalis are, on average, 21% lighter (dry weight), when the parasite was removed, than their uninfected counterparts (Wanink, 1992). In this study a similar assessment would have been useful, however, accurate weight measurements of the parasites could not be taken due to inexact balances.

The prevalence of L. intestinalis in R. argentea increased dramatically in individuals greater than 40 mm. One of the major explanations for this difference of infestation in different sized fish, may be a change in diet from small to large zooplankton as the fish grows. L. intestinalis larvae arguably have numerous intermediate hosts, and one is likely to be a zooplankton copepod (Wyatt and Kennedy, 1988). The fact that L. intestinalis only seems to infect larger individuals is an important finding, and may be linked to only larger R. argentea being able to ingest the primary host zooplankton. This infestation has important implications for reproduction in R. argentea because as fish length increases a higher proportion of individuals exhibit maturity stages five
and six, which means that they are ready to breed. If the presence of *L. intestinalis* has a detrimental effect on maturation and hence reproduction (Arme, 1975), there may be cause for concern, especially if *L. intestinalis* takes advantage of the perturbed Lake Victoria environment (Bugenyi and Magumba, 1996). This was confirmed by the present study as *L. intestinalis* apparently had an effect on *R. argentea* maturation. In the majority of *L. intestinalis* infected fish maturation was generally arrested at stage three.

Numerous explanations can be proposed as to why the presence of *L. intestinalis* effects maturation, including the suggestion that the parasite releases a sex steroid which may suppress gonadotrophin producing cells in the pituitary gland (Arme, 1968). However, the validity of this statement was negated, for when it was tested, no sex steroids were found to have been released by *L. intestinalis* (Arme, Griffiths and Sumpter, 1982). This leaves a number of other possibilities for the apprehended maturity progression. For example, the parasite may produce a non-steroid substance which inhibits gonadal development, or else it may produce a stress response in the fish host (Arme, Griffiths and Sumpter, 1982). Furthermore, being a parasite, *L. intestinalis* absorbs its nutrients from its host, thus reducing the energy that *R. argentea* can award to reproduction (Campbell, 1996). Although there is no one proven cause, whatever mechanism *L. intestinalis* uses to inhibit reproduction in the fish host, there is an apparent consensus (Arme, Griffiths and Sumpter, 1982), which corresponds to the results of this study, suggesting that *L. intestinalis* has a very real effect on *R. argentea* reproduction.

The length at which *L. intestinalis* becomes most prevalent is greater than 40 mm, and the length when most fish mature, and can therefore breed, is also around 39 - 40 mm. If the effect on reproduction augmented by *L. intestinalis* is as dramatic as suggested, the implications for the future viability of *R. argentea* populations are serious. Furthermore, *L. intestinalis* parasitism incurs a reduction in the space available in the visceral cavity (Dence, 1958). As the fish length increases so does the average number of *L. intestinalis* present in each fish host, as well as the average length of the parasite. Subsequently, the space available for maturation of the gonads must be reduced, which is detrimental for *R. argentea* reproduction. The increase in the intensity and average length of *L. intestinalis* must also logically exacerbate any effect it has, other than space availability, on its fish host. Significantly, it is the bigger fish, which are crucial for reproduction, which are the ones most affected by *L. intestinalis*, so if an outbreak of *L. intestinalis* ever occurs it may seriously affect the *R. argentea* fishery.

The presence of *L. intestinalis*, then, halts maturation and thus reproduction. However, it is possible for *R. argentea* which are affected by *L. intestinalis* to reach maturity stages five and six, and most probably reproduce. Nevertheless, the presence of *L. intestinalis* has the effect of diminishing the fecundity of the fish host at each length class, as well as the rate at which fecundity increases with fish size. These affects possibly correlate with the increase in both *L. intestinalis* intensity and parasite length with fish length, so the greatest effect will be apparent in the largest fish.

Comparisons between the depth and distance from the shore against *L. intestinalis* prevalence within the *R. argentea* populations showed no discernible trend. It would be expected that the prevalence of *L. intestinalis* would be at its highest levels close to
the shore for this is where its definitive avian host is most likely to feed (Dence, 1958). One explanation for the absence of any trend is the competitive release R. argentea received when the haplochromine population dramatically declined due to predation by Nile perch (Lates niloticus). As R. argentea dramatically increased in Lake Victoria (Wanink, 1998b), avian predators, such as the pied kingfisher and the cormorant, switched their diet from haplochromines to R. argentea (Wanink, Berger and Witte, 1993; Wanink and Goudswaard, 1994). Yet, as R. argentea is smaller than most haplochromine species, it offers a lower reward to the avian piscivores (Wanink and Goudswaard, 1994), forcing bird's to fly further afield to exploit the larger R. argentea. The assumption that the bird feeds on inshore fish is therefore negated, as it is necessary for the predator to gain as much benefit from its prey as it can, whilst minimising its efforts (Holmes, 1976). In short, the avian piscivor will fly further to feed, as long as the trade-off between effort expended and benefit gained is in its favour, illustrating how the correlation between the distance from the shore and L. intestinalis prevalence is not a valid argument.

Alternatively the lack of any relation between the parasite and the location of the fish can be attributed to the assumption that R. argentea's nursery areas are located in the littoral areas around the shoreline (Wanink, 1999). It is possible to argue that the fish host is infected in the inshore areas (Holmes, 1976; Dence, 1958) when it is a juvenile, or when moving towards a more pelagic habitat. In addition R. argentea populations are constantly moving to and from the shore line to breed, so L. intestinalis prevalence and distance from the shore is likely to be constantly changing.

As mentioned previously the R. argentea stock has increased in recent years as a result of the decline in the haplochromines (Witte, Goldschmidt, Goudswaard, Ligtvoet, Oijen and Wanink, 1992). This has left both aquatic and avian predators with a lack of prey as haplochromine populations have been decimated. R. argentea's generalist nature has enabled them to take the place of the haplochromines, and expand into the available niche (Wandera, 1993). Yet, as the avian piscivores are the definitive L. intestinalis host, the parasite causes behavioural changes in the intermediate host, to ensure that it fulfils its life cycle. So perhaps the most compelling argument for the haphazard correlation is due to the behavioural differences of the infected fish. For fish infected with L. intestinalis have a different feeding habitat than the unaffected population and will thus be spatially distinct (Wanink, 1992; Barber and Huntingford, 1995; Krause and Godin, 1994). It has also been noted in other studies that fish infected with L. intestinalis exhibit behavioural shifts which are likely to enhance transmission. These include positive buoyancy (Ness and Foster, 1999), or sluggish movement (Holmes, 1976; Dence, 1958), the habit of performing horizontal movements to and from shore, traversing towards the shore during the day and away at night (Wandera, 1993), and finally the tendency of shoaling together (Kennedy, pers. comm.). These factors may combine to create an unrealistic indication of prevalence levels of L. intestinalis in R. argentea populations. For, in a trawl the infected fish, which may be feeding at the surface (Wanink, 1992), may combine with the sample of unaffected R. argentea, feeding in their natural position at the oxycline during the daytime (Wanink, Kashindye, Goudswaard and Witte, 1998; Wanink, 1992). Furthermore, as Wandera (1993) recognises, at night the parasitised fish mix with the unaffected individuals which come to the surface, perhaps making it difficult to gain an accurate picture of the prevalence of the numbers of infected fish. These
changes in *R. argentea*’s behaviour, ensures that *L. intestinalis* reaches its definitive host, which in turn suggests that the prevalence of this parasite may increase in general. If this occurs then an ever increasing number of *R. argentea* may become infected, which will perhaps lead to a decreased population of *R. argentea* as the parasite diminishes their fecundity and often stops the fish host progressing past maturity stage three.

Although only four sites were analysed in this study with respect to the influence of *L. intestinalis* presence on host maturity, this is an important area for research and merits further investigation. If, for example, the definitive *L. intestinalis* host feeds upon *R. argentea* more frequently (Wanink, Berger and Witte, 1993), the prevalence level within the population may increase. This may have the effect of reducing the population density (Kennedy, 1996), forcing the avian predator to feed elsewhere, perhaps increasing *L. intestinalis* prevalence in other *R. argentea* populations, which are less accessible to the avian predator. If this cycle continues, there are serious issues raised concerning the productivity of the future *R. argentea* fishery. In addition, there is a distinct possibility that *R. argentea* is not the natural intermediate *L. intestinalis* host in Lake Victoria. Therefore, as is often the case with parasites and their hosts, an equilibrium may not exist between the two (Holmes, 1976), which could cause unpredictable effects which need to be monitored and managed.
5. CONCLUSION

The main point revealed by studying the CPUE and the length frequencies of *R. argentea* around Lake Victoria, provides further evidence to the argument that it is an inshore spawning species. This has a number of implications regarding the management of the fishery both now and in the future. In order to maintain a sustainable *R. argentea* fish stock, it is necessary to ensure that the recruitment of juveniles to the population is as unaffected by human influence as it possibly can be. Therefore, there is a need for regulation and restrictions to fishing in the inshore areas, to protect both spawning adults and juveniles. At present there is no clear management policies based on fishing restrictions in inshore areas, although a number have been proposed by various authors. These include, closed fishing seasons, especially around the peak breeding seasons, the control of mesh sizes, the licensing of nets and the registration of boats (Manyala, Vandenberghe, Dadzie, 1995; Wandera, unpublished (a)). It would also benefit the fishery to ensure more responsibility is placed upon the fishermen themselves, by implementation of fisheries co-operatives (Manyala, Vandenberghe, Dadzie, 1995). This would place the future of the fishery in the fishermen’s hands, thus making the concept of sustainability a very real one. It has also been noted that the mean length of *R. argentea* has decreased over the past few years, which is due to the exploitation of the larger individuals of the population. Combined with the concern about the overexploitation of the juveniles in inshore waters, there may need to be more research in the future on the selectivity of nets upon *R. argentea*.

The results concerning the size at first maturity for *R. argentea* populations over the lake suggested that in areas where fishing intensity was highest, *R. argentea* experienced a shift in life history tactics, enabling them to breed at a smaller size. This again raises concern about over-fishing, for if the fish become smaller, a greater number will need to be caught to give the same weight, which may in turn lead to the exploitation of the juvenile fraction of the population. This will require smaller net sizes which may decrease the mean length even further. This area will require constant and consistent evaluation in the future, for once this spiral starts there will be rapid deterioration and may be extremely difficult to halt the decrease in *R. argentea* stock.

The effect that *L. intestinalis* has on *R. argentea* is another area which needs careful and consistent management, as an out break of ligula could have dramatic effects on the population’s breeding capability, which would in turn effect the fish stocks. This problem is compounded as the definitive hosts now feed almost exclusively on *R. argentea*, perhaps making the fish the most important host for the parasite within the lake.

In an ever-changing environment, such as Lake Victoria, careful monitoring and constant evaluation is needed with respect to all aspects of the ecosystem to enable sound management decisions to be made to maintain a sustainable resource base both now and in the future.
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