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Acoustic estimates of commercial fish species in Lake Victoria: Moving towards ecosystem-based fisheries management

Inigo Everson[a,*], Anthony Taabu-Munyaho[b], Robert Kayanda[c]

[a] *Animal and Environment Research Group, Faculty of Science and Technology, Anglia Ruskin University, Cambridge, UK*
[b] *National Fisheries Resources Research Institute (NaFIRRI), P.O. Box 343, Jinja, Uganda*
[c] *Tanzania Fisheries Research Institute (TAFIRI), P.O. Box 475, Mwanza, Tanzania*

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ABSTRACT

Data from the first series of lakewide fisheries acoustic surveys of Lake Victoria, East Africa, have been re-analysed according to current protocols. Surveys took place in February and August each year between 1999 and 2002. The primary aim has been to estimate the standing stock of Nile perch and dagaa, the main species taken in commercial fisheries on the lake. The results show that over the period of the surveys from 1999 to 2002 there was no significant trend in the standing stock of either species with time although there was a significant seasonal effect higher values in February as compared to August. Information from bottom trawls during the surveys supports these conclusions. The results have been considered in the context of a food web from which it is concluded that in order for sufficient food to be present for the Nile perch there must be a significant proportion of the decapod crustacean Caridina present. It is noted that this species can be estimated acoustically using multifrequency echosounders but is very difficult with the single frequency system used on the 1999–2002 surveys. Refinements in the methodology will permit the simultaneous assessment of several key components in the food web and open the way to effective ecosystem-based fisheries management.

1. Introduction

Over the past century there have been enormous changes in the Lake Victoria fish community as it became transformed from a region where traditional fisheries using primitive equipment were the norm to one where increased fishing pressure caused major ichthyofaunal changes (Kudhongania and Chitamwebwa, 1995). The introduction of new species, of which the Nile perch (*Lates niloticus*) has arguably caused the greatest impact (Reynolds et al., 1995), produced major changes in the ecosystem. In addition, eutrophication as a result of deforestation and poor agricultural practices (Scheren et al., 2000) in the catchment, contributed to the changes as well. Previously dominated by diverse haplochromine species with different trophic specialisations the system has become dominated by Nile perch, a top predator (Witte and van Densen, 1995). In gross terms the new system can be represented in a much simplified form as shown in Fig. 1. Changes in the fisheries have caused concomitant changes in the socio-economic structure of the lakeside communities. Recognising the importance of maintaining sustainable fisheries in support of the lakeside communities, the Lake Victoria Fisheries Research Project (LVFRP) included acoustic surveys as a key component of the research programme.

The data from those acoustic surveys were analysed according to the protocols of the time and the results from all, except the last survey of the series, were published as Getabu et al. (2003). Although nominally analysed according to the same protocol, the results from the last survey in the series, that of August 2002 (Boyer, 2002), were extremely low. Following a revision of the acoustic protocols in 2005 (Anon, 2008) to increase objectivity in the analysis the survey series was recommenced. Fortunately the raw data from the LVFRP surveys had been collected in a manner that was suitable for re-analyse according to the Anon (2008) protocols.

The analytical protocol used by Getabu et al. (2003) involved a two stage process. Firstly echograms were examined and echotraces within each nautical mile, Elemental Distance Sampling Unit (EDSU), assigned to one of five categories based on the likely dominant acoustic scatterers. The second stage used the catch composition of net hauls to divide backscatter in each category to species, an approach that, to be effective, requires a large number of hauls using a standard net encompassing most of the water column.

Acoustic target strength (*TS*) to size relationships had been obtained from cage experiments (Getabu et al., 2003 and Tumwebaze et al., 2007). In the case of Nile perch the size range used for the study was very much less than that encountered in the

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[*] Corresponding author. Tel.: +44 845 196 2124.
E-mail addresses: ideverson@gmail.com (I. Everson), ataabum@yahoo.com (A. Taabu-Munyaho), bobkayanda@yahoo.com (R. Kayanda).

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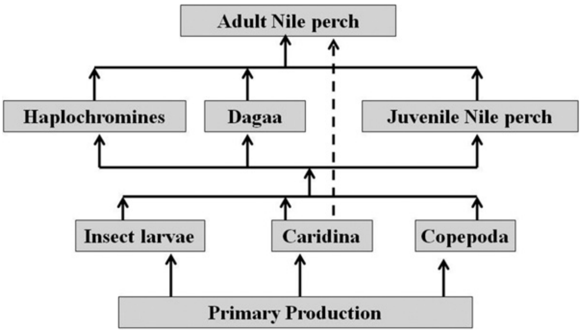

Fig. 1. Food web diagram of the Lake Victoria ecosystem following the upsurge in abundance of Nile perch.
Source: Ligtvoet and Witte (1991).

wild and recent studies (Kayanda et al. (2012)) have demonstrated that this introduces further error for large fish.

It was recognised that re-analysing the LVFRP data according to the Anon (2008) protocol would extend the time series of results of the most recent surveys back and potentially throw light on recent changes in the fisheries and the ecosystem. This paper presents the results of that re-analysis.

2. Materials and methods

Basic information on each survey was extracted from reports to LVFRP (Armstrong, 2000; Boyer, 2002; Fernandes, 2001; MacLennan, 1999; MacLennan, 2000; Reid, 2001). The dates of each survey and the abbreviated name used in this paper were as follows: 12–28 August 1999: Aug 99, 2–19 February 2000: Feb 00, 17 August–8 September 2000: Aug 00, 31 January–17 February 2001: Feb 01, 23 August–11 September 2001: Aug 01 and 10–28 August 2002: Aug 02. Survey spreadsheets and raw data were made available by LVFO, NaFIRRI, David MacLennan and, for the August 2002 survey, by David Boyer (Marine Acoustic Services). The raw acoustic data were held on CDs; in some instances parts of these were unreadable but sufficient data were available for the analyses reported here.

All of the surveys were undertaken using RV Victoria Explorer into which had been installed a Simrad EY500 echosounder with hull mounted transducer with an operating frequency of 120 kHz. Operational settings are shown in Table 1.

The echosounder had been calibrated in accordance with international standards (Foote et al., 1987) twice during each survey. For the original analyses the echosounder was set to log all data at the default gain values and a percentage adjustment, calculated from the calibration exercise on the survey, had been applied to the data for analysis. Over the survey series the mean *TS* gain was −23.655 dB (range 23.40–23.85) and the Sv gain −23.657 dB (range 23.23–24.11). Since there was no significant trend in these gain settings over the time series ($r^2 = 0.13$), the mean value of −23.66 dB was used for the analyses reported in this paper.

Table 1
Standard echosounder settings used for all surveys. For analysis the *TS* and Sv gain were set to 23.66 as explained in the text.

Setting	Value	Units
Power	63	Watts
Absorption coefficient	3	dB/km
Equivalent two way beam angle	−18.3	dB
Pulse duration	0.3	ms
Bandwidth	12	kHz
TS gain	23.80	dB
Sv gain	23.80	dB
Alongships 3 dB beamwidth	9.2	°
Athwartships 3 dB beamwidth	9.3	°
Alongships offset	0	°
Athwartships offset	0	°

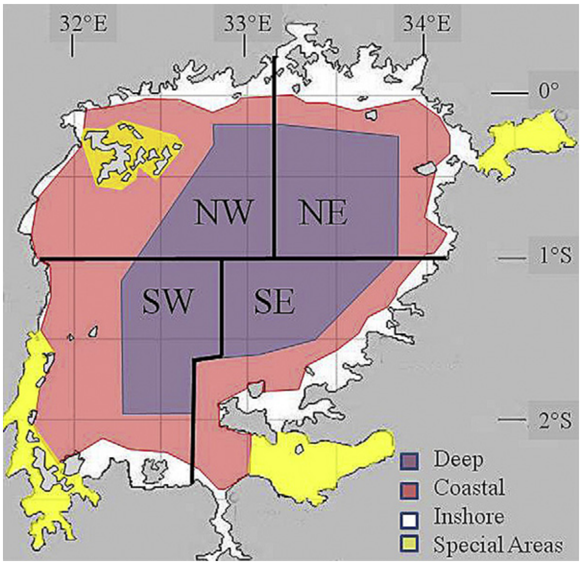

Fig. 2. Outline map of Lake Victoria to indicate the boundaries of the survey strata. The Special Areas are: NE: Nyanza Gulf, NW: Sesse Islands, SE: Speke Gulf and SW: Emin Pasha Gulf.

On all surveys a written log had been maintained of GPS positions at one nautical mile intervals. Where data sets did not include GPS positions the EDSU positions were estimated from the logged positions.

2.1. Survey design

The stratified design set out in Anon (2008) for the recent surveys was used for the analyses, whereby the lake is divided into four quadrants, Northeast (NE), Northwest (NW), Southeast (SE) and Southwest (SW), within which there are three depth strata. A Deep stratum had been designated so as to include water deeper than 40 m; a Coastal stratum extended from the shoreward region of the lake out to the Deep stratum and an Inshore stratum was composed of regions for which the formal survey design for the main lake body was impractical due to the presence of shallow water, rocks and islands. The design also includes the following ‘special regions’ within the Inshore stratum of each quadrant, Nyanza Gulf (NG), Speke Gulf (SG), Sesse islands (SI) and Emin Pasha Gulf (EP). The stratum boundaries are shown in Fig. 2 and a schematic representation for presentation of the results in Fig. 3. Logged positions from the original analyses were used to determine into which stratum a particular transect should be allocated. The cruise track design was the same for all surveys (Fig. 4) except August 1999.

Transects were defined as periods when the survey vessel was moving at a near constant cruising speed of 8–10 knots along the same course. In line with Anon (2008) each activity was identified as an ‘Event’ and given a unique identifier within each survey. This was a code to identify the type of activity (T = Transect) and stratum (D = Deep, C = Coastal and I = Inshore, NG = Nyanza Gulf, SG = Speke Gulf and SI = Sesse islands), followed by a number, unique for each survey. For example TC010 would represent Event 10 a ‘Coastal Transect’. All events were included in an Eventlog for each survey. No sampling had taken place within the SW Inshore or Emin Pasha Gulf strata of the Anon (2008) design on any of the surveys reported in this paper.

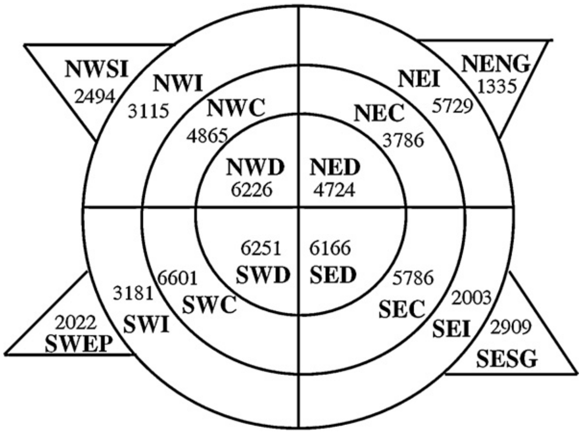

Fig. 3. Schematic outline of Lake Victoria showing the strata for the presentation of results. Numbers are the area of lakebed (km^2) within each stratum.

2.2. Net hauls

Fish were sampled with one or more of the following gears during the surveys: bottom trawl (headline height 3.5 m, wingspread 10 m, codend mesh 25 mm with 6 mm stretched mesh liner), frame net (3.5 m × 3.5 m) and pelagic trawl (headline height10 m, codend mesh 25 mm with 6 mm stretched mesh liner) had been made during the surveys. No information on the performance of these trawls had been reported and no studies are reported to compare their sampling efficiency. The results used for this study, total catch by species for each survey and gear type, were taken from the survey reports of Armstrong (2000), Boyer (2002), Fernandes (2001), MacLennan (1999), MacLennan (2000) and Reid (2001).

2.3. Analytical procedures

Under the original protocol for acoustic surveys there was a two stage process for data analysis (Getabu et al., 2003). Firstly, a visual interpretation of the echograms was used to assign echotraces to one of the following five categories:

1. Near surface schools mainly composed of dagaa (*Rastrineobola argentea*); which appear as isolated strong marks to about 15 m depth.
2. Mixed pelagic layer; mostly dagaa and haplochromines with some Nile perch
3. Mixed bottom layer; mostly haplochromines and Nile perch, with some dagaa.
4. Diffuse deep layer; mostly composed of the freshwater prawn *Caridina nilotica* with some *Barbus profundus*.
5. Mixture of fish and plankton; diffuse traces everywhere only seen at night.

Category 1 is well defined by depth but designation of echotraces to the other categories is difficult, particularly for 2 and 3, which include the same species but with different emphases. Since the survey protocol specified sampling during daylight, night-time sampling only occurred sporadically, consequently systematic data within category 5 are sparse.

The second stage used the catch composition of net hauls to divide backscatter in each category to species. This approach requires that analysts are working according to the same assessment scheme and that the net hauls are adequate for determining the size and species composition in the region. Unfortunately, the overlap between the echotrace definitions is such that greater reliance had to be placed on the net haul catches. It appears that there was very little opportunity to cross-check the performances of the three nets used. Consequently, although the acoustic data collection was consistent between and within the surveys this is not the case for the supporting net haul information. Due to subjectivity in echotrace classification and the limited number of net hauls available for the analysis there is an unavoidable and unquantified error in the assignment of backscatter to the key species.

The revised protocol (Anon, 2008) is more prescriptive for echotrace classification, since it is dependent on single target detections (STDs) and traditional echo-integration. Although consistent in its application, the effectiveness of the STD method is dependent upon setting the best acceptance criteria. A full discussion on that topic is outside the scope of this paper, but a critique is to be found in Simmonds and MacLennan (2005) and further information on the complexity of the subject in Horne and Jech (2005). The key point is that since the same criteria have been used for all surveys, the acoustic analytical process is independent of the analyst and therefore consistent both within and between surveys.

The Anon (2008) analytical procedure was used throughout. In summary, this assumes that the bulk of the large fish present in the water column in water deeper than 10 m are likely to be Nile perch. Further it assumes that dagaa are the dominant small fish (<10 cm) in the near surface water down to 30% of the water depth and that the remainder of the water column contains predominantly Nile perch, haplochromines and the crustacean Caridina.

All analyses were undertaken using the proprietary software 'Echoview. Myriax, Australia' (Version 4.90.59.17028) and the following summary procedure (Anon, 2008) adopted:

1. All raw data files were loaded into daily Echoview files.
2. Bottom detection was checked and adjusted to remove spurious echoes.
3. Transect events were marked as 'Regions' specified by time.
4. A grid of 1 km EDSU, or, for situations when GPS data had not been logged, 4 min time intervals (equivalent to approximately 1 km of survey track) and 2 m depth layers was established.

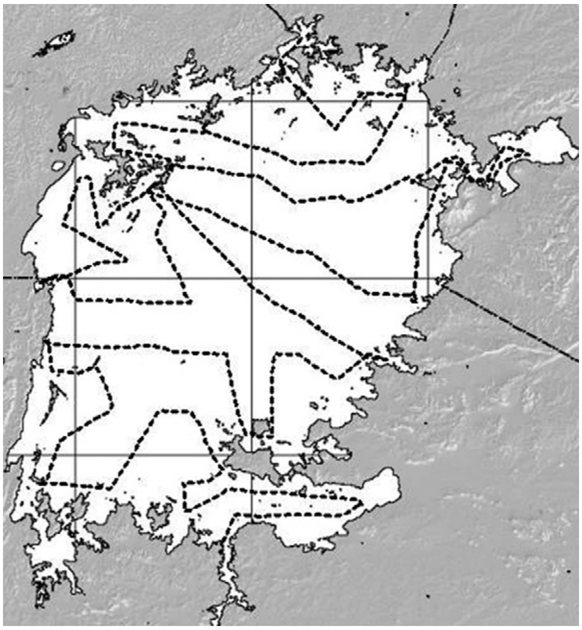

Fig. 4. Survey track used for all except the Aug 99 survey. The total transect distances used for analysis in this paper were Aug99: 1616 km, Feb00: 1501 km, Aug00:2071 km, Feb01: 1974 km, Aug01: 2040 km and Aug02: 2156 km.

Two approaches were used to analyse the echograms, STD and echo-integration.

2.4. Analysis of STDs

The following settings were used: Pulse length determination level: 6 dB, Minimum normalised pulse length: 0.8, Maximum normalised pulse length: 1.5, Maximum beam compensation: 6.0 dB, Maximum Standard Deviation on minor and major axis angles: 0.6°. The *TS* Threshold was set to −50 dB, the estimated TS of a fish of approximately 10 cm total length (*TL*) using Equation (1). The following *TL* to *TS* and *TL* to weight (*W*) relationships, reported by Kayanda et al. (2012) were used for all STDs:

$$TL = 10^\wedge((TS + 84.14)/30.15) \tag{1}$$

$$W = 0.0042 \times TL^{3.26} \tag{2}$$

The Echoview exports gave a mean *TS*, number of STDs and beam volume within cells 2 m deep by 1 km of distance (EDSU) that were used to calculate a weight density within each cell. Within each EDSU the weight densities, multiplied by the layer thickness were summed to give an overall density per unit area.

2.5. Correction for single beam STD

Acoustic data logged during the August 2002 did not include angular data telegrams so it was necessary to provide a correction to STDs to take account of their position in the acoustic beam. Series of mean *TS*, corrected (TS_c) and uncorrected (TS_u), within each cell from the other August surveys were compared to provide parameters for values for equation (3):

$$TS_c = (TS_u \times a) + (\text{Depth} \times b) + (TS_u \times \text{Depth} \times c) + d, \tag{3}$$

where *a*, *b*, *c* and *d* are constants.

2.6. Integration analyses

In Echoview, the Single targets were masked from the power echogram, the filtered echogram integrated and data for each time and depth layer exported. Dagaa are known to predominate near to the surface but are also found in deeper water. The bulk of the dagaa are thought to be present generally in the top 30% of the water column (Tumwebaze et al., 2007, and Anon, 2008) and a 'dagaa line' was set in Echoview at 0.3 of the water depth. All backscatter above this line was assumed to be due to dagaa and all backscatter from greater depths was assumed to be due to a mixture of haplochromines, small Nile perch and Caridina. Results from above the dagaa line were converted to dagaa biomass using the *TS* parameter −29.4 dB/Kg (Anon, 2008). Below the dagaa line, where the integrated backscatter was assumed to be due to other species, the biomass was estimated using the parameter value −25.17 dB/Kg (Anon, 2008).

2.7. Statistical analyses

The statistical package 'R' (R Development Core Team (2011)) was used for all analyses. The estimated density values from all EDSUs within each stratum and survey were combined in stratum series. These were bootstrapped with sample sizes of 50, repeated with replacement 10,000 times, to estimate the mean density and 95% confidence limits (Crawley, 2005). GLM analyses to determine differences between season, survey, strata and taxa were undertaken and the models described in Section 3.

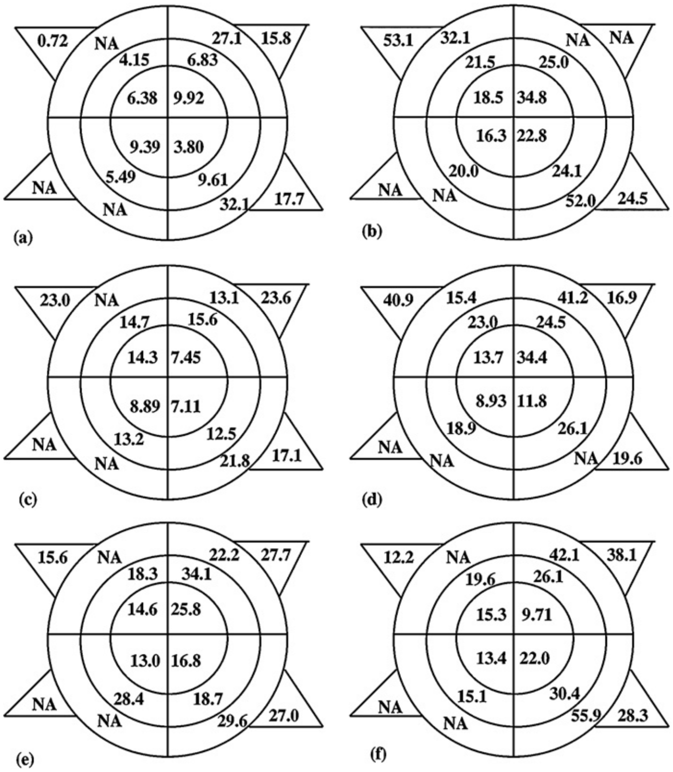

Fig. 5. (a–f) Mean weight density (g/m^2) for Nile perch for surveys. 5a:Aug99; 5b:Feb00; 5c:Aug00; 5d:Feb01; 5e:Aug01; 5f:Aug02. NA = No data.

3. Results

3.1. Area of coverage

The survey in August 1999 was largely exploratory and was of shorter duration than the others, consequently sampling did not take place in all strata of the Anon (2008) protocol. Sampling for subsequent surveys took place in all except Emin Pasha Gulf and the southwest inshore strata. In addition, there was very limited sampling in the northwest inshore stratum. The amount of all data that were available for analyses compared to that which had been collected were: Aug99:84%, Feb00:78%, Aug00:100%, Feb01:98%, Aug01:97% and Aug02:100%.

3.2. Adjustment for STDs without angle data

A least squares regression to estimate TS_c from TS_u and depth to apply to the Aug 02 STD results gave the following equation:

$$TS_c = (TS_u \times 1.076) + (\text{Depth} \times 0.149) + (TS_u \times \text{Depth} \times 0.0029) + 5.56 \tag{4}$$

r^2 = 0.840 with 3125°.

3.3. Weight density

Mean weight density derived from bootstrap analysis of EDSU results are shown plotted onto the schematic representation of the lake (Fig. 3) in (Figs. 5–7) for Nile perch, dagaa and other taxa, respectively.

3.4. Within taxa variations in weight density

Analysing the data from all surveys together, the distribution of mean values for each group, Nile perch, dagaa and

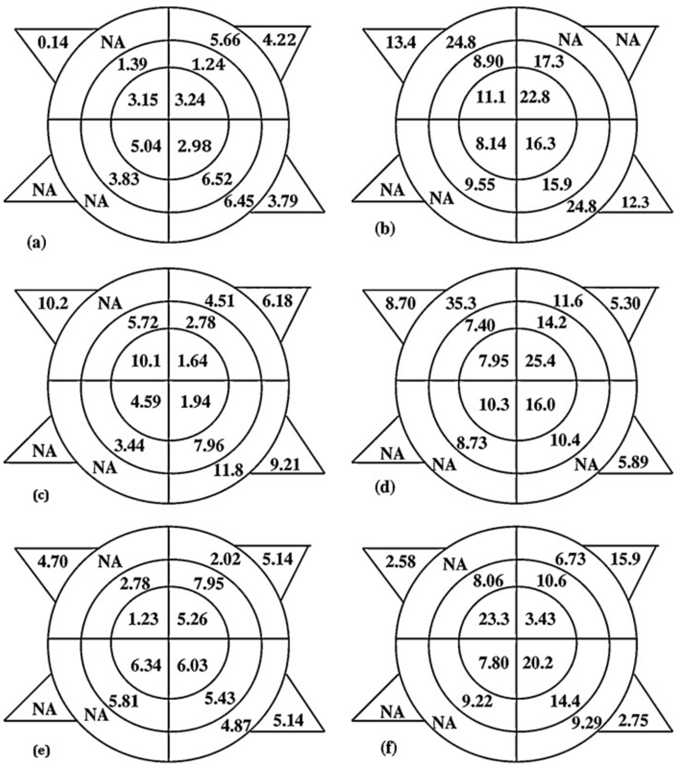

Fig. 6. (a–f) Mean weight density (g/m^2) for dagaa. 6a:Aug99; 6b:Feb00; 6c:Aug00; 6d:Feb01; 6e:Aug01; 6f:Aug02.

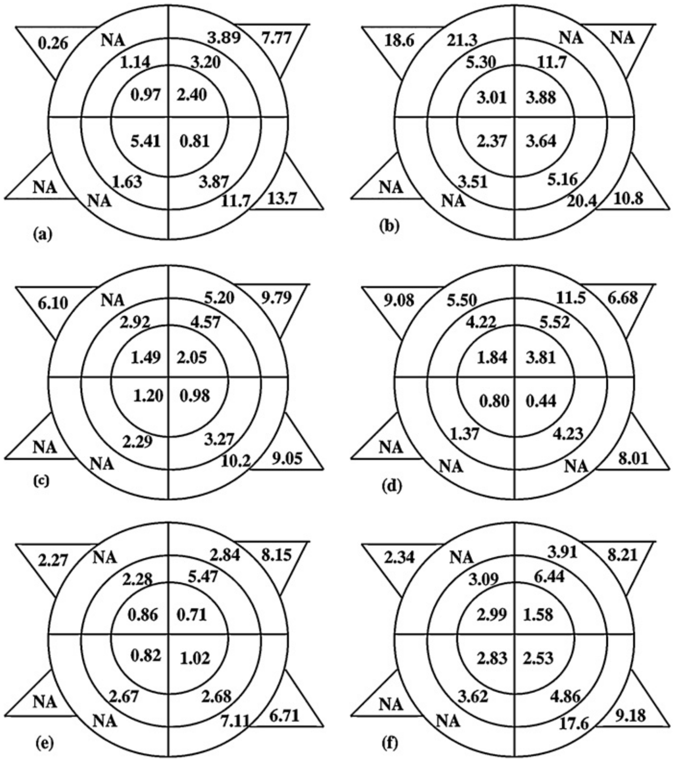

Fig. 7. (a–f) Mean weight density (g/m^2) for Other taxa. 7a:Aug99; 7b:Feb00; 7c:Aug00; 7d:Feb01; 7e:Aug01; 7f:Aug02.

Table 2
Mean densities of main taxa by season.

Taxon	NP	NP	Dagaa	Dagaa	Other	Other
Season	February	August	February	August	February	August
Stratum	Density (g/m^{-2})					
D	19.1	11.7	14.1	5.6	2.3	1.6
C	22.8	15.8	11.3	5.6	4.8	3.2
I	33.8	29.3	23.2	6.1	13.8	7.1
NG	16.8	25.7	5.3	7.2	6.7	8.5
SG	22.0	22.2	8.8	4.9	9.4	9.5
SI	46.8	10.7	10.9	3.3	13.4	2.3

Derived from results in Figs. 5–7.

others, was highly skewed to the left and this was normalised using a square root transformation. An initial GLM of the form: (sqrt(MeanDensity) ~ Survey + Season + Quadrant + Stratum) was run for each of the three groups. This indicated that there was no significant difference in the means for the quadrants so that factor was dropped for subsequent analyses. Summary GLM statistics for Nile perch were: Survey: NSD, Season: $p = 0.00099$, Survey and Season: $p = 0.0010$, Stratum I: $p = 9.5\text{e} - 05$, other strata: NSD. For dagaa the GLM statistics were: Survey: NSD, Season: $p = 0.0248$, Survey and Season: $p = 0.0250$, Stratum I, $p = 0.050$, Other strata: NSD. For the other species category the GLM statistics were: Survey: $p = 0.00060$, Season: $p = 0.00044$, Survey and Season: $p = 0.00044$, Strata: I: $p = 0.050$, D: $p = 0.00095$, NG: 0.00367, SG: $p = 5.6\text{e} - 05$, all other strata: NSD. This indicates that the variation in NP and dagaa densities between surveys is largely due to a seasonal effect rather than a trend over the time series of the surveys.

For the lakewide strata, as is shown in Fig. 8, there is a clear increase in Nile perch weight density sequentially from the Deep through the Coastal and into the Inshore strata, irrespective of quadrant. The weight density is also significantly higher in February than in August; this seasonal variation is responsible for most of the between survey variation (Table 2). The results for the special stratum SI match the pattern for the lakewide strata, although with by far the greatest values for the February season and an extremely low one for Aug 99 suggesting a great deal of heterogeneity in the distribution within this stratum. In contrast to the other strata, the NG results are lower in February than August whilst the SG results are the same for the two seasons.

In the case of Dagaa there is a strong seasonal effect for the lakewide strata with, like Nile perch, significantly higher values in February as compared to August (Table 2). Although variation is just significant for the inshore stratum this is not reflected in any of the other strata indicating that Dagaa are widespread at all times but their density varies seasonally. The seasonal pattern in the special strata for Nile perch is matched by dagaa in NG and SI but, in common with the lakewide strata, SG is higher in February than August.

In the case of the 'Other taxa' there is significant variation in both season and survey for the lakewide strata (Table 2). The results for the special strata follow those of the inshore stratum with the exception of SI for which the August results are significantly lower.

Arising from this analysis, the density estimates for each of the taxa for season and survey are internally consistent. This does not necessarily mean that the results are comparable between taxa: a topic addressed in the next section.

3.5. Comparison of densities between taxa

In this series of survey results several components of the simplified food web, Nile perch, dagaa and haplochromines shown in Fig. 1 have been quantified from the acoustic results. In this section quantitative interactions between taxa are explored. Nile perch is a large predatory species whose main prey is the crustacean *Caridina*, the fish species *Rastrineobola*, haplochromines and its own young

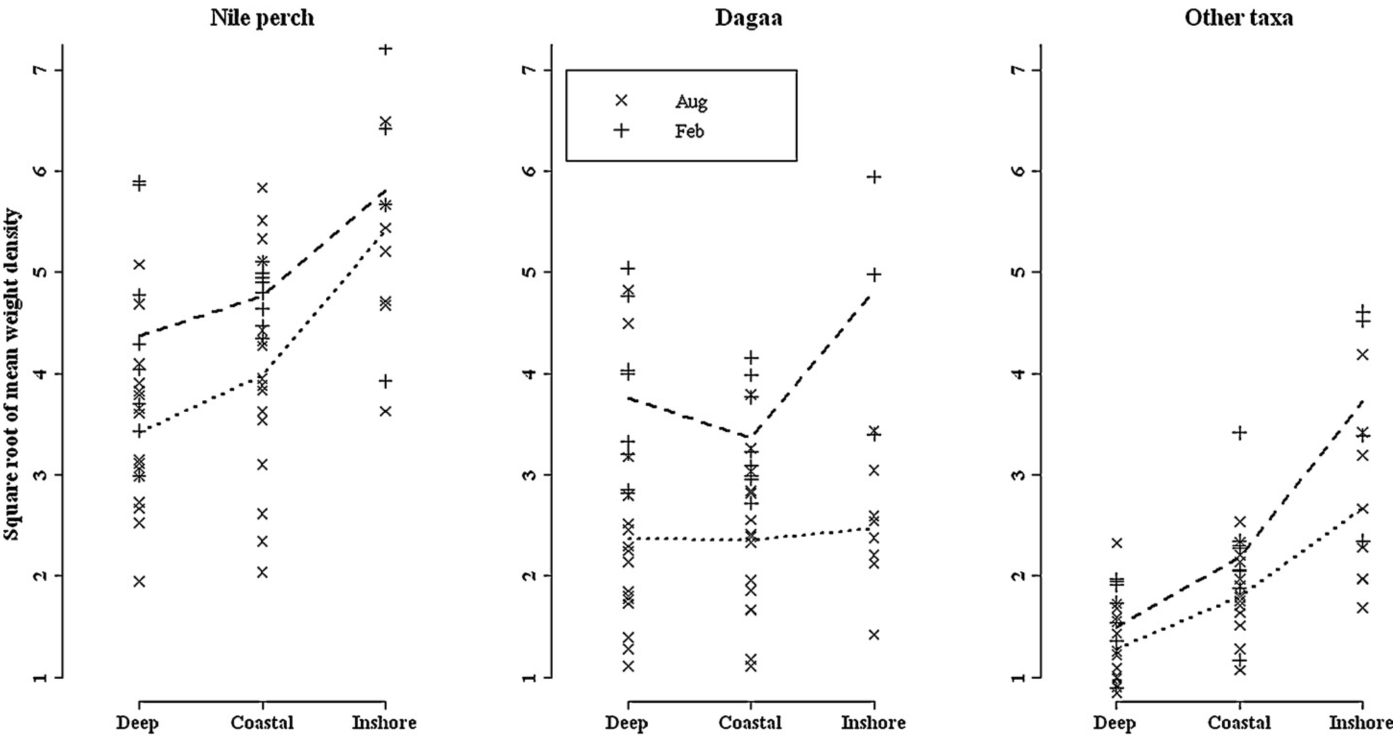

Fig. 8. Distribution of stratum values of mean weight density for Nile perch, dagaa and the Other taxa for all surveys. Dotted line is the stratum mean for August surveys and dashed line for February surveys.

(Ogari and Dadzie, 1988; Ligtvoet and Mkumbo, 1990; Ligtvoet and Witte, 1991; Ogutu-Ohwayo, 1990; Mkumbo and Ligtvoet, 1992) (Fig. 1), hence there is likely to be a positive relationship between the distributions of the predator and prey.

Transect results were used for this analysis to avoid problems of serial correlation in the EDSU data. Data were square root transformed to correct skew in the distributions and analysed by depth stratum.

GLM results comparing the taxonomic groups are shown in Table 3 and Fig. 9. These show that within all strata there is a strong relationship between Nile perch density and the haplochromine/*Caridina* grouping (termed ‘other’ group), a key prey component. The relationship of Nile perch with dagaa density is also highly significant for the deep and coastal strata but not inshore or within the special strata. This may be related to the higher density of the ‘other’ group in the inshore as compared to the deep and coastal strata. The relationship between dagaa and the other group is positive and significant in the deep and coastal strata but, with the exception of Sesse Islands, not so for the inshore strata.

These results demonstrate that on the spatial scale of the transect or stratum, tens of kilometres, the predator, Nile perch, is associated with its main prey. Further analysis is possible at smaller spatial scales but this has not been undertaken for the purposes of this paper.

3.6. Comparison of densities of taxa as estimated by acoustics and nets

Although net hauls were undertaken during the surveys, those results have not been used in this study to assist with determining the standing stock acoustically, consequently they can be used to provide independent estimates of species composition. Unfortunately insufficient hauls were made to make within survey comparisons but, even though different nets were used through the series, the proportions of total catches can be used as a guide of relative density between surveys.

The percentages of key taxa in the acoustic estimates of lakewide standing stock and the total catches from net hauls during each survey are set out in Table 4. The Nile tilapia (*Oreochromis niloticus*) was present in a few hauls in the inshore stratum, the deepest being from a bottom trawl in water 11 m deep. The only haul that contained a large amount of this species occurred in February 2001. Less than 10% of the sampled areas of the inshore stratum contained water shallower than this depth and consequently there is insufficient information to assess this species further for this paper.

In this study using the current single frequency protocols in Anon (2008), large Nile perch have been estimated using STD, whilst its prey species are included in the categories ‘dagaa’ and ‘other species’. The acoustic estimates indicate that, for the most

Table 3
Summaries of square root transformed transect mean weight density GLM statistics for relationships between main taxa.

Stratum	d.f.	Nile perch//Other		Nile perch//Dagaa		Other//Dagaa	
		F	*p*	*F*	*p*	*F*	*p*
Deep	133	45.1	**<0.001**	58.3	**<0.001**	9.7	**0.002**
Coastal	272	149.9	**<0.001**	86.5	**<0.001**	9.7	**0.002**
Inshore	45	22.87	**<0.001**	1.77	(0.19)	1.07	(0.31)
Nyanza Gulf	16	13.69	**0.002**	3.17	(0.094)	0.91	(0.35)
Speke Gulf	32	26.50	**<0.001**	0.34	(0.56)	2.35	(0.14)
Sesse Islands	21	146.3	**<0.001**	1.22	(0.28)	2.49	(0.13)

The bold numbers are to indicate those that were statistically significant.

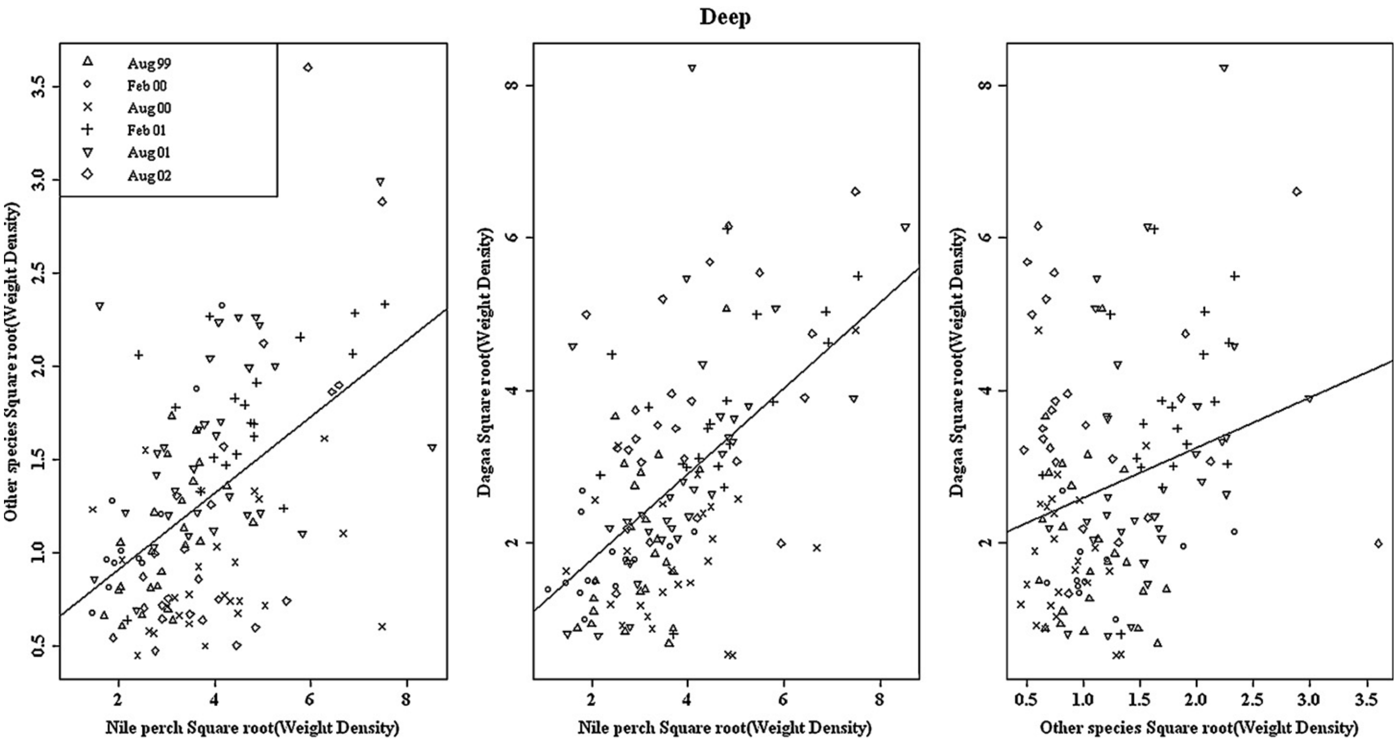

Fig. 9. Example from the Deep stratum of the comparison of densities of the main taxa as discussed in Section 3.5.

part, there is broad agreement with the net haul results which indicate that the weight density of Nile perch is similar too or much greater than that of the other taxa combined (Table 4). Since Nile perch is the 'top predator' this observation warrants further examination.

Wilcoxon tests comparing the acoustic and net haul percentages indicate that there is no significant difference for Nile perch and Dagaa but the difference is significant for the other taxa ($p = 0.015$). With the test reduced to just the bottom trawl series the differences for Nile perch and dagaa are significant ($p = 0.029$) but not for the other taxa. The reason for this result is because all acoustic percentages for Nile perch were lower than for the net hauls whilst the opposite relationship is present for dagaa.

No information was available from reports to indicate the sampling depth of net hauls, and furthermore, acoustic data were not logged during the tows, hence a thorough comparison of acoustics and nets is not possible. However, some general points arise. Since dagaa are known to predominate in the near surface layers (Tumwebaze et al., 2007) it is to be expected that they would form a very small proportion of bottom trawl catches. The frame net and pelagic trawl would likely catch all taxa depending on the fishing depths with near surface tows producing more dagaa.

In addition the bottom trawl catches can be used to investigate trends in density over the survey series. These estimates of density are highly skewed due to small numbers of high values; using a square root transformation, the slope of the GLM of catch rate against survey was not significantly different to zero ($F = 0.0012$ on 1 and 28 DF, $p = 0.93$), a result that is in agreement with the GLM of acoustic estimates of density (Section 3.4).

Combining length data for Nile perch into single frequency distributions for each type of net, as is shown in Fig. 10, provides a useful insight into the catches. Comparing length frequency results from all bottom trawl hauls into one distribution and comparing this with the pelagic trawl results indicates that the pelagic trawl results for Aug 01 are similar to those for the bottom trawl for that survey but are different for the Aug 02 survey. This difference

Table 4
Percentage by weight of taxa in acoustic estimates of standing stock and in total catches by nets during each survey.

Survey	Gear	Nile perch		Tilapia		Dagaa		Other taxa	Caridina/Total Catch	Caridina/Other taxa
	(N)	Acoustic	Net	Net	Acoustic	Net	Acoustic	Net	Net	Net
Aug 99	BT (4)	60.1	92.4	0	20.7	0.02	19.2	7.2	0.30	24.8
	FN (21)		2.3	0		47.1		50.4	0.18	0.4
Feb 00	BT (4)	53.9	89.9	2.7	30.5	1.3	15.6	12.0	0.01	0.11
	FN (23)		22.2	0.015		39.9		35.1	1.45	3.94
Aug 00	BT (9)	58.9	78.9	4.0	25.0	0.9	16.1	20.0	0.12	0.61
	FN (17)		7.8	0.007		26.6		58.2	7.3	27
Feb 01	BT (13)	56.2	72.9	17.4	32.6	1.2	11.2	7.5	1.08	14.0
	FN (14)		0.45	0		7.5		45.1	0	0
Aug 01	PT (28)	74.7	42.9	1.4	16.0	19.7	9.3	37.5	0.11	0.31
Aug 02	PT (29)	62.6	7.6	0.12	26.1	35.3	11.4	57.0	0.06	0.10

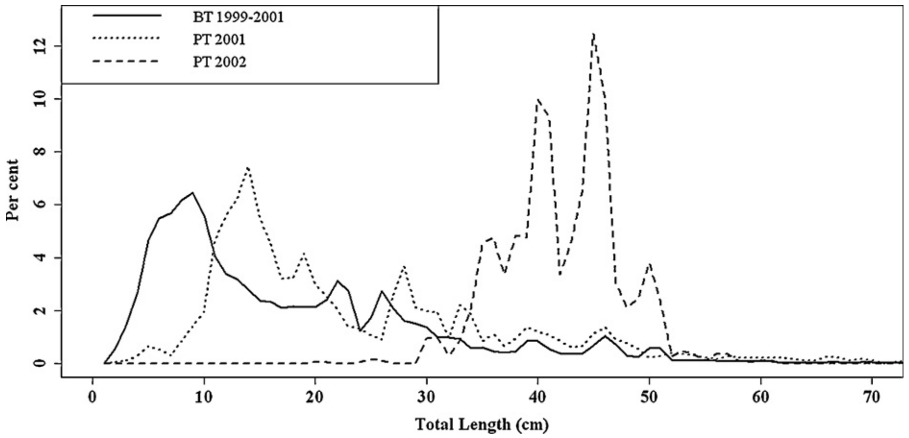

Fig. 10. Length frequency distributions of Nile perch from pelagic and bottom trawls. The values are the percentage of the total of all Nile perch caught by the bottom trawl (BT) on all surveys and the pelagic trawl (PT) on separate surveys.

Table 5
Estimated standing stock of Nile perch with 95% confidence limits for each survey.

Survey	Nile perch standing stock (t)	Lower 95% confidence limit	Upper 95% confidence limit
Aug 99	754,546	542,701	997,255
Feb 00	1,619,103	1,274981	2,012,501
Aug 00	820,892	625,824	1,046,382
Feb 01	1,321,900	964,785	1,754,735
Aug 01	1,447,029	1,099,280	1,874,333
Aug 02	1,601,497	978,842	2,579,921

cannot be because the pelagic trawl failed to catch small fish during the Aug 02 survey because both dagaa and the other taxa are well represented in the catches (Table 4). The results indicate a clear lack of small Nile perch during the Aug 02 survey.

Taking these points into account the evidence from the bottom trawls is indicative of a standing stock of Nile perch in excess of that for the other taxa. It should be noted that the bottom trawl does not sample dagaa at all effectively with the result that the weight for that taxon is low, thus increasing the proportion for Nile perch. In contrast the pelagic trawl in Aug 01 indicated a much smaller proportion, around 43%, by weight of Nile perch to be present. The Aug 02 net hauls results are unusual for two reasons, firstly because of the small proportion of Nile perch present in the catches and secondly due to the preponderance of 30 to 50 cm *TL* fish in those hauls. These results from comparing acoustics and net hauls indicate that, with the exception of the Aug 02 results, the proportion of Nile perch is broadly similar to the amount of small fish.

3.7. Estimated standing stock

The biomass within each stratum was calculated from the mean weight densities in Figs. 5–7 and the stratum areas in Fig. 3 and the lakewide estimates presented in Tables 5–7. The distribution of standing stock by stratum for all taxa was highly skewed to the left and, as with the density estimates, this was normalised using a square root transformation and the equivalent GLM to that used for the density estimates was run. There was no significant difference (NSD) in the means for the quadrants so that factor was dropped for the subsequent analyses. Summary GLM statistics for Nile perch were: Survey: NSD, Season: $p = 0.0139$, Survey and Season: $p = 0.0139$, Stratum NG, $p = 0.00021$ all other strata: NSD. For dagaa the GLM statistics were NSD for Survey, Season and Survey + Season, Stratum NG: $p = 0.0020$, SG: $p = 0.0162$, SI: $p = 0.0023$, all other strata NSD. For the other species category the GLM statistics were: Survey: $p = 0.000965$, Season: $p = 0.000567$, Survey + Season: $p = 0.000569$, Strata: D: $p = 0.000276$, I: $p = 0.00314$, SG: $p = 0.0464$, all other strata: NSD.

Table 6
Estimated standing stock of dagaa with 95% confidence limits for each survey.

Survey	Dagaa standing stock (t)	Lower 95% confidence limit	Upper 95% confidence limit
Aug 99	253,054	168,235	355,991
Feb 00	916,109	658,514	1,225,080
Aug 00	351,922	243,245	481,899
Feb 01	762,165	539,978	1,031,275
Aug 01	307,497	221,389	410,029
Aug 02	692,450	324,282	1,511,007

Table 7
Estimated standing stock of haplochromines with 95% confidence limits for each survey.

Survey	Other taxa standing stock (t)	Lower 95% confidence limit	Upper 95% confidence limit
Aug 99	244,132	183,608	317,829
Feb 00	490,544	329,887	699,623
Aug 00	210,285	150,848	287,636
Feb 01	249,898	162,134	377,770
Aug 01	192,476	126,311	297,786
Aug 02	307,622	209,452	452,120

4. Discussion

4.1. Weight density

Given the short time series of the surveys it is not surprising that there is not a significant trend in the weight density with time for acoustic estimates of density for either Nile perch or for dagaa (Table 3). The same conclusion comes from the bottom trawl results for Nile perch. The same net haul comparison is not appropriate for dagaa because the bottom trawl does not sample that species well (Table 4). Although Getabu et al. (2003) note that there has been a decline in Nile perch the slope of the trend line in their results is not significantly different to zero, a result in agreement with the results presented in Table 3 and further supported by the bottom trawl results.

In spite of there being no trend in weight density over the period of the surveys, it is noteworthy that the Nile perch length frequency distribution was different in Aug 02 to the earlier surveys (Fig. 10). Such a difference could have been due to a recruitment failure in months prior to the Aug 02 survey. Evidence for such an event might be found from a detailed analysis of the STDs, a task outside the scope of the current paper.

Even though there is no trend overall in the results, there are significant seasonal differences in all three groups. In the case of the Deep, Coastal, Inshore and Sesse Island strata, densities were higher during the February as compared to the August surveys (Table 3). Results from Nyanza and Speke Gulfs indicate either no difference or else higher values in August than February.

The same analytical procedures have been used for all of the surveys, which means that the observed seasonal differences must be due, either to changes in fish behaviour affecting their susceptibility to detection acoustically, or else real seasonal changes in density causing changes in abundance. It is important to note that STD, in the case of Nile perch, and echo integration, for the other taxa, are both showing the same pattern, so it is unlikely that the difference in procedures is the cause.

Relevant changes in behaviour could be through migration into regions where they were not or cannot be detected acoustically. Alternatively the *TS* could be affected through tilt angles or biochemical composition.

Whilst not impossible, it seems unlikely that, at the population level, the distribution of tilt angles necessary to double or halve the estimated standing stock would follow the same seasonal pattern in both Nile perch and dagaa. If this is the cause it indicates that field observation of *TS* would be needed associated with every survey. Such a procedure is not impossible when STD is used because the length frequency distribution from bottom trawls can be compared to the concurrent frequency distribution of *TS* as shown by Kayanda et al. (2012), a paper in which no seasonal differences were apparent.

A pattern of high density inshore and lower values for the deep stratum is present for Nile perch both for the August and February surveys (Fig. 8) providing no evidence for onshore/offshore movement. In the case of dagaa there is no obvious offshore/onshore trend in the results present in Fig. 8 to counter the seasonal difference.

Echoes from fish close to the lakebed are liable to coincide with the much stronger echo from the bottom and as a consequence be excluded from the analysis whether by STD or integration. This 'dead zone' effect, discussed at length by Ona and Mitson (1996), is dependent on pulse length and beamwidth, the settings for which (Table 1) would indicate a dead zone of 1 or 2 m. Were half of the February standing stock compressed into a layer within the dead zone the density would have been impossibly high and also would likely have manifest itself as a serious difference in the appearance of the lakebed echoes.

A significant seasonal pattern was also noted by Getabu et al. (2003) for Nile perch but in that analysis the results showed higher densities to be present in August, the opposite to the results reported here. In their paper Getabu et al. (2003) note that the mean Dissolved Oxygen Concentration (DOC) is consistently high at around 6.2 mg l^{-1} during the August surveys but lower in inshore waters during February surveys (4.3 mg l^{-1}) and very low in deep water during that season (1.2 mg l^{-1}) and infer that the oxygen concentration is the cause of the seasonal difference. Were that the case then it would be expected that the Nile perch would be concentrated in shallow water during the February season and widely dispersed over the lake in August. Our results in Fig. 8 indicate the same pattern in both seasons but with different densities. Whilst oxygen concentration may influence the distribution of Nile perch, the seasonal difference noted by the results in this paper are more indicative of the seasonal difference in the balance of production over mortality.

Analysis of the results within the 'Other taxa' category is made more difficult because it contains both fish and crustacea, groups that, owing to the presence of a swimbladder in the fish, an organ contributing over 90% of the backscatter (Foote, 1980). A swimbladder or equivalent source of high backscatter is absent in decapod crustacea (Foote, 1980; Foote and Stanton, 2000).

Using models of acoustic backscatter for zooplankters of similar size, Foote and Stanton (2000) estimated the *TS* of a prawn at 120 kHz, a species with no gas bladder, to be −75 and a siphonophore with a gas inclusion to be −66 dB. Such a difference between Caridina and haplochromines would indicate an approximately eight times higher density of the decapod over the fish for the same level of backscatter.

Although precise measurements have not been made on the *TS* of Caridina it is reasonable to assume that its acoustic scattering properties will be akin to those of prawns which would mean that a given weight density of haplochromines would reflect around eight times as much sound as the same amount of Caridina. In order to determine the weight densities of these two taxa in a mixed grouping it is necessary to know their proportions in the water column. This is possible directly using multifrequency systems (see, for example, Mitson et al., 1996) but has not been achieved using the acoustic data from single frequency systems such as used for these surveys.

Estimation of the proportion of Caridina cannot be done from a single frequency and the only other available indicator might be found in the net haul results. Table 4 shows that the catches contained very small proportions of Caridina; the exceptions being the Frame net in August 1999 and bottom trawl in February 2001 where around 4% of the catch was Caridina, all other catches were much less than 1% of the 'other species' category. Results from the net hauls suggest that at the time of the surveys Caridina made up a very small proportion of the biomass in the lake. This assumption is dependent on the catchability of all taxa by the different nets being quantified so that adjustments can be made. This has not been reported even though it is clear from the results in Table 7 that there is considerable variation.

The size distribution of the different taxa ranges from <1 cm up to >150 cm. Large specimens are likely to be retained by the net whilst small ones, such as Caridina will only be retained by the codend. This problem is compounded by the lack of information on behavioural differences between taxa to the presence of a net. Sampling Caridina quantitatively is known to be difficult, Witte and van Densen (1995) advocate a vertical net or light traps rather than a conventional trawl. These differences mean that caution needs to be exercised when comparing results over a large size range and that this caution needs to be extended for comparisons between taxa. Bearing in mind these cautions it is likely that the small proportion of Caridina in the net hauls is an artefact of the sampling methods rather than an approximation to the true variation.

Caridina was present at low abundance levels before the expansion of the Nile perch stock (Ligtvoet and Witte, 1991) whereas recent studies indicate that there has been a major shift to the type of food web structure described by Ligtvoet and Witte (1991) and shown in Fig. 1. It is therefore likely that the relative abundance of Caridina is greater than that indicated by the results in Table 4. Caridina is reported to be one of the main prey species of Nile perch over the size range from 5 to 60 cm *TL* (Hughes, 1986, 1992, Ogari and Dadzie, 1988, Ogutu-Ohwayo, 1990; Mkumbo and Ligtvoet, 1992). Consequently, it is to be expected that it will have a high standing stock and/or turnover rate. This topic is considered further in the section on Food web considerations.

4.2. Standing stock estimates

Lakewide estimates of standing stock for Nile perch and dagaa from the analyses reported here indicate that there are significant differences between individual surveys (Tables 5 and 6) but there is no significant trend over the survey series (Section 3.7). Any variation from the pattern in the weight densities can therefore only be attributed to redistribution within the strata or major differences in area. The results do not lend support to there being a major redistribution of biomass between strata and the same conclusions with respect to weight density, that there is no significant trend in standing stock with time and that the seasonal differences are not a result of redistribution, therefore apply.

4.3. Food web considerations

Although the preceding analyses provide information on the standing stock of Nile perch, a top predator, and its prey, in order to set the results into an ecosystem context envisaged in Fig. 1, it is necessary to investigate their trophic relationships. It is generally assumed that in the conversion of biomass from one trophic level to the next higher there is an approximately 10% efficiency, a figure that may be as low as 5% or as high as 20% depending on the ecosystem (King, 2007). Standing stock alone cannot be used for this purpose because it provides no indication of production or turnover, a generally accepted norm for which is that there is an approximately tenfold requirement in prey abundance to support a predator. In the context of the present study this is important because the standing stock of Nile perch is similar to that of its prey, a situation that is unsustainable unless its productivity is very much less than that of its prey.

In developing an ECOPATH model for the Lake Victoria species, Moreau (1995) used the food web structure described by Ligtvoet and Witte (1991) along with the following Production to Biomass ratios (P/B) from the literature: Nile perch: 0.95, Predatory haplochromines: 2.5, Planktivorous haplohromines: 3.0, Dagaa: 2.2, and Caridina: 16.0.

Using the current Anon (2008) acoustic protocol, Nile perch are estimated using STD, dagaa from integration in the near surface layer whilst haplochromines, whether predatory or planktivorous, along with the decapod Caridina are contained within the haplochromine integration layer. Applying these P/B ratios to the mean estimates of standing stock from Tables 5–7 gives Nile perch production of 1.260 Mtonnes and its prey of 1.201 Mt of dagaa and 0.705 Mt for the haplochromine group. Although this estimate of prey production is higher than that of the predator it falls far short of the tenfold norm. This discrepancy is reduced if a large proportion of the prey component is the decapod crustacean Caridina. If Caridina were responsible for half the backscatter within the haplochromine layer this would raise the total prey amount to around 3.8 Mt. In the context of the Lake Victoria ecosystem in Fig. 1, if half the backscatter within the haplochromine layer were due to Caridina this would indicate a near sixteenfold difference in prey production over Nile perch, more than sufficient to satisfy the needs of energy flow through the system.

As Moreau (1995) has pointed out, there are several links in the food web leading to Nile perch as the top predator. These are:

1. via Caridina to Nile perch;
2. via Caridina to juvenile and then to adult Nile perch;
3. via insect larvae to juvenile and then to adult Nile perch;
4. via juvenile dagaa and juvenile and then adult Nile perch.

The foregoing discussion has demonstrated that the estimated standing stock values within each category are plausible within the context of an ecosystem analysis. However, at this stage some important assumptions are necessary when quantifying some of the key links. The most critical is the partitioning of the backscatter between Caridina and small fish. In order to develop trophic models it is also necessary to obtain good information on the diet of Nile perch and in particular to determine the proportion of Caridina, juvenile Nile perch, dagaa and other small fish.

The analysis presented in this paper has demonstrated that the acoustic method can be used to quantify several links in the Lake Victoria food web. This approach has the major advantage that the same sampling procedure is being used throughout, obviating the need for inter-comparison studies of methods. For completeness there is the need to ensure that the *TS* to size relationships for all components are equally comparable.

Further research on the *TS* of all taxa would further enhance the quality of the basic information that could be incorporated into ecosystem models. That information combined with stomach content analyses from net hauls would enable the development of realistic ecosystem models.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fishres.2012.09.019.

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