VERTEILUNG UND ABUNDANZ VON ZOOPLANKTON UND *RASTRINEOBOLA ARGENTEA* (PISCES: CYPRINIDAE) UND IHRE TROPHISCHEN INTERAKTIONEN IM NORDLICHEN VIKTORIASEE, OST AFRIKA.

DISSERTATION

ZUR ERLANGUNG DES AKADEMISCHEN GRADES
DOKTOR DER NATURWISSENSCHAFTEN
AN DER FORMAL UND NATURWISSENSCHAFTLICHEN
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EINGEREICHT VON

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WIEN, IM APRIL 1998

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DATE Nov 2000

DISTRIBUTION AND ABUNDANCE OF ZOOPLANKTON AND *RASTRINEOBOLA ARGENTEA* (PISCES: CYPRINIDAE) AND THEIR TROPHIC INTERACTIONS IN NOTHERN LAKE VICTORIA, EAST AFRICA.

THESIS

SUBMITTED FOR THE DOCTORATE DEGREE IN THE
FORMAL AND NATURAL SCIENCES FACULTY
UNIVERSITY OF VIENNA

BY

LUCAS MWEBAZA-NDAWULA M.Sc.

VIENNA, APRIL 1998

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DEDICATION

This research work is dedicated to my dear parents,

SAMUEL M.R. NDAWULA (Late)

and

TOFISA GRACE NANTUME

in recognition of their great resolve and inspiration to make me what I am today.

CONTENTS

Zusammenfassung

Seit drei Jahrzehnten ist der Viktoriasee Schauplatz tiefgreifender Änderungen des Ökosystems, wie auch seiner physikalischen und chemischen Eigenschaften. Der starke Besatz des räuberischen Nilbarsches (*Lates niloticus*) führte während den 80er Jahren zu einem massiven Zusammenbruch der ursprünglich sehr abundanten und artenreichen Gruppe der Haplochrominen (Pisces: Cichlidae), sowie zahlreicher anderer Fische. Im Laufe dieser Entwicklung konnte sich *Rastrineobola argentea* (Pellegrin), eine kleinwüchsige, endemische Cyprinidenart, die vormals im Pelagial des Sees nur von geringer ökologischer Bedeutung war, etablieren und erreichte einen Dichtezuwachs um das Dreifache. Gleichzeitig wuchs das kommerzielle Interesse an dieser Fischart als Nahrungsquelle für die Bevölkerung der angrenzenden Länder. Die rasche, großflächige Ausbeutung dieses Fisches erfordert die Ausarbeitung eines vernünftigen Fischereimanagements, für welches die umfassende Erforschung der Biologie und Ökologie von *R. argentea* von enormer Bedeutung und Dringlichkeit ist. In diesem großen Untersuchungsfeld fällt besonderes Augenmerk auf die Ernährungsökologie. Eine fundierte Analyse dieses Aspektes ermöglicht erst das Verständnis der funktionllen Rolle dieser Fischart in der Nahrungskette, sowie der nahrungsbedingten Faktoren, die ausschlaggebend für die Fischproduktion sind.

Thema dieser Untersuchung ist die Ernährungsökologie von *R. argentea* im nord-westlichen Teil des Viktoriasees (Uganda) in den Jahren 1994 bis 1996. Für die Besammlungen wurden sowohl ufernahe, seichte als auch uferferne, tiefe Standorte ausgewählt. Die Hauptziele dieser Studie waren eine detailierte Analyse der Nahrung sowie der Abhängigkeit des Nahrungsspektrums von der räumlichen und zeitlichen Verteilung und der Abundanz der Fische und deren Beute (Zooplankton). Für die Interpretation von den Verteilungsmustern von *R.*

argentea und vom Zooplankton wurden sowohl Profile von Temperatur und gelöstem Sauerstoff, als auch Wassertransparenz, Lichtextinktion und Phytoplanktonbiomasse gemessen.

Der potentielle Einfluß des Räuberdruckes auf die Beutegemeinschaft konnte mittels Vergleichen der Größen- und Biomassestruktur der Zooplanktongesellschaft zwischen ufernahen Stellen mit hohen Fischdichten und uferfernen Stellen mit viel geringeren Fischdichten ermittelt werden. Saisonale Vergleiche der Zooplanktongrößenstruktur wurden zwischen Dezember 1995 (niedrige Zooplanktondichten; hohe Fischdichten) und Juli 1996 (hohe Zooplanktondichten; niedrige Fischdichten) angestellt. Dank historischer Zooplankton- und Fischproben aus den 60er Jahren (prä-Nilbarsch-Ära; charakterisiert durch hohe Dichten planktivorer Cichliden) und modernen Proben (diese Studie) (post-Nilbarsch-Ära; *R. argentea* als wichtigste planktivore Art) war es möglich, Langzeiteffekte aufgrund von Planktivorie festzustellen. Darüberhinaus wurde die Beutegrößenselektivität mittels Vergleich von relativen, mittleren Beutegrößen in den Fischdärmen und im Nahrungsspektrum, sowie durch Anwendung eines Selektivitätsindex für zwei unterschiedliche Beutetypen und unterschiedliche Fischgrößenklassen ermittelt.

Die Struktur der Wassersäule wechselte zwischen thermaler Stratifizierung mit gut ausgebildeter Thermoklilne und Oxykline (Oktober bis März) und Durchmischung (März bis Juli) sowohl im ufernahen als auch im tiefen Bereich. Während des Höhepunktes der thermalen Schichtung im Dezember wurde eine beträchtliche Sauerstoffzehrung (bis zu $<1.0 mg\ O_2 l^{-1}$) festgestellt. Die vertikale Verteilung von Zooplankton und *R. argentea* erwies sich als abhängig von der saisonalen Schichtung bzw. Durchmischung. So konnte eine Konzentration von Organismen über dem anoxischen Hypolimnion im Verlauf der thermalen Schichtung beobachtet werden, während die

durchmischte Wassersäule durch homogene Verteilungsmuster charakterisiert war. Diese Verteilungsmuster von *R. argentea* (und offensichtlich auch vom Zooplankton) lassen sich auf die Vermeidung niedriger Sauerstoffbedingungen im Hypolimnion während der Stratifizierung zurückführen.

Die generelle Verdrängung von bodenaufsuchenden Organismen in höhere Wasserschichten aufgrund der Sauerstoffzehrung während der thermischen Schichtung ermöglicht eine zusätzliche räumliche Überlappung von *R. argentea* mit Beuteorganismen als auch mit dem größten natürlichen Räuber, dem Nilbarsch. Diese Art bevorzugt tiefere Wasserschichten und ist während anoxischer Bedingungen gezwungen, in höhere Wasserschichten auszuweichen. Obwohl der Nilbarsch ursprünglich zu einer Verbesserung der Nahrungsbedingungen für *R. argentea* geführt hat, könnte er in Phasen hoher Überlappung einen starken Fraßdruck auf die kleine Cyprinidenart ausüben. Zur Zeit ist noch nicht bekannt, wie gut Populationen von *R. argentea* dem Druck durch wandernde Nilbarsche, Befischungen und den beobachteten Fraß durch Vögel widerstehen können.

Zooplankton und Fischdichten, Wassertransparenz, Lichtextinctionkoeffizienten und Phytoplankton Biomasse (Chl a) wiesen Gradienten vom Ufer zum offenen Wasser hin auf. Im Oktober 1996 korrelierte am ufernahen Standort niedrige Wassertransparenz mit einem hohen Extinktionskoeffizienten, während am uferfernen Standort das Gegenteil vorherrschte. Der Chlorophyll-a Gehalt war ufernah fast zwei mal höher als im offenen Wasser während November/Dezember 1995 und Oktober 1996. Das Chll-a-Vertikalprofil zeigte an beiden Standorten Biomassespitzen zwischen 1 und 10m Tiefe. Zwischen Fisch- und Zooplanktondichten bestand eine klare quantitative Beziehung. Im offenen Wasser stand einer hohen Zooplanktonabundanz niedrige Fischdichten gegenüber, während in Ufernähe

niedrigere Zooplankton- und höhere Fischdichten beobachtet wurden. Die Zooplanktongesellschaft setzt sich zusammen aus cyclopiden Copepoden (3 Gattungen: 8 Arten), calanoiden Copepoden (2 Gattungen: 2 Arten), Cladoceren (7 Gattungen: 8 Arten), Rotatorien (12 Gattungen: 19 Arten), der Süßwassergarnele (*Caridina nilotica*), aquatischen Dipterenlarven und –puppen und Milben. Alle Gruppen kamen an beiden Beprobungsstellen vor. Allerdings gab es einige Unterschiede in der relativen Abundanz entlang des horizontalen Gradientens. Rotatoriendichten waren im ufernahen Bereich höher. Darüberhinaus wurde für diesen Standort eine höhere Artendiversität festgestellt. Dagegen waren große Diaptomiden (900-1400µm), sowie Cyclopiden im Größenbereich 500-700µm im offenen Wasser abundanter. Obwohl cyclopide Copepoden numerisch die größte Gruppe darstellten, dominierten die weniger zahlreichen aber größeren Diaptomiden die Biomasse.

Die Größenstruktur der Population von *R. argentea* am ufernahen Standort war gekennzeichnet von einem Wechsel zweier modaler Längenklassen (10-35 und 40-60mmsl.) zwischen den Besammlungsterminen, während die Größenverteilung im offenen Wasser von kleinen Fischen (Modallänge von 20mm sl.) an beiden Terminen dominiert wurde. Die saisonale Entwicklung der Populationsstruktur ließ sich in Ufernähe verfolgen. Im Dezember 1995 dominierte eine einzige Kohorte von großen Fischen (Modallänge 45mm sl.), während im März und September-Oktober 1996 ein zweimodales Muster mit Längen von 10 und 50mm bzw. 15 und 30mm sl. beobachtet wurden. Diese saisonale Längenverteilung widerspiegelt den jährlichen Brutzyklus und das Wachstum juveniler Fische in seichten ufernahen Arealen.

Verschiedene pelagische Arten (z.B. *R. argentea,* juvenile Cichliden und Nilbarsche) wiesen unterschiedliche saisonale Muster in der Abundanz in ufernahen Gewässern auf. *R. argentea* und Cichliden waren zahlreich im

Dezember (bis zu 20 Fische/ Netzzug), nahmen von März bis Juli 1996 ab (<3 Fische/Netzzug). Die erste Gruppe erreichte im September und Oktober Höchstdichten bis zu 80 Fischen/Netzzug. Die Cichlidendichten dagegen blieben bis September 1996 niedrig. Juvenile Nilbarsche wiesen die höchste Dichte von März 1996 bis Juli 1996 (<40 Fische/Netzzug) auf und nahmen während September und Oktober 1996 (<10 Fische/Netzzug) ab. Das offene Wasser war charakterisiert durch sehr geringe Fischdichten und Fischbiomasse an beiden Besammlungsterminen. Die Fischbiomasse in Ufernähe folgte dem saisonalen Verlauf der Fischdichten. Diese Muster scheinen mit den Brutzyklen der gefundenen Arten, die Uferbereiche als Laichgründe und Aufwuchsareale nützen, übereinzustimmen. *R. argentea* repräsentierte während der Untersuchungszeit die Art mit den höchsten Dichten und der höchsten Biomasse für alle Besammlungsstandorte.

Das Nahrungsspektrum von R. *argentea* der Größenklasse 10-60mm sl. wurde dominiert von cyclopiden Copepoden, welche >75% der aufgenommenen Beuteindividuen bzw. >65% des Trockengewichtes des Darminhaltes ausmachten. Zusätzlich bestand die Nahrung aus Diaptomiden, Cladoceren, Rotatorien, Chaoboruslarven und adulten Insecten. Die Süßwassergarnele, *Caridina nilotica*, die während der Nachtstunden in sehr hohen Dichten in der Wassersäule vorkommt, wurde, trotz Beobachtungen in Fischdärmen von Individuen vom Mwanza-Golf (südlicher Teil des Sees), im untersuchten Darminhalten nicht vorgefunden. Eine mögliche Erklärung könnte die unterschiedliche Befischungstechnik und die Auswahl der Besammlungstermine sein.

Der Anteil von cyclopiden Copepoden im Nahrungsspektrum von *R. argentea* vom Befischungsstandort am offenen See (BG) war wesentlich höher (ca. 98%), als der ermittelte Anteil von ufernahen Standorten (MSE und NG)

(78 bzw. 53%). Den zweitwichtigsten Beutetyp am offenen See stellten Chaoboruslarven (4.8%) dar, während in Ufernähe adulte Insekten (42%, NG) sowie Rotatorien (16%, MSE) in beträchtlichen Mengen gefressen wurden. Generell repräsentierten Cyclopiden auch den Hauptanteil der Biomasse, obwohl Chaoboruslarven bzw. adulte Insekten periodisch je nach Standort und Zeit an Wichtigkeit zunahmen.

Im Laufe der Ontogenie von *R. argentea* zeigte sich die zunehmende Aufnahme größerer Mengen von Diaptomiden bzw. der gegenläufige Trend für kleine Nauplien als Nahrung. Analysen von Fischen, die 1966 im Windy Bay Napoleon Golf (nahe von NG und MSE) gefischt worden waren, bestätigten die dominante Stellung cyclopider Copeoden, obwohl in einem etwas geringerem Anteil von >50% am Gesamtdarminhalt. Außerdem wurden vermehrt Cladoceren (13%) und Diaptomiden (30%) im Vergleich zu einem viel geringerem Anteil von 0.5-3.7% in den modernen Proben aufgenommen. Der relative Anteil der drei Schlüsselbeutetypen an Trockengewicht betrug in der historische Probe 47.1% für Cyclopiden, 23.6% für Diaptomiden und 24.1% für Cladoceren, insgesamt 95% des Totalinhaltes. In den modernen Proben bildeten Cyclopiden 69.9%, Diaptomiden 2.8% und Cladoceren 1.3% des Trockengewichtes, insgesamt 74% des totalen Darminhaltes. Keine wesentlichen Änderungen des Nahrungsspektrum wurden bei Individuen des Befischungsstandortes NG festgestellt. Cyclopiden repräsentierten in allen Sammelterminen die dominante Beute. Rotatorien erreichten den höchsten Nahrungsbestandteil im September-Oktober 1994 und Dezember 1995, obwohl ein Zusammenhang mit dem annuellen Abundanzzyklus nicht feststellbar war. Der mittlere Trockengewichtsanteil von Chaoboruslarven in der Nahrung war relativ hoch im September-Oktober 1994, Oktober1995 und Dezember 1995, während sie im August 1995 kaum gefressen wurden. Die Aufnahme dieser Makrozooplankter schien eher mit der Größenstruktur der Fische als mit der

saisonalen Dichteverteilung übereinzustimmen. Ein Vergleich von Tag- und Nachtdarminhalten ergab, selbst unter Berücksichtigung der vertikalen Position, keinen Unterschied des Nahrungsspektrums. Allerdings zeigten die Trockengewichtsanalysen einen relativ höheren Anteil von Chaoboruslarven in der Nacht, was sich durch die nächtliche Migration dieser Dipterenlarve in höhere Wasserschichten erklären läßt.

Die Preferenz von cyclopiden Copepoden in den historischen wie den modernen Proben ist auf den hohen Anteil dieser Gruppe im Zooplankton zurückzuführen. Als sehr artenreiche Form bilden sie ein sehr weites Spektrum an Partikelgrößen für planktivore Fische. Die warmen tropischen Bedingungen ermöglichen hohe Produktionsraten und Konzentrationen, die selbst bei starken Fraßdruck aufrecht erhalten bleiben können.

Die Analyse der mittleren Beutegrößen im Darm und im verfügbaren Zooplankton zeigte im Dezember 1995 am Befischungspunkt NG Nahrungspreferenz für größere Cyclopiden. Im Gegenteil wurden aus dem verfügbaren Größenspektrum von Diaptomiden kleinere Individuen von *R. argentea* konsumiert. Individuen der Fischgrößenklasse <50mm sl. selektierten, Copepoden der modalen Größe 500µm, während für Fische >50mm sl. eine Preferenz von Beutetieren von 600-700µm festgestellt wurden. Die mittlere Größe der gefressenen Copepoden stieg mit zunehmender Fischstandardlänge an. Der Jacobs Index zeigte positive Selection für Cyclopiden in allen Fischgrößenklassen (10-60mm sl.). Calanoide Copepoden und Cladoceren wurden von juvenilen Fischen (<20mm sl.) vermieden, jedoch von größeren Individuen mehr oder weniger entsprechend ihres Vorkommens aufgenommen. Unter Berücksichtigung der Beutegröße war für Fische der Größe 10-50mm sl. eine starke Preferenz für Copepoden von 500µm zu verzeichnen (D= +0.58 - +0.71). Die größten Individuen (>50mm sl.) bevorzugten Beutetiere von 900µm

Länge (D=+0.87). Dagegen wurden Copepoden <400µm und >1000µm sehr stark von allen Fischlängenklassen vermieden.

Die hervorstechende Selektion von Cyclopiden und die Vermeidung von Diaptomiden und Cladoceren demonstriert, daß die relative Beuteabundanz ein entscheidender Faktor für die Nahrungswahl von *R. argentea* ist. Die Vermeidung kleinerer Copepoden und die positive Selektion von Beute von 500-700µm Länge sind ein Hinweis auf eine größenabhängige Nahrungswahl dieser Fischart und bestätigen die den „Optimal Foraging" Theorien (OFT) zugrundeliegende Vermutung, daß Fische ihre Nahrungsaufnahme durch aktive Beutewahl optimieren können. Die Vermeidung der größten Individuen der Gruppe der Diaptomiden ist wahrscheinlich auf ihre geringen Dichten und ihr effizienteres Fluchtverhalten zu zurückzuführen.

ABSTRACT

The diet, spatial-temporal distribution and abundance patterns of the pelagic cyprinid, *Rastrineobola argentea* (Pellegrin) and zooplankton were investigated in conjuction with limnological conditions in nothern Lake Victoria, between September 1994 and October 1996. Samples were collected from the shallow inshore and deep open waters. Fish and zooplankton were sampled with a small mid-water trawl net of 5 mm stretch mesh size and a Schindler trap respectively from the surface, mid-waters and near-bottom vertical positions. Concomitant measurements of temperature, dissolved oxygen (DO), light attenuation, Secchi depths and chlorophyll-a were made. Water column structure exhibited seasonal alternation of thermal stratification (October-March) and mixing March-July), synchronous in inshore and offshore waters. Oxygen depletion (up to < 1.0 mg O_2l^{-1}) was common in the hypolimnion during stratification, in contrast with high DO throughout the water column during turnover. Vertical distribution of fish and zooplankton revealed higher concentrations above the oxycline during stratification while a near homogeneous dispersion occurred during mixing. Low zooplankton-high fish densities inshore contrasted with high zooplankton-low fish densities offshore. Low water transparency-high extinction coefficients inshore contrasted with high water transparecy-low extinction coefficients offshore. Phytobiomass was nearly twice as high inshore compared to offshore. Zooplankton community was dominated by cyclopoid copepods, with minor proportions of diaptomids, cladocerans, rotifers etc. Higher, relative proportions of diaptomids and cladocerans, in the historical (1961) sample, however, prompted suggestions of long-term changes in zooplankton community structure. Most zooplankters attained highest numerical abundance during the annual turnover, (July), declining thereafter to lower levels in subsequent months. Zooplankton size distribution in December 1995 indicated lower relative abundance of large copepods inshore compared to offshore,

while both copepods and cladocerans showed higher abundances (inshore) during July 1996. Pelagic fish community, was dominated by *R. argentea*, and the three co-habiting taxa exhibited different seasonal patterns of abundance. *R. argentea* fed heavily on cyclopoids, with minor supplements from diaptomids, and cladocerans. Proportions of diaptomids increased with fish size while nauplii showed the reverse pattern. Comparision of propoportions of diaptomids and cladocerans in the diet of historical (1966) and modern (December 1995) fish diet suggests substantial decline in their relative contributions. No major and consistent variations in diet composition were observed on different sampling dates, day and night samples or different vertical positions in the water column. Dominance of the diet by cyclopoids seemed to be largely due to their much greater pelagic abundance, higher species diversity and wide size range of food particles. Sustained prominence of cyclopoids in the environment may be partly explained by high productivity under warm tropical conditions where a taxon may be be mantained at high concentrations despite heavy predation.

LIMNOLOGICAL CONDITIONS, COMPOSITION, DISTRIBUTION AND ABUNDANCE OF ZOOPLANKTON AND PELAGIC FISHES AND THE DIET OF *RASTRINEOBOLA ARGENTEA* (PELLEGRIN)

1. INTRODUCTION

Over the past three decades, Lake Victoria ecosystem has undergone remarkable transformations following radical changes in its physical, chemical and biological characteristics (Ogutu-Ohwayo, 1990; Kaufman, 1992). Witte et al., 1992 & 1995; Hecky, 1993; Hecky et al., 1994) To date, various human perturbations continue to impact the lake ecology through increased pressure on the fisheries and irrational land use practices in the catchment area (Bugenyi & Balirwa, 1989). Scientific opinion on these ecological challenges and strategies to keep apace with the new unfolding lake processes have been well articulated by Branstrator et al., (1996). Understanding of the mechanisms of cause and effect underlying such ecological changes entails in part, a firm grasp of knowledge of the lake's past and present food webs.

At the time when the previously dominant haplochromine cichlids were declining during the 1980s, the small pelagic cyprinid, *Rastrineobola argentea,* increased remarkably in abundance in the period between 1982-1987 (Wanink, 1991; Witte et al., 1992), becoming the second most important commercial species after the Nile perch in Kenya and Tanzania waters of Lake Victoria (Arunga 1991) and third after *Lates* and *Oreochromis* in the Uganda waters (Ogutu-Ohwayo, 1990). The new ecological and economic status of *R. argentea* came against a backdrop of a dearth of scientific information necessary for preservation and management planning of its fishery. Current information suggests a continuous annual breeding cycle of the fish in shallow inshore areas

one in December - Janua

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Previous records indicate that *R. argentea* feeds on zooplankton , and in

ticular copepods (Corbet, 1961; Greenwood, 1966; Wandera, 1991;1992).

part from the study by Hoogenboezem (1985), vital details of the feeding ecology of the fish are lacking. The importance of zooplankton in the Lake Victoria food webs deserves emphasis. Currently the zooplankton community constitutes a major harvester of the lake's primary production and is vital food resource to the Nile perch and several birds of prey around the lake (Wanink, 1992; Goudswaard & Wanink, 1993; Wanink et al., 1993; Wanink & Goudswaard, 1994).

Virtually all larval fish in Lake Victoria, regardless of taxon, are to a great extent planktivorous (personal observation). However, current knowledge on the ecology of the zooplankton community is very limited. Detailed accounts of the spatial-temporal patterns of distribution and abundance are lacking. Potenti

impacts on the community structure by planktivory have not been studied and the food chain link between zooplankton and fishery production is poorly understood. The few early studies on Lake Victoria zooplankton were largely descriptive (Daday, 1907; Delachaux, 1917; Rzoska, 1957). The first quantitative data (Worthington, 1931) reported relative abundancies for various taxa and aspects of vertical migration. Recent studies by Mavuti and Litterick (1991), Branstrator et al. (1996), and Mwebaza-Ndawula (1994) provide some preliminary understanding of the quantitative aspects of distribution and abundance patterns.

Understanding of the mechanisms and extent of trophic interaction between a predator and its food resources requires adequate knowledge on the distribution and abundance of both the predator and prey in time and space. Such knowledge is a pre-requisite towards understanding the functional role and significance of *R. argentea* in the Lake Victoria ecosystem. In this study an attempt is made to investigate and answer the following ecological questions:

1. How does the distribution and abundance patterns in fish and zooplankton relate to the limnological regime in Lake Victoria ?
2. To what extent do the distribution and abundance patterns in fish and zooplankton relate to trophic interaction ?
3. What constitutes the food base of *R. argentea* in Lake Victoria and how does the diet vary in time and space ?
4. What are the impacts, if any, of planktivory on the zooplankton community ?
5. How does historical planktivory by *R. argentea* compare with modern planktivory under changed lake conditions and what are the ecological implications of this ?
6. How sustainable is *R. argentea* and its fishery in the modern Lake Victoria ecosystem ?

of the lake, with two peaks: one in December - January and another in August - September (Wandera, 1992). Size of the smallest ripe females varies with locality; but are in a range of 36 to 44 mm sl (Okedi, 1973; Wanink, 1988; Wandera, 1992). These values, however, appear to have gone down in time. Wanink (in preparation), has found a value of 33 mm for the smallest ripe females in the southern part of the lake.

Maximum size of *R. argentea* decreased over the period of its increase in abundance in the lake (Wanink, 1991), largely as a result of increased fishing mortality (Wandera, 1992) and predation by the Nile perch, *Lates niloticus* (Wanink, 1988). An increasing inshore-offshore trend in biomass of *R. argentea* over a depth range of 2-30 metres has been reported in the areas of the lake (Wanink, 1988). Diurnal vertical migrations have also been reported and are believed to be influenced by seasonal variations in water column structure (Wandera, 1992).

Previous records indicate that *R. argentea* feeds on zooplankton , and in particular copepods (Corbet, 1961; Greenwood, 1966; Wandera, 1991;1992). Apart from the study by Hoogenboezem (1985), vital details of the feeding ecology of the fish are lacking. The importance of zooplankton in the Lake Victoria food webs deserves emphasis. Currently the zooplankton community constitutes a major harvester of the lake's primary production and is vital food resource to the Nile perch and several birds of prey around the lake (Wanink, 1992; Goudswaard & Wanink, 1993; Wanink et al., 1993; Wanink & Goudswaard, 1994).

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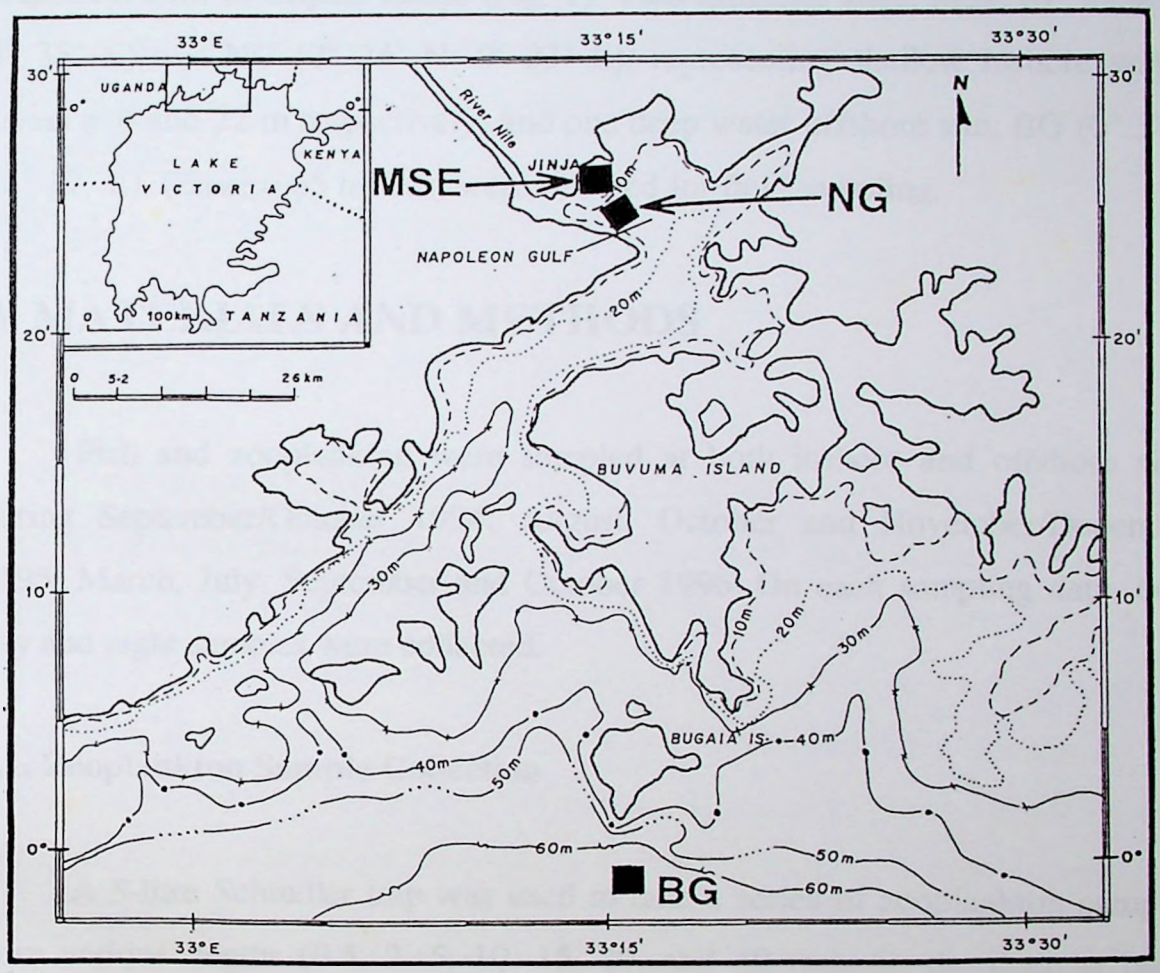


Figure 1. Map of northern Lake Victoria showing the study areas: MSE, NG and BG.

2. STUDY AREA

The geographical boundaries of Lake Victoria are 0° 20' N - 3° 0' S, 31° 39'-34° 53' E (Welcomme 1972) and lies at an altitude of 1134 m above sea level. The study area is located in the northern part of the lake, stretching from Napoleon Gulf to Bugaia Island (Fig. 1). Two sampling sites: MSE (0° 25.9' N; 0° 33' E) and NG (0° 24' N; 0° 33' E), representing shallow inshore waters (Z_{max} = 6 and 22 m respectively) and one deep water offshore site, BG (0°.3' S; 33° 17' E), (Z_{max} = 65 metres) were selected for field sampling.

3. MATERIALS AND METHODS

Fish and zooplankton were sampled at both inshore and offshore sites during September/October 1994; August, October and November/December 1995; March, July, September and October 1996. On each sampling date, both day and night samples were collected.

3.1. Zooplankton Sample Collection

A 5-litre Schindler trap was used to take a series of zooplankton samples from various depths (0.5, 2, 5, 10, 15, 20, and 40 metres); the deepest point depending on the maximum depth at each site. From each depth level, three hauls were taken, pooled, filtered through a 60 µm nitex mesh net and the sample preserved in sugar-4% formalin solution.

3.2. Fish Sample Collection

Fish samples were taken with a small midwater trawl net of the design described by Matena (1995). The conical net was of 5 mm stretch mesh size, had a mouth opening of 1 X 1 metre and was approximately 6 metres long. The net was secured to the back of a canoe and towed through water with a 25 HP outboard motor. At each sampling station, five horizontal tows, each of 5 minutes duration were taken at vertical depths representing the surface, intermediate and near-bottom water strata. Fish samples were preserved in 10% formalin for subsequent laboratory examination.

3.3. Physical-chemical Measurements

Vertical profiles of underwater light and water transpareny were measured with a lightmeter and Secchi disk repectively, while temperature and dissolved oxygen were determined using a Hydrolab Surveyor 11. Water samples for chlorophyll-a determination were collected at various depths using a dark-painted bottle sampler. Phytoplankton chlorophyll-a was determined by filtration of 100 mls of the sample on to a GF/C filter and the latter immersed in 10 mls of 95% methanol for approximately 20 hours at 4°C in the dark until final reading on a Turner fluorometer.

3.4. Zooplankton Sample Analysis

Species identification of zooplankton was carried out in collaboration with the laboratory of Ecology, Ghent, Belgium. Taxonomic sorting and enumeration was carried out under an inverted microscope (x100). For computational purposes, organisms were assigned to broad taxonomic groupings: i.e. cyclopid

and diaptomid copepods (copepodid instars C1 to C6), nauplii, cladocerans, rotifera, chaoborid instars, adult insects and 'other' (minor constituents). Body lengths of copepods, (excluding antenae and posterior terminal spines and setae) were measured with the aid of a calibrated Camera Lucida mounted on a compound stereo microscope. Dry weight estimates were made using existing length-weight regressions (Botrell et al. 1976). For *Chaoborus* larvae and adult insects dry weights were estimated from mean weights of randomly selected individuals (n = 20-50) dried for 24 hours at 80°C in an oven.

3.5. Fish Sample Analysis

Fish standard lengths (mm sl) were measured to the nearest 0.1 mm (from the snout to the base of the hypeural bones) with an electronic digital caliper Fresh weight of each individual fish was measured to the nearest 0.1gm on a Sartorius research balance (R180D). Each fish was dissected, its entire gut removed, and its length measured. The gut was opened up by a longitudinal incision with a pair of scisors and a preparation of its entire contents mounted on to a glass slide (plus coverslip) in artificial wax (gelvatol) for subsequent microscopic examination. Identification of prey taxa and enumeration was carried out under a stereo compound microscope (x 40). Where gut contents were in an advanced state of digestion, resistant body parts were identified (i.e. furcal rami in copepods, mandibular structure in cladocerans, trophi in rotifers, head capsules in chaoborid larvae and adult insects) and used as enumeration units in subsequent data analysis.

3.6. Statistical analysis

For comparision of the vertical distribution of zooplankton and fish densities, a Chi-square test (Sokal & Rohlf 1981) was used.

4. RESULTS AND DISCUSSION

4.1.0. Limnological conditions

An assessment of limnological conditions prevailing in the study area (Figures 2a & b and Figure 3; Table 1 and Table 2a & b) was based on comparisions of vertical profiles of temperature and dissolved oxygen at the three sampling sites (MSE, NG and BG; for the months of December 1995 and October 1996), an examination of seasonal trends in temperature and dissolved oxygen depth profiles at NG station and comparisions of inshore-offshore data of Secchi records, light extinction coefficients and chlorophyll-a levels.

4.1.1. Temperature and Dissolved Oxygen Profiles: Inshore vs Offshore waters

The December 1995 and October 1996 temperature and dissolved oxygen (DO) profiles for inshore (NG, MSE) and offshore (BG) stations indicate certain similarities and differences among the three study sites. Near-surface thermoclines, indicative of diurnal heating under brief spells of calm weather, were common to all three stations (Fig. 2a and Appendix 1). Thermal stratification with well developed deep water thermoclines and oxyclines characterised the water column structure at NG and BG during both periods.

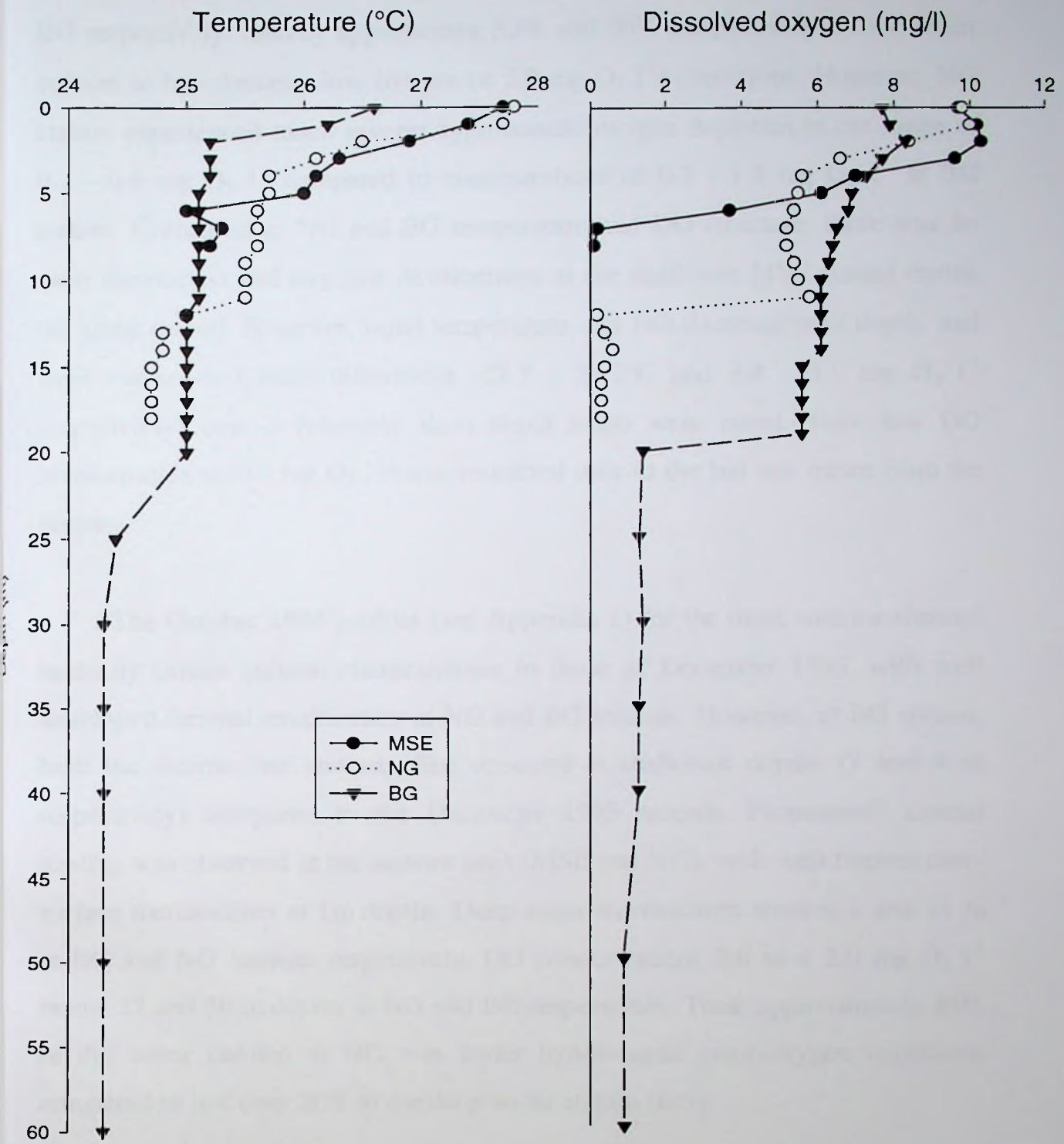


Figure 2a. Temperature (^{0}C) and dissolved oxygen (mgl^{-1}) depth profiles at MSE, NG, and BG sampling sites, November/December 1995.

During December 1995, the thermocline was at 11 m and 20 m in NG and BG respectively; thereby apportioning 50% and 70% (respectively) of the water column to hypolimnetic low oxygen (< 2.0 mg O_2 l^{-1}) conditions. However, NG station experienced much severer hypolimnetic oxygen depletion in the range of 0.2 - 0.6 mg O_2 l^{-1} compared to concentrations of 0.7 - 1.4 mg O_2 l^{-1} at BG station. Compared to NG and BG temperature and DO structure, there was no clear themocline and oxycline development at the shallower MSE station during the same period. However, rapid temperature and DO decrease with depth, and large surface-to-bottom differences (27.7 - 25.2°C and 9.8 - 0.1 mg O_2 l^{-1} respectively) over a relatively short depth range were noted. Very low DO concentration (< 0.2 mg O_2 l^{-1}) was restricted only to the last one metre from the bottom.

The October 1996 profiles (see Appendix 1) for the three stations showed basically similar column characteristics to those of December 1995, with well developed thermal stratification at NG and BG stations. However, at BG station, both the thermocline and oxycline occurred at shallower depths (7 and 9 m respectively) compared to the December 1995 records. Pronounced diurnal heating was observed at the inshore sites (MSE and NG), with well formed near-surface thermoclines at 1m depths. Deep water thermoclines were at 9 and 11 m in BG and NG stations respectively. DO concentrations fell to < 2.0 mg O_2 l^{-1} below 12 and 50 m depths at NG and BG respectively. Thus, approximately 45% of the water column at NG was under hypolimnetic poor-oxygen conditions compared to just over 20% at the deep water station (BG).

The deeper water strata at MSE station remained largely unstratified and maintained relatively high DO concentrations (> 4.0 mg O_2 l^{-1}) from surface to bottom. Lack of strong thermal stratification at this littoral station is an attribute

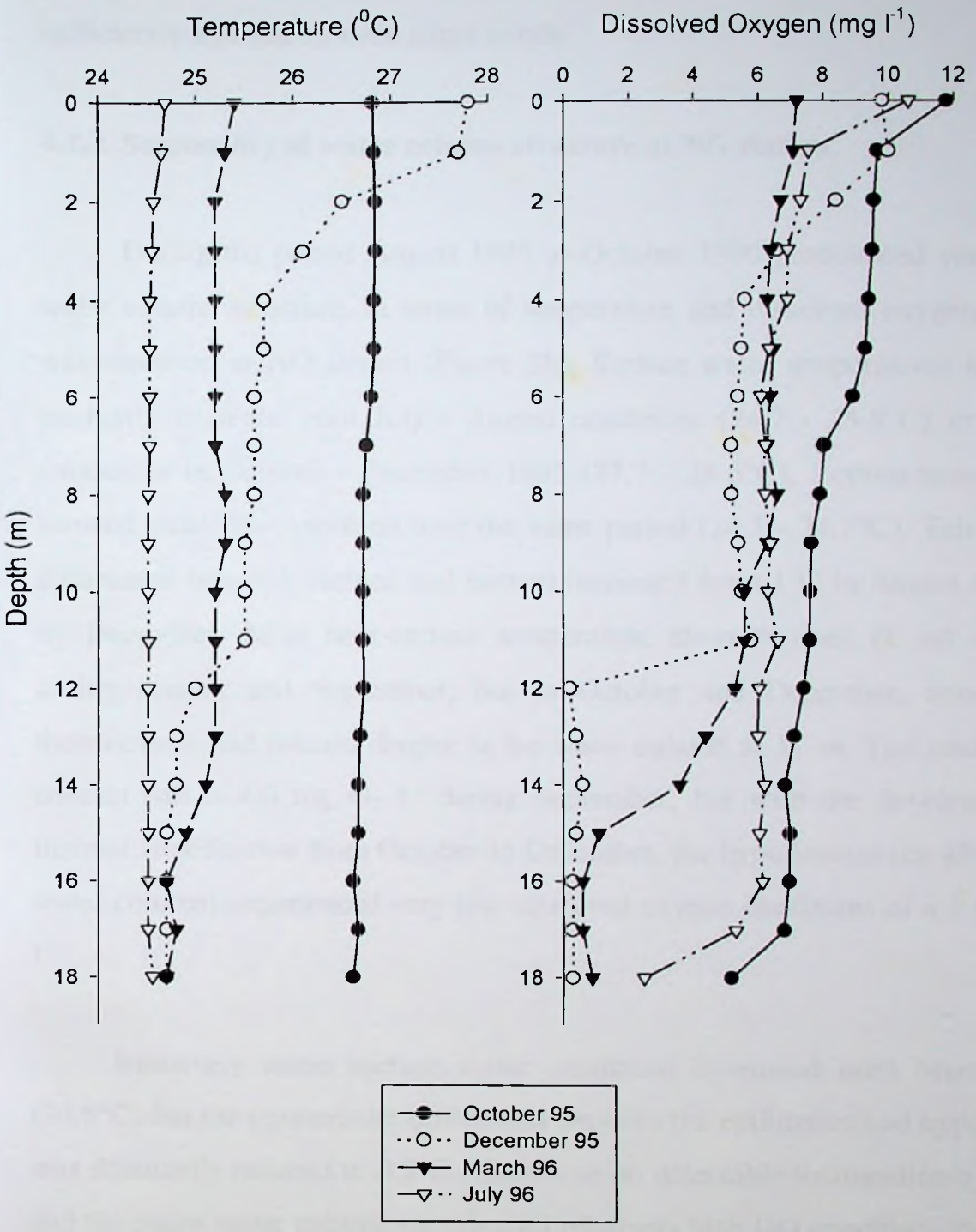


Figure 2b: Temperature and dissolved oxygen depth profiles at NG station

of shallowness of the water column whereby the its entire depth can be kept sufficiently agitated by even slight winds.

4.1.2. Seasonality of water column structure at NG station

During the period August 1995 to October 1996 pronounced variation in water column structure, in terms of temperature and dissolved oxygen profiles was observed at NG station (Figure 2b). Surface water temperatures increased gradually from the cool July - August conditions (24.7 - 25.8°C) to warmer conditions in October - December 1995 (27.7 - 28.6°C). Bottom temperatures showed much less variation over the same period (24.3 - 24.7°C). Temperature differential between surface and bottom increased from 1°C in August to 3.1°C by December. Mild near-surface temperature discontinuities (1 m) occurred during August and September, but in October and December, conspicuous thermoclines had formed deeper in the water column at 11 m. The entire water column had > 4.0 mg O_2 l^{-1} during September, but with the development of thermal stratification from October to December, the hypolimnion (ca 45% of the water column) experienced very low dissolved oxygen conditions of < 2.0 mg O_2 l^{-1}.

Relatively warm surface water conditions continued until March 1996 (26.8°C) but the temperature differential between the epilimnion and hypolimnion was drastically reduced to 0.2°C. There was no detectable thermocline by March and the entire water column experienced relatively high DO conditions.(> 5.0 mg O_2 l^{-1}). The pattern of distribution of temperature and dissolved oxygen for March, which indicated virtual breakdown of thermal stratification and the enhancement of mixing of the entire water column (holomixis), must however be interpreted with caution, as the DO levels recorded seem to be too high for the

corresponding temperatures. Comparable mixing conditions were still prevailing by July 1996, though at lower mixing temperatures (24.6 - 24.7°C) attained during the cool and wet season (April - August). Temperature and DO profiles during September and October 1996 were comparable to corresponding patterns in 1995, with the exception of an apparently early onset of thermal stratification conditions.

4.1.3. Secchi depths and Light extinction coefficients

Secchi depth records for December 1995 (Table 1) indicated nearly similar water transparencies at MSE (inshore) and BG (offshore) stations (1.45 and 1.48 m respectively), while water at NG station (inshore) was much less transparent (0.78 m). On the other hand, the October 1996 comparison showed similar low transparencies for the two inshore stations (MSE, 0.81; NG, 0.86 m) while the offshore water (BG) was markedly more transparent (1.64 m). The source of disparity in the two late-year Secchi observations is not clear. Nonetheless, the October 1996 data suggest low inshore transparencies relative to offshore waters and appear to be consistent with NG and BG records for December 1995. Parallel estimates of light attenuation showed higher extinction coefficients inshore compared to offshore waters and were consistent with the observed inshore-offshore trends in water transparency.

Seasonality in Secchi depths was evident from the NG data. A decreasing trend from 1.20 m in August 1995, through 1.16 m in September, 1.09 m in October culminated into a low record of 0.78 m in December. July 1996 had the highest transparency with Secchi depth as high as 2.20 m, which eventually fell to 0.86 m during October 1996. On the assumption that water transparency is primarily a function of biogenic turbidity in this lake, the seasonal pattern of

Table 1. Secchi depths (m) for inshore and offshore waters of Lake Victoria 1995/96. - indicate no data available. Figures in brackets show corresponding light extinction coefficients (per metre) where data were available.

	1995				1996		
	August	September	October	Nov./Dec.	March	July	October
MSE							
Zmax = 8m	-	-	-	1.25	1.3	-	0.81
INSHORE							(3.16)
NG							
Zmax = 22m	1.24	1.16	1.09	1.0	-	2.2	0.86
INSHORE	(3.10)	(1.48)					(3.98)
BG							
Zmax = 65m	-	-	-	1.95	-	-	1.64
OFFSHORE				(2.47)			(2.34)

water transparency observed may be associated with annual algal production cycle in the lake. Mugidde (1993) reported two peaks of Chll-a at BG: a major one in October - December and a smaller one in May. She pointed out that July - August minima were synchronous at offshore and inshore waters and are associated with severe light limitation due to the deeper mixing depth during the turnover period.

4.1.4. Chlorophyll-a distribution: horizontal and vertical gradients

Phytobiomass (as chll-a) in December 1995 and October 1996 showed clear inshore-offshore gradients (Table 2a). Good agreement was achieved in both data sets showing that offshore phytobiomass levels are an order of magnitude lower than corresponding estimates for inshore waters. Comparison of the present data with chlorophyll-a estimates by Mugidde (1993) (Table 2b; for the years 1989-1991) revealed fair consistency both in magnitude of the estimates as well as inshore-offshore gradients. A similar comparison with data from the Kenyan waters of the lake (Mavuti & Litterick 1991) (Table 2c) provides further confirmation of inshore-offshore trends observed in the Ugandan part of the lake.

Vertical distribution of Chlorophyll-a in NG and BG stations during December 1995 showed the occurrence of higher phytobiomass concentrations at 5 and 10 m while the corresponding peaks in the shallow MSE station were at 1 and 4 m (Fig. 3). The strata of maximum phytobiomass lay within the well lit and mixing (trophogenic) zone at this time of the year (see Fig. 2a). In NG station both chlorophyll-a determinations made on 2 and 12 December 1995 showed double peaks at 1 and 5 m. The peaks may be associated with primary and secondary thermoclines observed at this station (see Fig. 2a). The surface water layer above 1 m and deeper water below 10 m (NG,BG) supported much lower

Table 2. Chlorophyll-a values ($\mu g l^{-1}$) for inshore and offshore waters of Lake Victoria: (a) present study, (b) Mugidde (1993), (c) Mavuti & Litterick (1991). Note: Mugidde (1993) determinations were for inshore station Pilkington Bay (PB) and offshore station Bugala (B G) in Uganda waters, 1989-1991; Mavuti & Litterick (1991)determinations were for inshore and offshore stations in Kenya waters, 1984-1987.

		(a) Present study		(b) Mugidde (1993)	(c) Mavuti & Litterick (1991)
		Nov./Dec. **1995**	October **1996**		
Inshore	MSE	51,2	62,2	range: 22,2-67,1 mean: 46,7	50,6
Inshore	NG	60,9	59,5		
Offshore	BG	24,9	29,9	range: 8,4-40,0 mean: 24,5	40,7

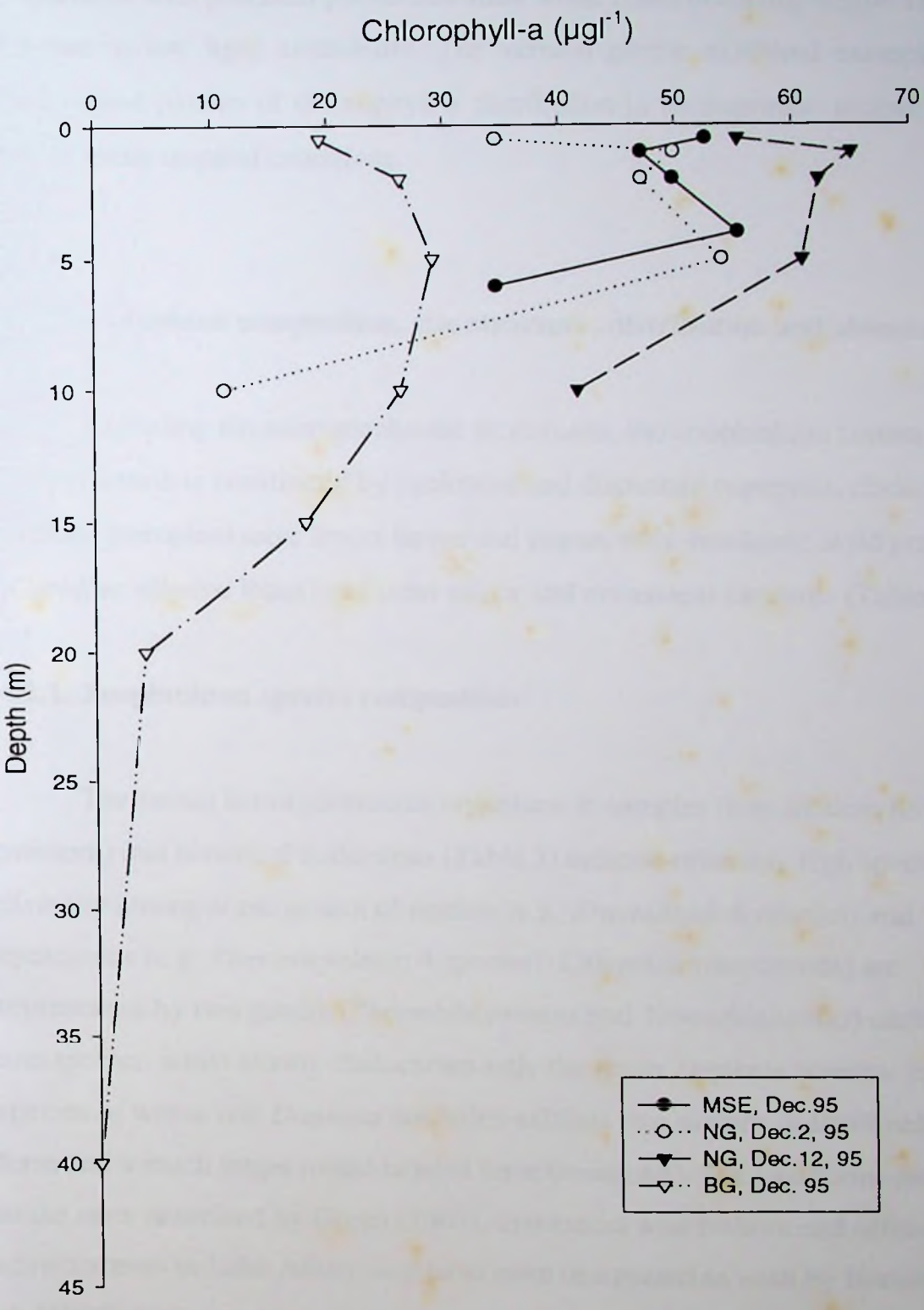


Figure 3. Chlorophyll-a depth profiles for MSE, NG (inshore) and BG (offshore) stations in Dece

chlorophyll-a concentrations. Low chlorophyll values at the surface may be associated with potential photo-inhibition while those occurring below 10 m may be due to low light availability. The vertical profile exhibited examplifies the generalised pattern of chlorophyll-a distribution in an eutrophic system (Wetzel 1983) under tropical conditions.

4.2. Zooplankton composition, size structure, distribution and abundance

Excluding the microplanktonic protozoans, the zooplankton community of Lake Victoria is constituted by cyclopoid and diaptomid copepods, cladocerans, rotifers, meroplanktonic insect larvae and pupae, semi-benthonic atyid prawns (*Caridina nilotica* Roux) and other minor and occasional elements (Table 3).

4.2.1. Zooplankton species composition

The faunal list of planktonic organisms in samples from modern (inshore, offshore) and historical collections (Table 3) indicate relatively high species diversity among some genera of rotifers (e.g. *Brachionus*: 6 species) and cyclopoids (e.g. *Thermocyclops*: 4 species). Calanoids (diaptomids) are represented by two genera (*Thermodiaptomus* and *Tropodiaptomus*) each with one species, while among cladocerans only the genus *Daphnia* contains two species of which one *Daphnia lumholtzi* exhibits two morphs: a small helmeted form and a much larger round-headed form.(*monacha*). The two forms are similar to the ones described by Green (1967), associated with inshore and offshore environments in Lake Albert, and have been designated as such by Branstrator et al. (1996). The remaining 6 cladoceran genera support a single species each. No rotifers were recovered in the historical zooplankton collection (shown as

blanks in Table 3). This may have been due to the mesh size of the net used to take or concentrate the sample. Absence of *C. nilotica* and *Chaoborus* larvae in the historical sample may have been due to the timing of sampling as these two macroplankters spend the day time near bottom sediments and ascend into the water column at night (Lehman et al. 1994; personal observations).

There has been considerable taxonomic controversy especially with the more complex cyclopoid copepod group. At the turn of the twentieth century, Sars (1909) reported occurence of the genus, *Cyclops* containing twenty species from Lake Victoria. Worthington (1931) accordingly grouped all cyclopoid copepods under this genus. On the other hand, Rzoska (1957) reported five cyclopoid species belonging to three genera: *Thermocyclops, Mesocyclops* and *Tropocyclops*. He included in his list the species *Thermocyclops schuurmanae*, while admitting doubts to its true specific identity. In the early 1990s Mavuti and Litterick (1991) reported three genera from the Kenyan part of the lake, one of which, *Microcyclops* had not been reported before. Most of the studies cited above reported the occurrence of *Mesocyclops leukarti* in the lake which was later shown not to exist on the African continent by van de Velde (1984). Mwebaza-Ndawula (1994) identified three genera *Thermocyclops*, *Mesocyclops* and *Tropocyclops*) containing a total of eight species including two species: *Thermocyclops incisus* and *Tropocyclops tenellus* which had not been previously reported from Lake Victoria.

Details of relative proportions of the various taxa in the community are found in recent publications by Branstrator et al. (1996), Mavuti and Litterick (1991) and Mwebaza-Ndawula (1994). The faunistic list adopted in the present study is largely based on identifications of the latter author.

Zooplankton taxa encountered in samples from inshore and offshore waters of Lake Victoria a
historical sample (1961, off Dagusi Island). A and P indicate absence and presence respectively,
ms in the samples. See text for the blanks under historical.

	Inshore	Offshore	Historical
FERA			
Brachionus angularis GOSSE	P	A	
B. calyciflorus GOSSE	P	P	
B. caudatus AHSTROM	P	P	
B. falcatus O.F. MÜLLER	P	P	
B. forficula WIERZEJSKI	P	P	
B. plicatilis O.F.M.	P	P	
Filinia longiseta ZACHARIAS	P	A	
F. opoliensis ZACHARIAS	P	A	
Keratella tropica APSTEIN	P	P	
K.cochlearis GOSSE	P	P	
Polyarthra vulgaris CARLIN	P	A	
Lecane spp.	P	A	
Asplanchna brightwelli GOSSE	P	P	
Trichocerca spp.	P	A	
Anureupsis fissa GOSSE	P	A	
Epiphanes sp.	P	A	
Euclanis spp.	P	A	
Hexathra sp.	P	A	
Pompholyx sp.	P	A	
STACEA			
poida			
Thermocyclops neglectus SARS	P	P	P
T. emini MRAZEK	P	P	P
T. incisus KIEFER	P	P	P
T. oblongatus SARS	P	P	P
Mesocyclops aequatorialis KIEFER	P	P	P
M. major VAN DE VELDE	P	P	P
Tropocyclops confinis KIEFER	P	P	P
T.tenellus SARS	P	P	P

Contd.

lida			
Thermodiaptomus galeboides SARS	P	P	P
Tropodiaptomus stuhlmanni MRAZEK	P	P	P
era			
Daphnia lumholtzi SARS	P	P	P
D. lumholtzi var. *monacha*	A	P	P
D. longispina LEYDG.	P	P	P
Ceriodaphnia cornuta SARS	P	P	P
Diaphanosoma excisum SARS	P	P	P
Bosmina longirostris O.F.M.	P	P	P
Chydorus sphaericus O.F.M.	P	A	P
Alona sp.	P	A	P
Moina micrura KURTZ	P	A	P
poda			
Caridina nilotica ROUX	P	P	
CTA			
Chaoborus larvae and pupae	P	P	
CHNIDA			
Acarid mites	P	A	A

1.2.2. Zooplankton size distribution and abundance: inshore vs offshore and modern vs historical communities

Zooplankton size distributions in modern samples from inshore (NG, December 1995 and NG, July 1996), offshore (BG, December 1995) waters of the lake and one historical sample (open lake off Dagusi island, July 1961) (Fig. 4; see also Appendix 2) show interesting contrasts and similarities in the community structure. The size scale ranging from < 100 µm to > 1500 µm is dominated by mesoplanktonic nauplii and rotifers at the lower side and by adult diaptomid copepods at the upper end; with cyclopoid copepodids and adults and to some extent cladocerans lying between the two extremes. This size analysis excludes the largest and mostly meroplanktonic elements such as the atyid prawns, *Caridina nilotica* and *Chaoborus* larvae and pupae which were relatively rare in the samples; largely due to limitations of the sampling method, time and frequency of sampling. In all four data sets there is a remarkable domination of the communities by cyclopoid copepods (copepodids, adults and naupliar larvae), while diaptomid copepods and to a great extent cladocerans rank relatively low in terms of proportions across all size classes (Figure 4). Comparision of the December 1995 inshore and offshore samples revealed the occurence of lower proportions of large diaptomid.copepods (> 900µm) in the inshore sample. In contrast, mean numbers of the mesoplanktonic rotifers and naupliar larvae indicated higher abundance inshore compared to offshore. Cyclopoid copepods in the size range 500 - 700 µm were found to be less abundant in inshore relative to offshore plankton. Cladocerans, of which the main constituent was *Diaphanosoma excisum* were very rare (not depicted in Fig. 4) in both inshore and offshore plankton.

The inshore zooplankton size distribution during July 1996, though

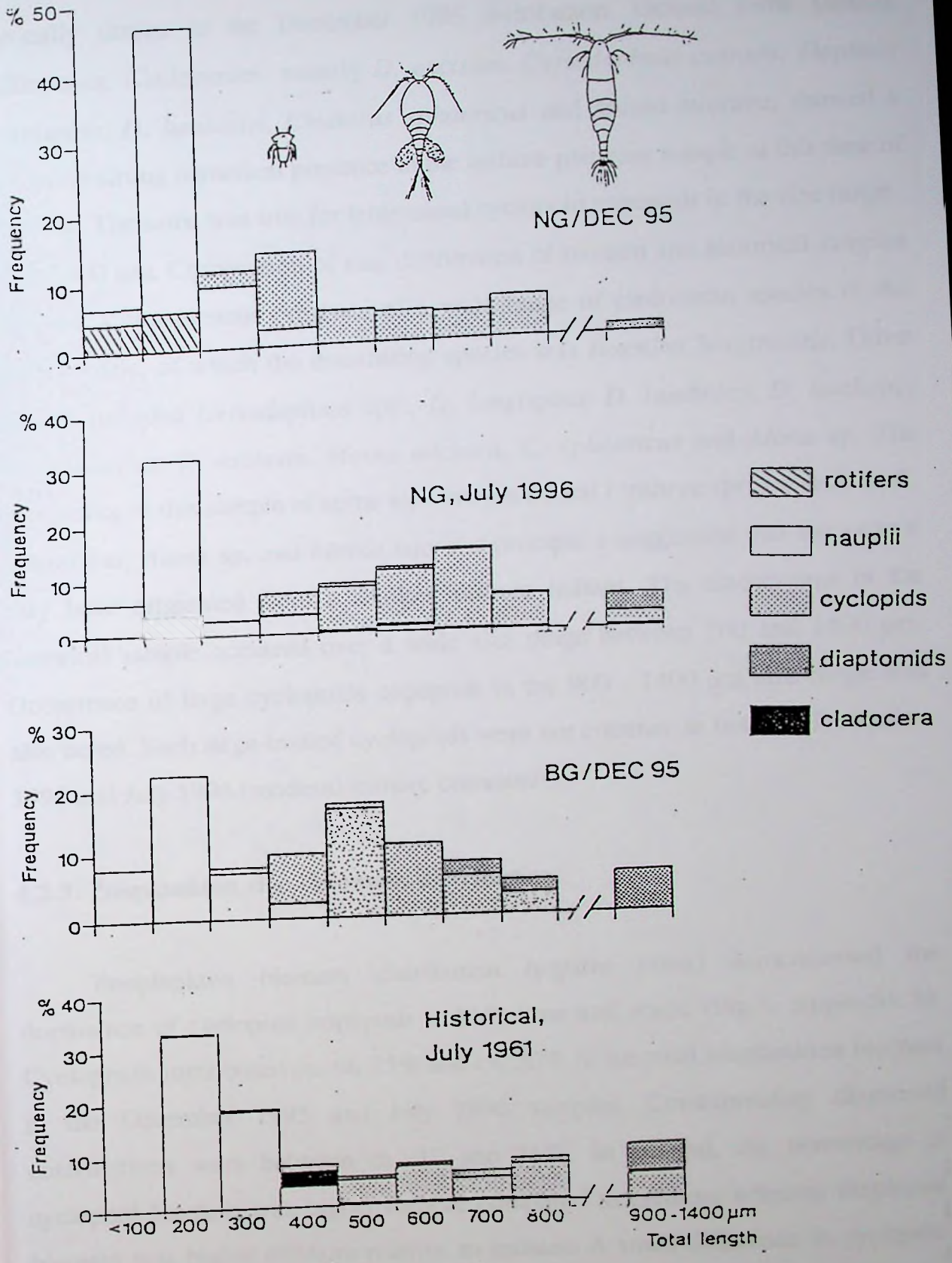


Figure 4. Zooplankton size structure for NG (inshore: December 1995 and July 1996), BG (offshore: December 1995) and a historical sample (July 1961, off Dagusi Island).

basically similar to the December 1995 distribution, showed some striking differences. Cladocerans, namely *D. excisum*, *Ceriodaphnia cornuta*, *Daphnia longispina*, *D. lumholtzi*, *Chydorus sphaericus* and *Moina micrura*, showed a relatively strong numerical presence in the inshore plankton sample at this time of the year. The same was true for large-sized cyclopoid copepods in the size range 900 -1400 µm. Comparison of size distribution of modern and historical samples revealed a conspicuous presence of a wide range of cladoceran species in the latter sample, of which the dominating species was *Bosmina longirostris*. Other species included *Ceriodaphnia* spp., *D. longispina*, *D. lumholtzi*, *D. lumholtzi* var. *monacha*, *D. excisum*, *Moina micrura*, *C. sphaericus* and *Alona* sp. The occurrence in this sample of some well known littoral / inshore species such as *C. sphaericus*, *Alona* sp. and *Moina micrura* prompts a suggestion that the sample may have originated from a shallow inshore habitat. The cladocerans in the historical sample occurred over a wide size range between 200 and 1400 µm. Occurrence of large cyclopoids copepods in the 900 - 1400 µm size range was also noted. Such large-bodied cyclopoids were not common in both the December 1995 and July 1996 (modern) inshore community.

4.2.3. Zooplankton size - biomass distribution

Zooplankton biomass distribution (µg/size class) demonstrated the dominance of cyclopoid copepods in both time and space (Fig.5; Appendix b). Cyclopoids contributed ca. 68-75% and ca. 50% of the total zooplankton biomass in the December 1995 and July 1996 samples. Corresponding diaptomid contributions were between ca. 12 and 46%. In general, the percentage of cyclopoid biomass was higher inshore compared to offshore whereas diaptomid biomass was higher offshore relative to inshore. A small difference in cyclopoid biomass occurred between the December 1995 and July 1996 inshore samples

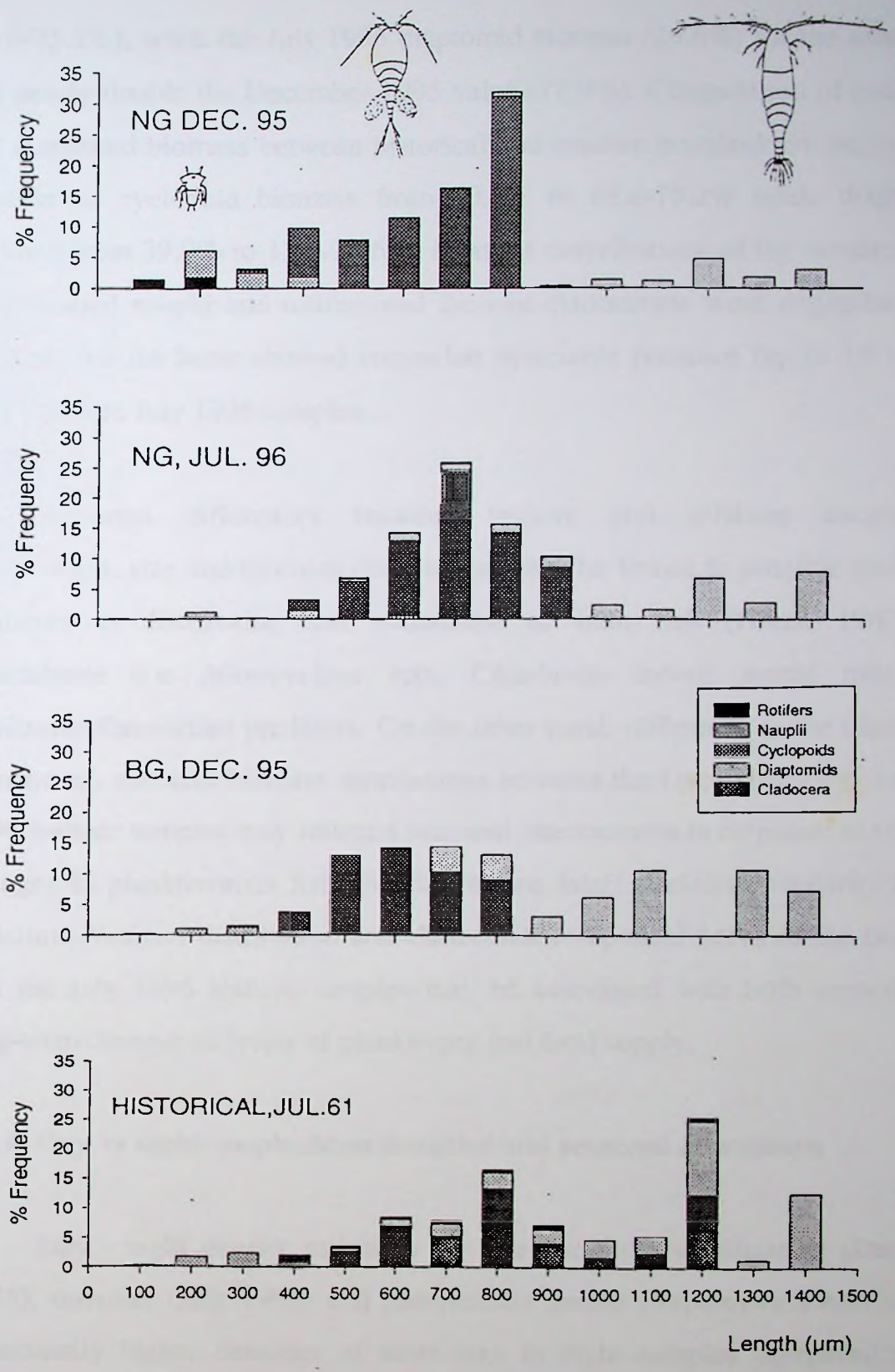


Figure 5. Zooplankton size-biomass distribution for NG (inshore: December 1995 and July 1996), BG (offshore, December 1995) and a historical sample (July 1961, off Dagusi Island).

(68.6-75.2%), while the July 1996 diaptomid biomass (26.6%) for the same area was nearly double the December 1995 value (12.9%). Comparision of cyclopoid and diaptomid biomass between historical and modern zooplankton indicated an increase of cyclopoid biomass from 50.7% to 68.6-75.2% while diaptomids declined from 39.9% to 12.9-26.6%. Biomass contributions of the numerous but small-bodied nauplii and rotifers and the rare cladocerans were negligible in all samples, but the latter showed somewhat detectable presence (up to 1%) in the historical and July 1996 samples.

Apparent differences between inshore and offshore zooplankton composition, size and biomass distributions may be linked to possible horizontal gradients in distribution and abundance of both fish (Green 1967) and invertebrate (i.e. *Mesocyclops* spp., *Chaoborus* larvae, acarid mites and planktonic flatworms) predators. On the other hand, difference in the cladoceran component, size and biomass distributions between the December 1995 and July 1996 inshore samples may reflect a seasonal phenomenon in response to seasonal changes in planktivorous fish abundance (see later). Relative similarity in size structure, biomass distribution and cladoceran component between the historical and the July 1996 inshore samples may be associated with both seasonal and long-term changes in levels of planktivory and food supply.

4.2.4. Day vs night zooplankton densities and seasonal abundance

Day - night density estimates for three periods: stratification (December 1995), turnover (July 1996) and intermediate period (September 1996) showed consistently higher densities of most taxa in night samples compared to day samples (Table 4). This day - night pattern of abundance is a confirmation of earlier observations (Worthington 1931; Goldschmidt et al. 1990; Lehman, pers.

comm.). Notably, rotifers and cladocerans showed no marked differences in abundance between day and night samples. Smaller day catches may have been due to a proportion of zooplankton settling near the bottom beyond the sampling range (> 0.5 m above the bottom) during this study. The possibility of net avoidance was considered to be minimal due to the generally small size of tropical zooplankton relative to their temperate counterparts.

Patterns of seasonal change among larger zooplankters i.e. cyclopoids, diaptomids and cladocerans were quite similar, showing highest abundances during the turnover period relative to the stratification and intermediate periods. Mesoplankters, i.e. rotifers and nauplii peaked later during the intermediate period. During the turnover, mean densities of diaptomids and cladocerans indicated as much as 10-fold and 13-fold increases compared to their respective abundances at stratification time. Corresponding increases among cyclopoids and nauplii were 2.8 and 1.2 times respectively. Rotifers were the only group with lower mean density during turnover compared to stratification time. Mean densities of cyclopoids, diaptomids and cladocerans indicated a marked decrease during the intermediate period relative to the turnover levels, but were still higher than the respective densities at stratification time.

The seasonal pattern of zooplankton abundance described here is in agreement with earlier descriptions for PB station (inshore) and BG station (offshore) by Branstrator et al. (1996). A nearly similar seasonal cycle was observed by Begg (1976) in Lake Kariba (a large tropical reservoir), showing diminishing zooplankton mean densities from mixing time (August 1972), to stratification time (May 1973). Relative numerical percentage proportions of the various taxa during the three periods remained nearly constant and ranked as: nauplii, cyclopoids, diaptomids/rotifers and Cladocera in decreasing order.

Table 4. Seasonal variation in zooplankton densities (no./litre) and relative abundance at NG station, 1995/96.

		day	night	mean	%
cember 1995: STRATIFICATION					
	Cyclopoids	20,8	31,0	25,9	22,5
	Diaptomids	0,9	1,2	1,0	0,9
	Cladocera	0,1	0,1	0,1	0,1
	Rotifera	9,7	8,6	9,2	8,0
	Nauplii	61,4	96,5	78,9	68,5
ly 1996: MIXING					
	Cyclopoids	89,8	54,4	72,1	39,8
	Diaptomids	12,5	8,0	10,3	5,7
	Cladocera	1,3	1,2	1,3	0,7
	Rotifera	5,7	7,3	6,5	3,6
	Nauplii	72,0	109,7	90,9	50,2
eptember 1996: INTERMEDIATE					
	Cyclopoids	38,8	81,6	60,2	31,8
	Diaptomids	1,9	2,5	2,2	1,2
	Cladocera	0,5	0,2	0,4	0,2
	Rotifera	26,2	14,5	20,4	10,8
	Nauplii	85,8	126,3	106,1	56,0

4.2.5. Zooplankton diurnal vertical distribution

A comparison of day and night zooplankton density estimates from samples taken at different vertical positions indicated heterogeneous distribution along the water column (Table 5). At stratification time (December 1995), total zooplankton densities at NG station were significantly different across depths both during the day and night ($P < 0.01$, and $P < 0.05$, respectively). Day time distribution depicting dispersion away from the surface (above 1m) was exhibited by all five taxa. Comparison of day and night surface densities showed clear indications of night time enrichment of surface waters presumably by recruits of organisms from the deeper layers. Highest concentrations were however found at 5-10 m depths in the majority of taxa; with the exception of the rarer Cladocera which tended to be evenly distributed across depths both during the day and night times. At the offshore station (BG), a similar tendency for zooplankton dipersion away from the surface during the day and night time enrichment of surface waters was observed. Day time densities were significantly different over a depth range of 0.5 - 20 m ($P < 0.05$), while the night distribution showed no significant difference across the same depth range ($P > 0.05$). Offshore day time vertical pattern showed cyclopoids, diaptomids and cladocerans concentrated in a layer 10 - 15 m, nauplii at 0.5 - 5 m while rotifers, which were extremely rare at this station, exhibited a near homogeneous dispersion across depths. During the turnover period (July 1996) all taxa at NG station were concentrated in the 5 -10 m layer both during day and night and total zooplankton densities were highly significant across depths ($P < 0.01$).

During the intermediate period (September 1996), highly significant differences of zoolankton densities across depths were observed in both day and night distributions ($P < 0.01$). Highest day time densities were located at 10 m

Table 5. Mean density estimates (no./litre) of different zooplankton taxa in vertical depth series: NG (inshore) and BG (offshore) 1995/96 data.

December 1995: STRATIFICATION

NG (Inshore)

	day			night			
	0.5m	2m	10m	0.5m	2m	5m	10m
Cyclopoids	4,0	17,6	40,7	28,3	26,2	43,3	23,2
Diaptomids	0,2	0,6	1,8	1,3	0,9	1,5	1,1
Cladocera	0,0	0,1	0,1	0,1	0,1	0,1	0,1
Rotifera	2,3	14,0	12,7	4,5	7,7	14,0	8,3
Nauplii	13,7	81,9	88,5	56,9	60,7	70,9	36,5
Others	0,1	0,0	0,3	0,2	0,0	0,0	0,0
All taxa	20,3	114,1	144,0	91,3	95,7	129,9	69,1

December 1995: STRATIFICATION

BG (offshore)

	day						night			
	5m	2m	5m	10m	15m	20m	0.5m	2m	5m	10m
Cyclopoids	4,7	9,8	39,3	52,6	32,3	32,8	35,3	35,9	32,7	30,9
Diaptomids	0,0	0,4	3,2	6,6	7,4	6,8	5,5	5,0	8,5	5,9
Cladocera	0,0	0,0	0,0	0,1	0,2	0,1	0,2	0,1	0,0	0,3
Rotifera	0,4	0,4	0,4	0,3	0,4	0,0	0,6	0,3	0,3	0,6
Nauplii	45,9	47,1	47,5	29,6	28,0	23,1	19,1	21,9	21,7	48,9
Others	0,0	0,0	0,0	0,0	0,1	0,0	0,1	0,1	0,0	0,2
All taxa	51,0	57,7	90,4	89,2	64,8	62,8	60,7	63,1	63,3	86,6

July 1996: Mixing

NG (Inshore)

	day			night		
	0m	5m	10m	0m	5m	10m
Cyclopoids	24,7	127,5	119,1	6,9	88,2	68,0
Diaptomids	0,9	15,3	21,3	4,5	8,5	11,1
Cladocera	0,0	2,9	0,9	0,0	2,0	1,8
Rotifera	5,1	9,8	2,3	4,5	9,1	9,6
Nauplii	50,7	111,6	53,8	7,1	158,0	164,0
Others	0,0	0,0	0,0	0,0	0,2	0,0
All taxa	81,3	265,1	198,5	22,3	266,0	254,4

September 1996: Intermediate

NG (Inshore)

	day				night			
	0m	5m	10m	15m	0m	5m	10m	15m
Cyclopoids	13,5	46,3	64,2	31,1	114,0	53,3	92,9	66,0
Diaptornids	0,5	1,7	2,0	3,3	4,0	1,8	2,2	2,0
Cladocera	0,0	0,7	0,9	0,2	0,0	0,0	0,0	0,7
Rotifera	29,9	23,1	37,1	14,5	11,3	14,2	17,8	14,5
Nauplii	56,2	99,9	132,9	54,0	126,2	124,5	148,2	106,2
Others	0,0	0,0	0,0	0,0	0,7	0,0	0,0	0,0
All taxa	100,0	171,8	237,1	103,1	255,6	193,8	261,1	189,3

epth for all taxa. Night time high concentrations were on the other hand found in urface waters (0 - 1 m) for cyclopoids and diaptomids, while rotifers and nauplii eaked at 10 m. Cladocerans were very few in the sample and did not show any lear vertical trends.

The first documented investigation of diurnal vertical distribution of zooplankton in Lake Victoria, by Worthington (1931) was carried out at an offshore point approximately 0° 34' S 33° 40' E, i.e. north east end of the lake (Z_{max} = 69 m) in 1927. Temperature records at the time of sampling indicated a mildly stratified profile with a thermocline at 30 m. Most zooplankters, namely *Daphnia longispina* and other cladocerans, diaptomids and cyclopoids were found to be concentrated in surface waters above 16 m at 6.0 pm, 9.0 pm and 3.0 am. The deepest concentration of zooplankton was found at a depth range of 33 - 50 m at 3.0 pm. Thus, the night time vertical distribution observed then, showing concentration of organisms in the epilimnion compares quite favourably with present observations showing persistent concentrations at 5 - 10 m depth; well above the thermocline. Worthington's day time peak concentration at 33 - 50 m, however, can not benefit from a comparison with the present data because this depth range falls outside the vertical sampling range during the present study.

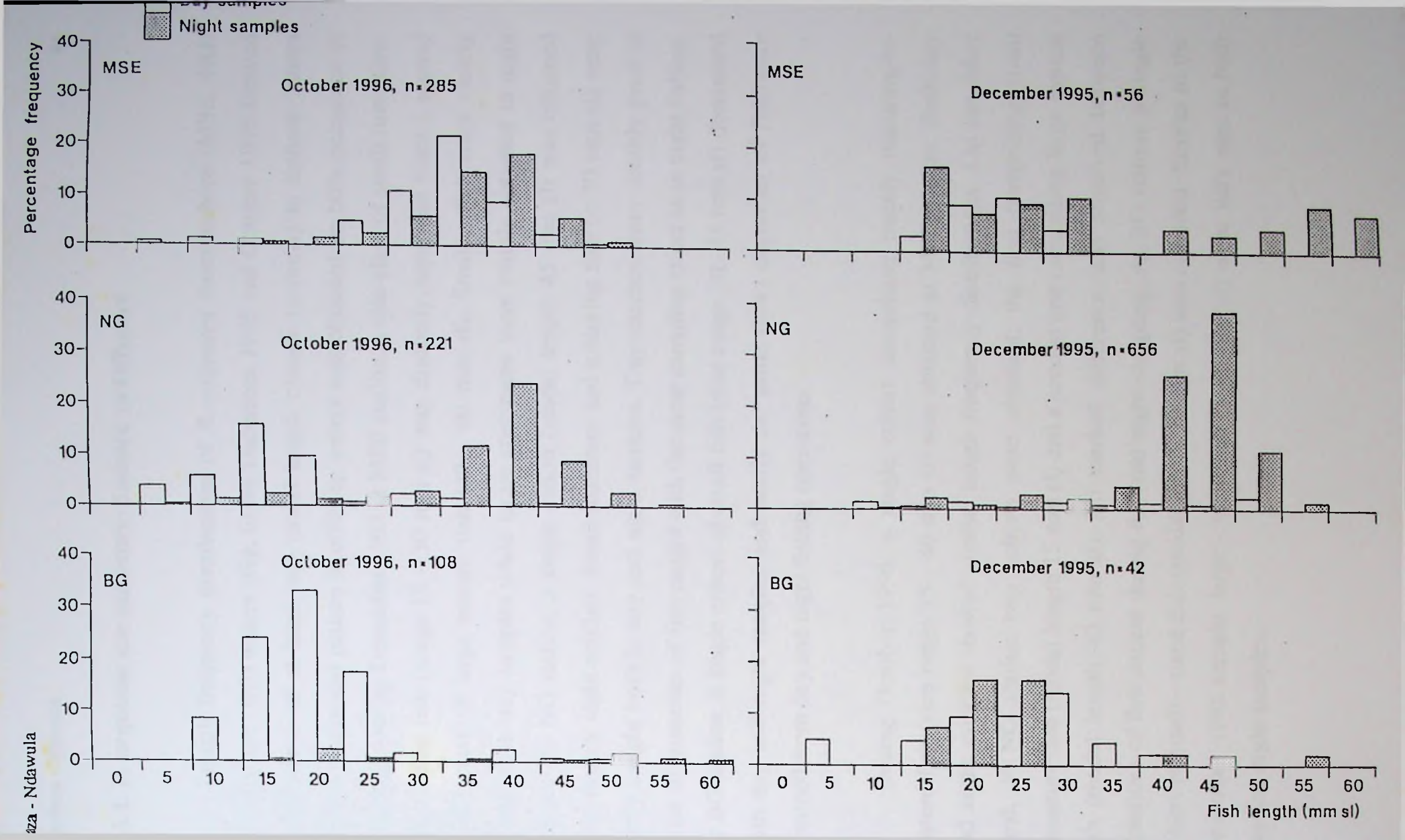
More recent observations at a 14 m deep station in the Mwanza Gulf (southern part of the lake) by Goldschmidt et al. (1990) showed high day time densities of copepods in the top six metres of the water column and a peak for cyclopoids in the top two metres. Night time distributions depicted a similar vertical distribution, but with much higher densities near the surface for both cyclopoids and diaptomids. Chaoborids were absent in the column by day but their night time distribution showed a vertical pattern similar to the copepods.

Present data on diurnal vertical distribution is in general agreement with the findings of Goldschmidt et al. (1990) and provides evidence to suggest that the amplitude of day time descent by most zooplankters has since shifted upwards, in line with a similar shift in the depth of the thermocline and concomitant increase of the (anoxic) hypolimnetic volume; both attributes of eutrophication of the lake (Hecky 1993; Hecky et al 1994;Ochumba 1995) over the past three decades.

Gophen (1979) reporting on bathymetric distribution and diurnal vertical migrations of zooplankton in Lake Kinneret (Israel) found that most of the organisms were concentrated at the 5-10 metre depths and in the metalimnionic layer during stratification and with much less concentrations at 1 metre depth and 1 metre below the metalimnion; an observation which compares favourably with results of the present study (Table 5). He argued that the metalimnic layer is rich in suspended detrital particles, algae, protozoa, bacteria and small zooplankters which would attract filter feeding zooplankters because of the enrichment of food resources there. In addition, the low oxygen concentrations in the hypolimnion may restrict the vertical dispersion of most organisms to their normal daytime depths.

4.3. Fish population structure, distribution, and abundance

The size composition of fish among samples usually ranged between 10 and 60 mm sl., regardless of site or sampling date (Figures 6 & 7). A small proportion of larval fish ($\leq$ 10mm sl.) was sometimes present in some samples. Such a wide size range ensured the presence of different life stages of fish i.e. juveniles, maturing and adult fishes at any one sampling occasion.


Night samples
Percentage frequency
MSE
October 1996, n=285
MSE
December 1995, n=56
NG
October 1996, n=221
NG
December 1995, n=656
BG
October 1996, n=108
BG
December 1995, n=42
0
10
20
30
40
0 5 10 15 20 25 30 35 40 45 50 55 60
Fish length (mm sl)

3.1. *R. argentea* size structure: Inshore vs Offshore

Length frequency distributions of *R. argentea* from inshore (MSE, NG) and offshore (BG) waters (Fig. 6) for December 1995 and October 1996 showed the presence of at least two modal length classes (cohorts) in inshore waters while an unimodal pattern in offshore waters was obtained on both occasions of sampling. During December 1995 at MSE station, a size class of small immature-to-maturing fish (range 15 - 30 mm sl) was distinctly separated from a second modal class of large mature fish (40 - 60 mm sl). Smaller fish were clearly dominant in day samples while larger specimens were mainly obtained in night catches. At NG station, a single cohort (modal length 45 mm sl) was obtained from mainly night catches. Small immature and maturing fish (< 30 mm sl) were rarely caught both in day and night samples. Day catches were notably poor in terms of quantities of fish caught with the same sampling effort as in night fishing. At BG station, a single cohort of small fish (size range 20 -35 mm sl) dominated both day and night samples and nearly the same (low) quantities of fish were obtained from day and night fishing operations.

During October 1996, a single cohort comprising mainly maturing-to-mature fish (size range 35 - 40 mm sl) was obtained at MSE station. Both day and night samples showed similar length frequency distributions. On the other hand, at NG station two cohorts were obtained; the first comprising small immature fish (modal length 15 mm sl) and a second one comprising large mature fish (modal length 40 mm sl). No marked difference was observed between quantities of fish caught during day and night sampling. At BG station, a single cohort of small - sized fish (modal length 20 mm sl) was obtained. Similar to the December 1995 sample, large - sized fish (> 40 mm sl) were very rare in both day and night samples.

4.3.2. Seasonal variation in fish size structure at NG station

Length frequency distribution of *R. argentea* at NG station (Fig. 7) shows the variation of modal length classes at different times over the period December 1995 to October 1996. A unimodal pattern of distribution depicting domination of the population by large mature fish (modal length 45 mm sl) in December 1995 was replaced by a bimodal pattern with modal lengths at 10 and 50 mm sl in March 1996. Bimodality in fish length distribution was still in place by September and October 1996; the shift in modal class lengths to 15 and 30 mm sl notwithstanding.

Interpretation of the seasonal pattern of fish described above is rendered difficult by insufficient fish length frequency data for successive months, but limited inferences are possible on the basis of what is known about the annual breeding cycle of *R. argentea* in the lake. Previous findings have shown that breeding activity occurs continuously throughout the year but with two peaks: a major one in December-January and a minor one in August - September (Wandera 1992). Accordingly, larval *R. argentea* are abundant in the Napoleon Gulf (NG) during the months of January and September. Based on this information, the single and prominent cohort of large fish in the December population most probably represents the adult breeding stock at this time of the year.

In conjunction with trends in growth and recruitment of *R. argentea* (Wandera1991; Wandera and Wanink 1995), the conspicuous March 1996 cohort of juvenile fish is likely to be largely the brood of the August-September breeding peak of the previous year. This appears to be the same cohort observed by Wandera (1991) during April - May. The second and somewhat subdued cohort

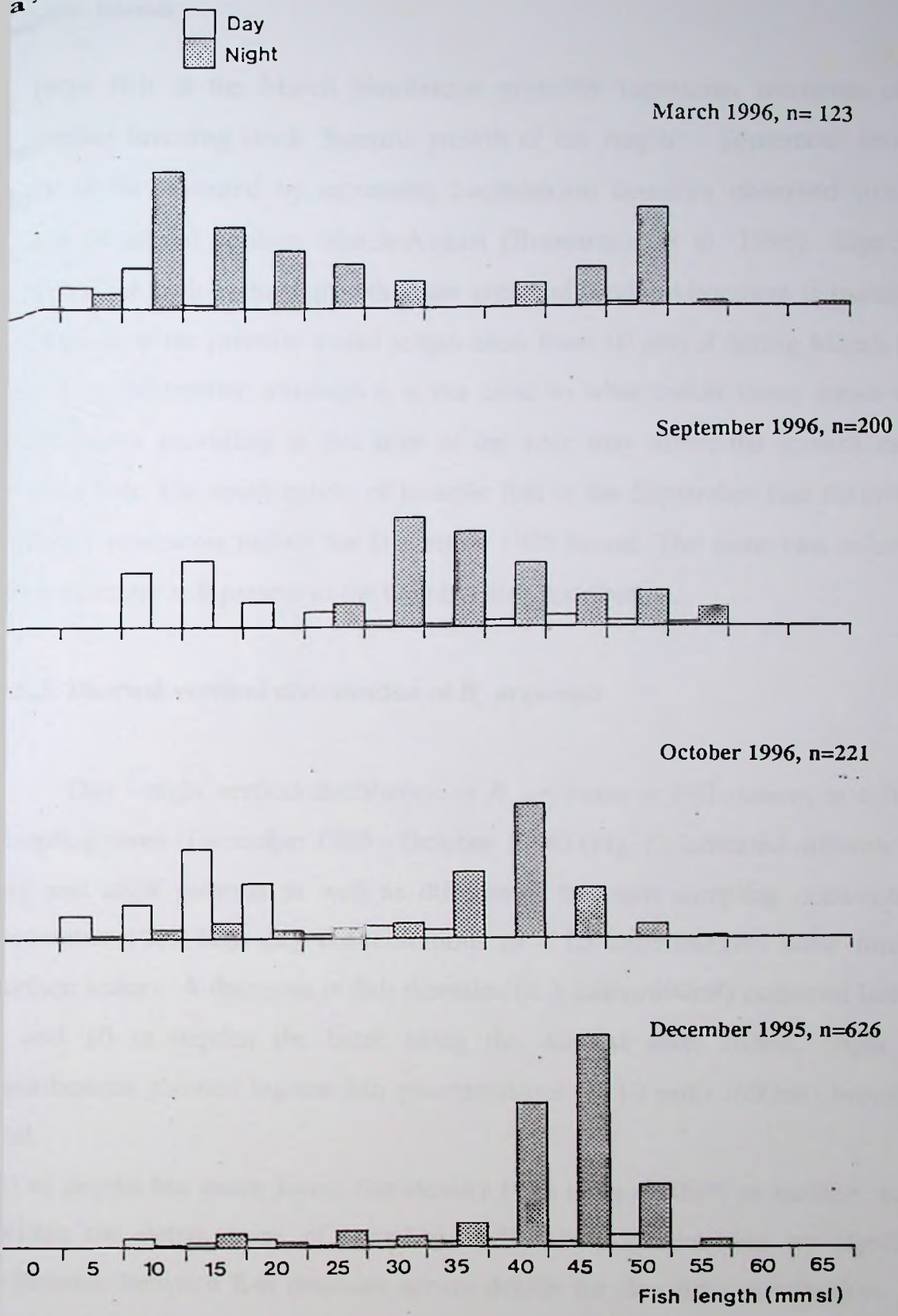


Figure 7. Variation of the size structure of *R. argentea* at NG station on different sampling dates (1994/1996 data).

f large fish in the March distribution probably represents remnants of the December breeding stock. Somatic growth of the August - September brood is likely to be favoured by increasing zooplankton densities observed over the period of annual cooling, March-August (Branstrator et al. 1996). Supporting evidence for such optimal growth under enriched food environment is manifested in increase of the juvenile modal length class from 10 mm sl during March to 30 mm sl by September; although it is not clear to what extent lower mean water temperatures prevailing at this time of the year may affect the growth rate of juvenile fish. The small cohort of juvenile fish in the September size distribution probably represents mainly the December 1995 brood. The same two cohorts in September are still present in the October size distribution.

4.3.3. Diurnal vertical distribution of *R. argentea*

Day - night vertical distribution of *R. argentea* at NG station, at different sampling times (December 1995 - October 1996) (Fig. 8) indicated differences in day and night patterns as well as differences between sampling occasions. In December 1995 high day concentrations (3 - 10 indiv./600m^3) were found in surface waters. A decrease in fish densities (< 3 indiv./600m^3) occurred between 5 and 10 m depths; the latter being the deepest level fished. Night time distributions showed highest fish concentrations (> 10 indiv./600m^3) between 5 and
10 m depths but much lower fish density (< 3 indiv./600m^3) in surface waters. Within the depth range of sampling (0-10 metres) there was no significant difference between fish densities across depths for day time distributions ($P > 0.05$), while night time densities were highly significant ($P < 0.01$).

March 1996 day time distributions revealed a homogeneous fish density

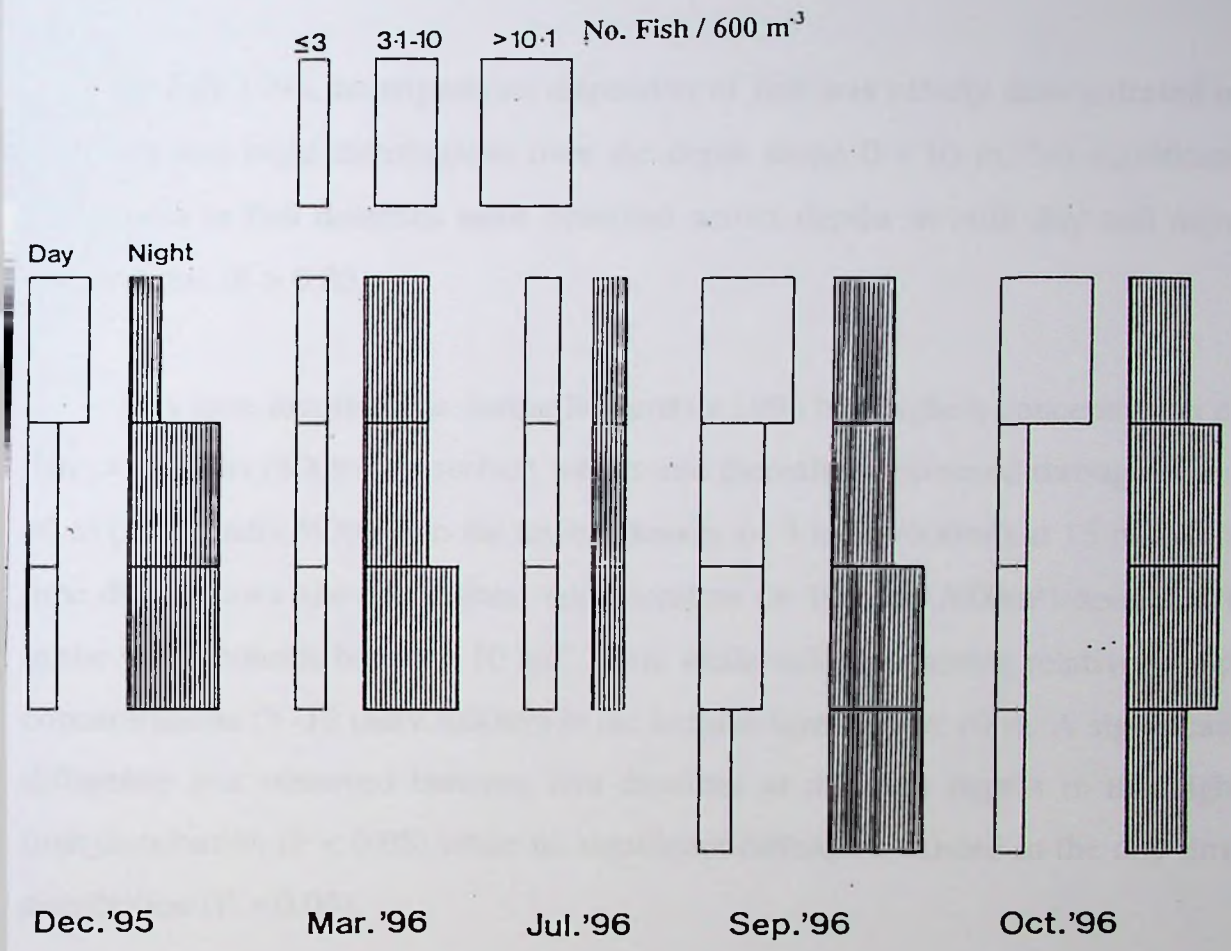


Figure 8. Diurnal vertical distribution and abundance of *R. argentea* at NG station (1995/1996 data).

The day - night, seasonal and vertical distribution patterns observed at NG station during the study appear to be related to variations in water column structure especially with regard to temperature and dissolved oxygen profiles (see Fig. 2a &b). Day time concentrations of fish around surface waters observed during December 1995, September and October 1996 may appear to be contradictory to previous observations (Wanink 1988) indicating concentrations of fish near the bottom during the day and near the surface at night time. However in this study, the majority of fish inhabiting near - surface waters during the day were mainly small juveniles (> 10 - 30 mm sl) and few large adults infected with a visceral cestode worm, *Ligula intestinalis*. These two categories were the main constituents of day time fish catches. Members of the adult population were nearly always captured from deeper water layers during day sampling. Night samples on the other hand contained a mixture of both juvenile and adult fishes and there was no evidence of size - dependent segregation between juvenile and adult fish.

The December 1995 day and night distributions indicated high concentrations of fish above the thermocline and oxycline boundaries (epilimnion) at a time of strong thermal stratification. With the apparent breakdown of the thermal stratification over the period March - July, a near homogeneous vertical dispersion of fish seems to be largely in response to favourable conditions of dissolved oxygen prevailing throughout the the entire water column during the period of mixing. The September and October 1996 diurnal distributions indicating higher fish concentrations between 5 and 10 m, occur during the period of transition between water circulation (July) and thermal stratification (December) events. Figure 2b shows the initiation of thermal stratification during October 1996 with a discernible discontinuity zone at 11 m depth. It would therefore appear that the December 1995 and October 1996 vertical distributions with peak fish concentrations in the epilimnion tend to

characterise trends in vertical distribution of fish during spells of thermal stratification when hypolimnetic anoxia may constrain dispersion further downwards. These distribution trends are further supported by mostly significant statistical differences in fish densities observed across depths during months of thermal stratification (October, December) while such differences did not exist during the mixing period (March , July).

4.3.4. Seasonality in pelagic fish densities

Variation in mean catch rates (number of fish / 5-min. 600m³) of three pelagic fishes, *R. argentea*, juvenile *Lates niloticus* and Cichlid species (tilapine and haplochromines) at the three sampling sites shows that different species become abundant at different times around inshore waters (Figure 9). At MSE and NG stations, *R. argentea* were more abundant during December 1995 (> 20 fish / 600m³), declined in March through July (<10 fish / 600m³) before rising in September and October 1996 (up to 80 fish / 600m³ at MSE). Juvenile cichlid species exhibited a nearly similar pattern except that they tended to remain at low abundance from July through September and October. On the other hand, juvenile *Lates niloticus* were abundant during March and July (> 40 fish / 600m³) and declined during September and October. Much lower fish catch rates (< 2 fish / 600m³) of all three fish species characterised the offshore BG station on each of the two occasions when the offshore waters were sampled (December 1995 and October 1996).

Owing to the long sampling intervals during this study, the seasonal trends described here are at most just indications of possible seasonal patterns in pelagic fish abundance and therefore require confirmation from more intensive, monthly fish catch data. Tentatively therefore, higher abundances of *R. argentea* and

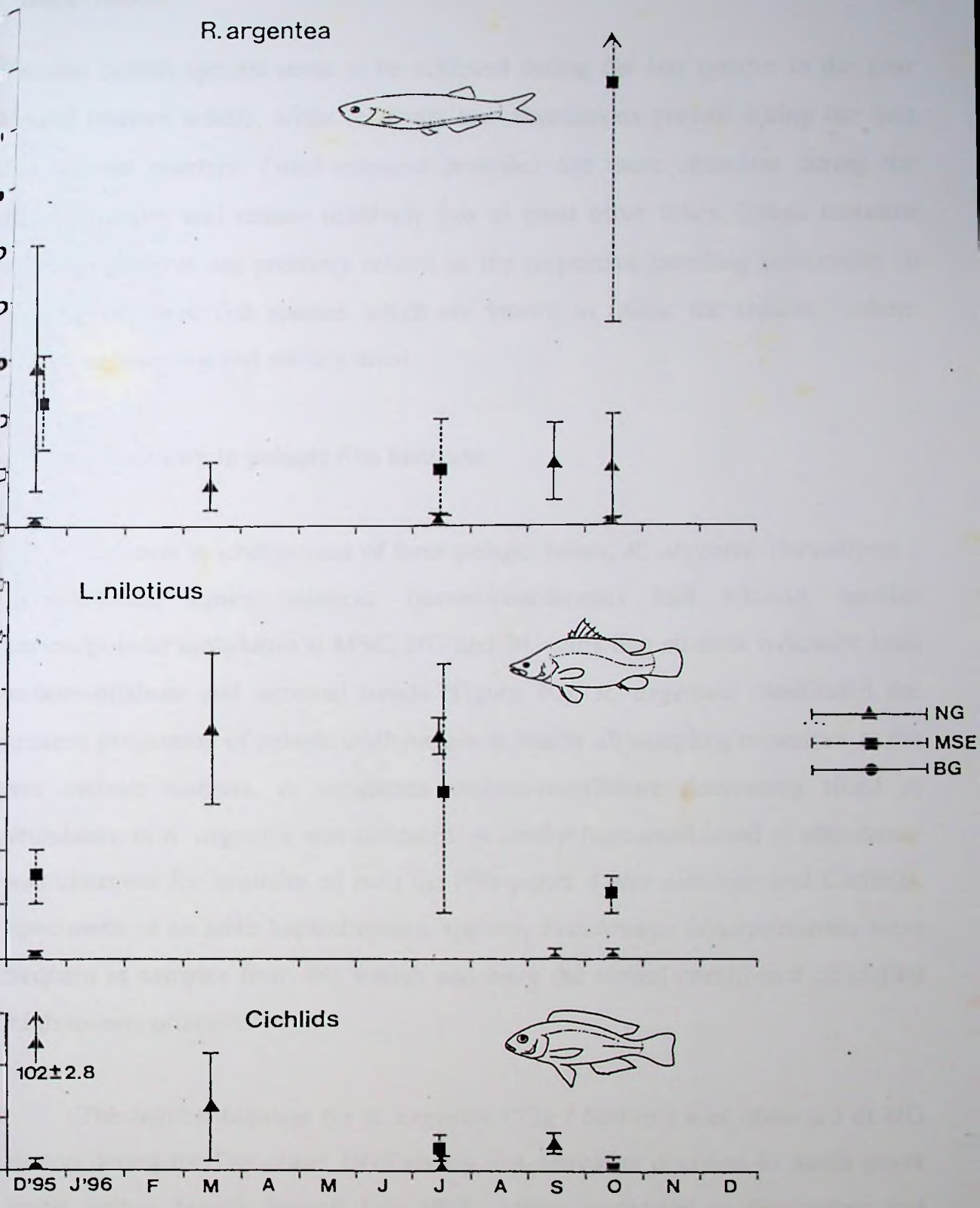


Figure 9. Seasonal variation in pelagic fish (*R. argentea* and juveniles of *Lates niloticus* and cichlid species) densities at MSE, NG (inshore) and BG (offshore) sampling stations (1995/1996 data).

uvenile cichlid species seem to be achieved during the last quarter in the year around inshore waters, while relatively low abundances prevail during the first and second quarters. *Lates niloticus* juveniles are more abundant during the second quarter and remain relatively low at most other times. These tentative seasonal patterns are probably related to the respective breeding seasonality in each of the three fish species which are known to utilise the shallow inshore waters as breeding and nursery areas.

4.3.5. Seasonality in pelagic fish biomass

Variation in ichthyomass of three pelagic fishes, *R. argentea* (larvae/post - larvae/adults), *Lates niloticus* (larvae/post-larvae) and Cichlid species (larvae/post-larvae/adults) at MSE, NG and BG sampling stations indicated both inshore-offshore and seasonal trends (Figure 10). *R. argentea* constituted the greatest proportion of pelagic ichthyomass at nearly all sampling occasions at the two inshore stations. A significant inshore-to-offshore decreasing trend in abundance of *R. argentea* was indicated. A similar horizontal trend of abundance was observed for juveniles of both the Nile perch, *Lates niloticus* and Cichlids. Specimens of an adult haplochromine species, *Yssichromis laparogramma* were frequent in samples from BG station and were the virtual contributor of cichlid ichthyomass offshore.

The highest biomass for *R. argentea* (73g / 600 m^3) was observed at NG station during the December 1995 survey, but thereafter declined to much lower levels during March through July 1996, before increasing in September and October 1996. Total numbers of individual fish in the corresponding samples showed a similar trend, indicating that fish catches were dominated by a particular size range of fish; in this case sub-adult and adult fishes (see also

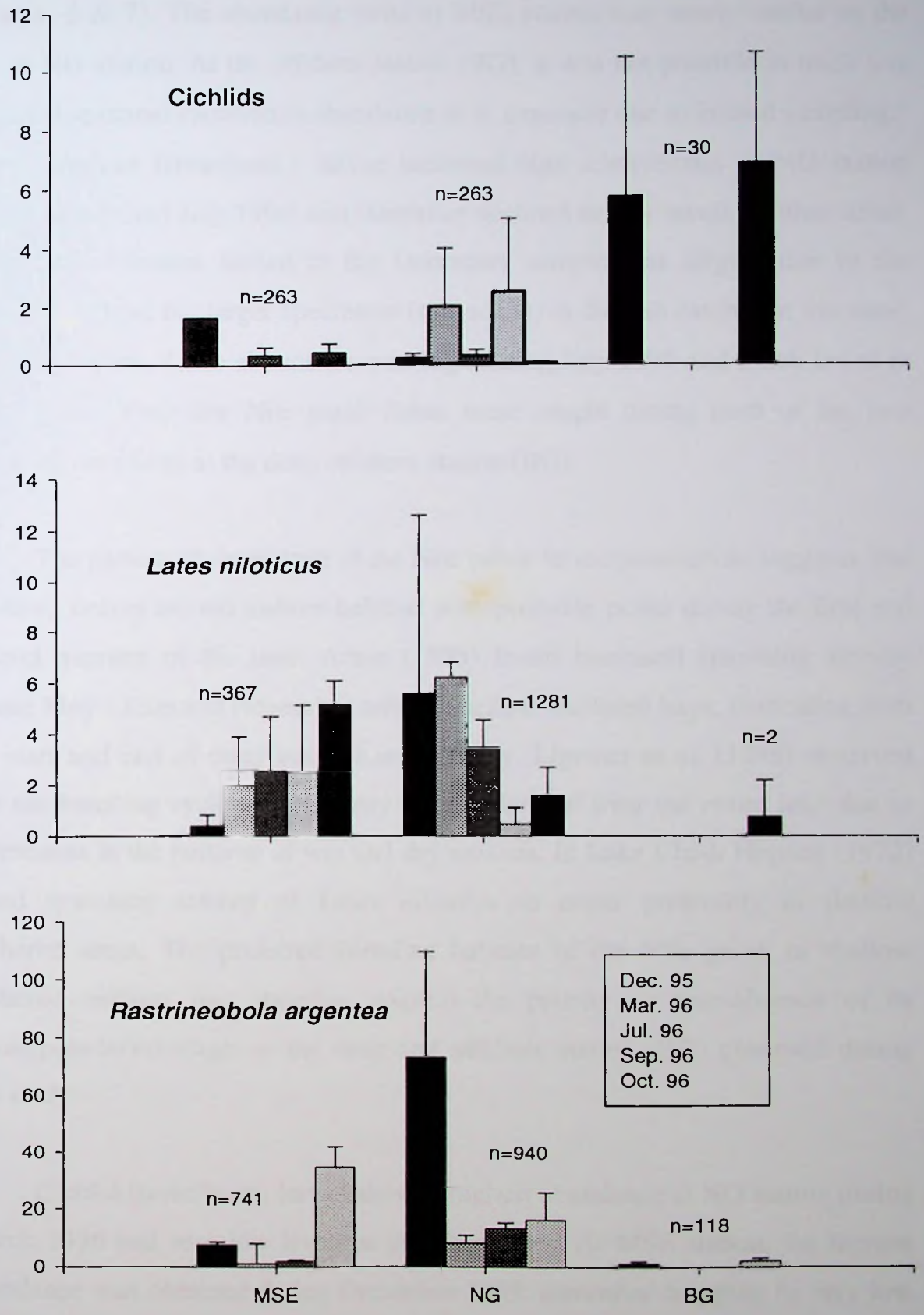


Figure 10: Seasonal variation in pelagic fish biomass at MSE, NG (inshore) and BG (offshore) sampling sites, 1995/1996 data.

gures. 6 & 7). The abundance trend at MSE station was nearly similar to the e at NG station. At the offshore station (BG), it was not possible to track any tential seasonal variation in abundance of *R. argentea* due to limited sampling. *tes niloticus* larvae/post - larvae indicated high ichthyomass at NG station ring March and July 1996; and thereafter declined to low levels at other times. gh *Lates* biomass shown in the December sample was largely due to the esence of few, but larger specimens (sub-adults) in the fish catches at this time. MSE station, *Lates* abundance was high during July 1996 and much lower at her times. Very few Nile perch fishes were caught during each of the two mpling occasions at the deep offshore station (BG).

The pattern of abundance of the Nile perch larvae/post-larvae suggests that eeding occurs around inshore habitats with probable peaks during the first and cond quarters of the year. Acere (1985) found increased spawning activity ring May - June and November around shallow sheltered bays, coinciding with e start and end of rainy seasons respectively. Ligtvoet et al. (1988) observed at the breeding cycle of *Lates* may not be identical over the entire lake due to fferences in the patterns of wet and dry seasons. In Lake Chad, Hopson (1972) und spawning activity of *Lates niloticus* to occur preferably in shallow eltered areas. The preferred breeding habitats of the Nile perch in shallow eltered habitats may therefore explain the paucity or near-absence of its rvae/post-larval stages at the deep and offshore station (BG) observed during is study.

Cichlid larvae/post - larvae showed highest abundance at NG station during arch 1996 and very low levels at all other times. At MSE station, the highest undance was obtained during December 1995; thereafter dropping to very low vels at other times. Large adult haplochromines (*Yssichromis laparogramma*)

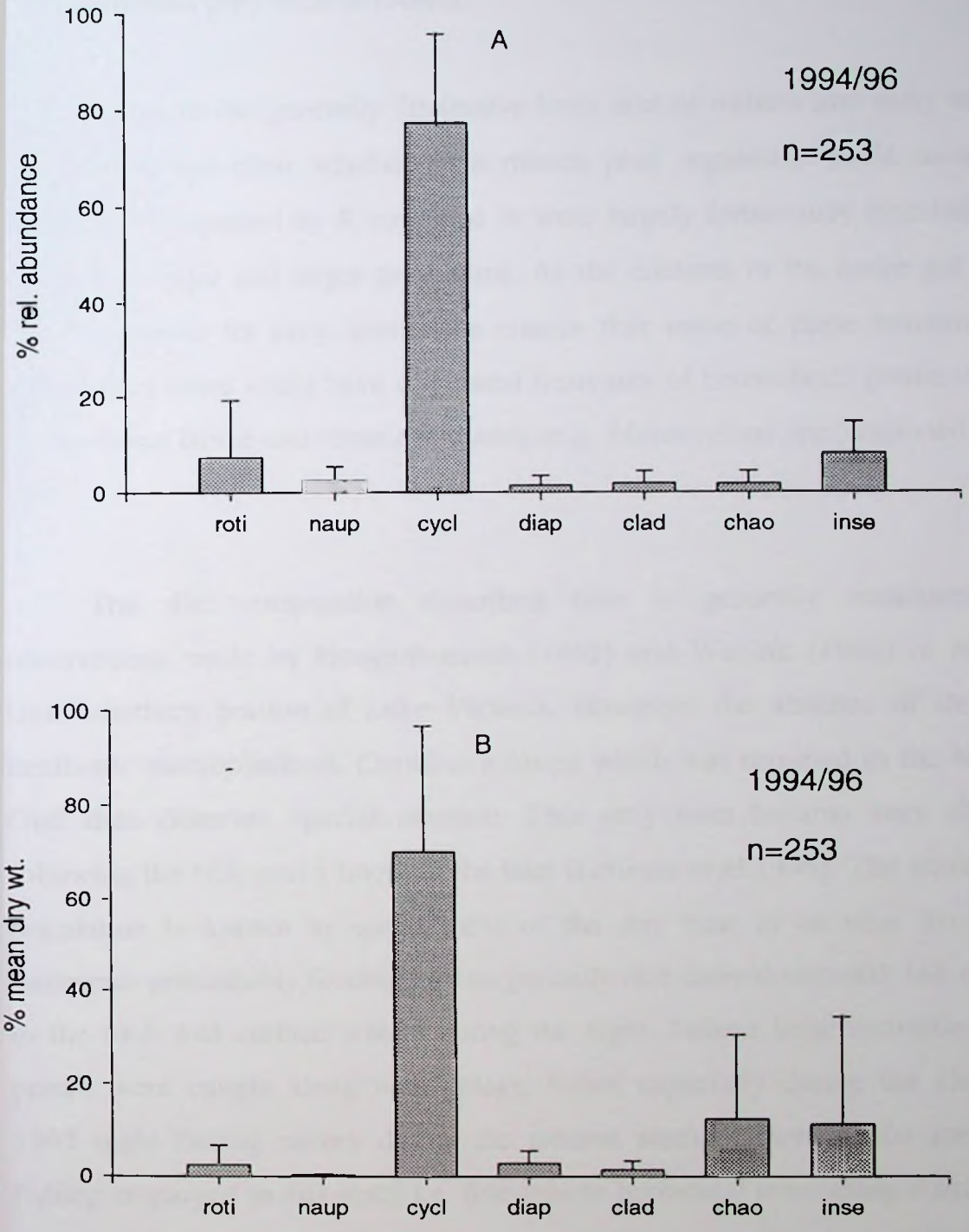
haracterised the cichlid component of samples from BG station on both casions of sampling.The seasonal trend suggests the occurrence of a breeding eak (for at least the main cichlid species, *Oreochromis niloticus*) sometime uring the last quarter of the year, around inshore waters of the lake. The deep ffshore waters appear to offer suitable habitat(s) for the re-establishment of ocks of the pelagic haplochromine species, *Yssichromis laparogramma* in the ost - Nile perch era.

4.4. The Food and feeding habits of *R. argentea*

An examination of 253 guts of *R. argentea* (10 - 60 mm sl) from the three study sites, with data pooled by sampling dates, time of day and water column depths, showed a diet composed of copepods (cyclopoids, diaptomids and copepodids, nauplius larvae), cladocerans, rotifers, chaoborid larvae/pupae, ostracods adult insects and acarid mites (Figures 11 - 17).

4. 4.1. Diet composition: modern samples (1994 - 1996)

Cyclopoid copepods contributed by far the highest proportion of the diet, with > 75% of the total number of prey items (Figure 11a). Of the remaining proportion (> 20%), diaptomid copepods, cladocerans, rotifers, nauplii, chaoborid larvae/pupae were regular contributors to the diet, while chironomids, ostracods, acarid mites were occasionally ingested. Adult insects, 'lake flies' (mostly chaoborids, chironomids and the Ephemeropteran *Povilla adusta*) were common in fish guts from night samples (see later). Conversion of the ingested prey items into their respective mean dry weights (Fig. 11 b) showed cyclopoid copepods still as the major prey component with > 65% of the total dry weight. Larger prey items such as chaoborid larvae/pupae and adult insects which were often not



'e 11. Diet composition of *R. argentea* (A, % rel. abundance ± sd and B, % mean dry wt. ± sd) odern samples (1994-1995) from all three sampling sites.Note: roti = rotifers; naup = nauplii; = cyclopoids; diap = diaptomids; chao = chaoborid larvae; inse = insects.

consumed in large numbers contributed greater dry weight proportions to the diet relative to their low numerical abundance in fish guts and in comparision to small, often numerous prey such as rotifers.

Owing to the generally diminutive body size of rotifers and early naupliar stages, it is not clear whether such minute prey organisms could have been intentionally captured by *R. argentea* or were largely fortuitously ingested along with other major and larger prey items. As the contents of the entire gut length were examined for prey, there is a chance that some of these numerous but minute prey items could have originated from guts of invertebrate predators such as chaoborid larvae and some cyclopoids (e.g. *Mesocyclops* spp.) ingested by the fish.

The diet composition described here is generally consistent with observations made by Hoogenboezem (1985) and Wanink (1988) in Mwanza Gulf, southern portion of Lake Victoria. However, the absence of the semi-benthonic macroplankton, *Caridina nilotica* which was reported in the Mwanza Gulf data deserves special mention. This prey item became very abundant following the Nile perch boom in the lake (Lehman et al.1996). The adult prawn population is known to spend most of the day time in or near the bottom sediments presumably feeding on energetically rich detrital material, but migrates to the mid- and surface waters during the night. Indeed large quantities of the prawn were caught along with pelagic fishes especially during the December 1995 night fishing survey during the present study. However, the method of fishing employed in this study i.e. five-minute horizontal tows using a small mid-water trawl net, deployed several metres above the bottom sediments could have possibly missed catching fish that had fed on *C. nilotica* at the water-sediment interface. In contrast, Wanink (1988) caught fish specimens for diet analysis

ng top-to-bottom set gillnets (13 mm stretch mesh size) over a 24-hour cycle. ch fish samples consisting of mainly large adult specimens would have a high elihood to contain a proportion of fish that had fed on *C. nilotica* during the y time near the bottom sediments. Long sampling intervals which characterised e present study may constitute an additional factor that could possibly conceal otential utilisation of *C. nilotica* as prey by *R. argentea*. *C. niolotica* are ported to exhibit seasonal variation in abundance in Lake Victoria (Lehman et l. 1996). It is assumed that their optimal utilisation as a food source to redaceous fish would more likely be achieved seasonally at times of maximum bundance of *C. nilotica*.

From the extent to which different prey organisms are consumed vis- a- vis heir respective abundances in the environment (see Table 4), a picture emerges hat the more abundant and ubiquitous cyclopoid copepods constitute the primary ood base of *R. argentea* stocks in both sub-littoral and pelagic habitats which were sampled in the present study. Besides, Cyclopoids offer a wide range of prey sizes for the potential predator to choose from (see Figure 4). The less abundant elements of the zooplankton appear to be consumed in proportionately lower quantities, although they may temporarily become important during their respective seasonal peak abundances. As an example, Hoogenboezem (1985) found fish guts with a high component of 'lake flies' shortly after the latter's mass emergence in the Mwanza Gulf.

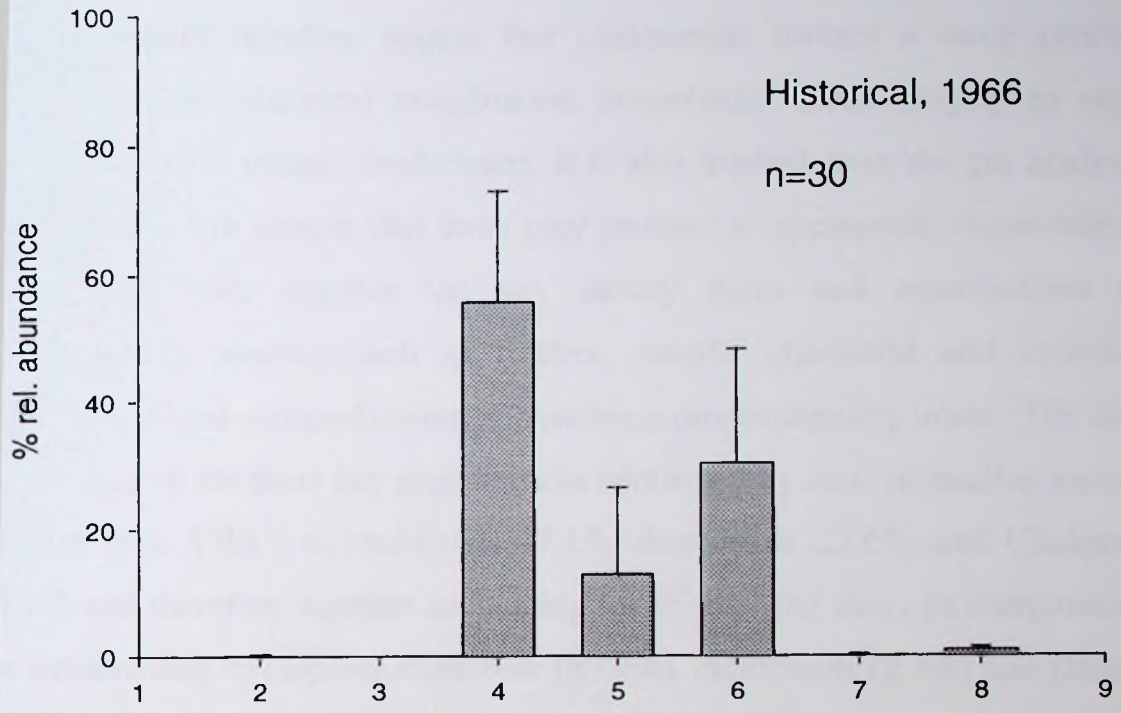
Judging from the *R. argentea* prey composition which includes dead floating adult insects (presumed to have been caught from the water surface), pelagic crustacean zooplankton and rotifers and benthic elements such as chironmid larvae and the prawns, there is a clear indication that *R. argentea* is capable of feeding along the entire water column over a 24-hour period and in

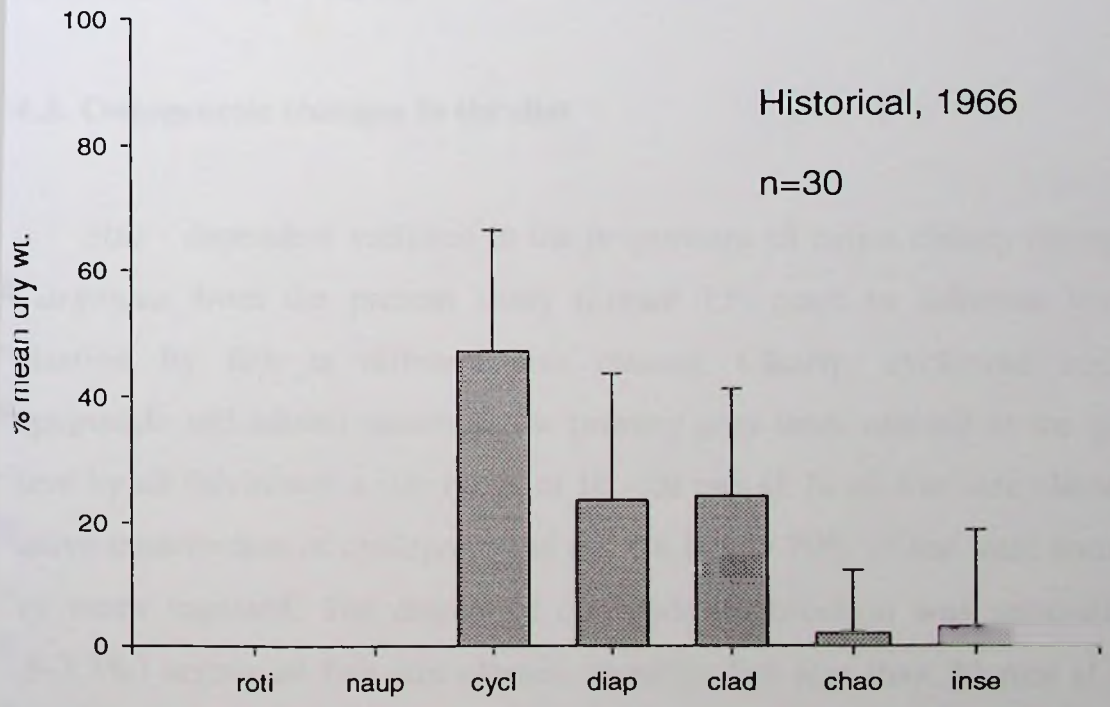
is way is able to take advantage of the various food resources associated with fferent vertical positions. The capacity to utilise such a wide range of food -sources appears to be one of the key factors behind the ecological success of *R. "gentea* during the post-Nile perch era in Lake Victoria.

.4.2. Diet composition of *R. argentea* from historical (1966) fish sample

Guts of 30 fish (45 - 61 mm sl) captured at Windy Bay (to the south west f NG station) during 1966 were examined. The data showed a diet composed of asically similar prey species as in the modern fish samples, except one dditional item, nematodes occuring in very low numbers (Figure 12a). Cyclopoid opepods constituted the major prey item but with a markedly lower numerical bundance (just > 50%) compared to their dominant contribution to modern fish iet (Fig 11a). On the other hand, cladocerans and diaptomid copepods ontributed much higher proportions (approximately 13% and 30% repectively) ompared to their much lower contributions in the modern diet (see Figure 11a).

The cladoceran component in the historical sample was composed of *)aphnia longispina, D. lumholtzi, Ceriodaphnia cornuta, C. dubia,)iaphanosoma excisum, Moina micrura* and chydorid species but was lominated by *Bosmina longirostris*. The latter formed an average of (26 % of the otal number of cladoceran prey in the diet) compared to (5.5 %) for *)iaphanosoma excisum* which is the more frequent cladoceran prey in the nodern fish diet. With the exception of *D. excisum*, and *D. longispina*, which are he relatively more common species in modern zooplankton community, most ther cladoceran species have become very rare; more so around inshore habitats personal observation). The greater contribution of cladocerans to the diet in istorical fish samples is in agreement with their abundance as shown in the


Historical, 1966
n=30
% rel. abundance
100
80
60
40
20
0
1
2
3
4
5
6
7
8
9


Historical, 1966
n=30
% mean dry wt.
100
80
60
40
20
0
roti
naup
cycl
diap
clad
chao
inse

torical zooplankton sample (Figure 4), although the latter originated from a ferent part of the lake.

It would therefore appear that cladocerans formed a more prominent ember of the historical zooplankton assemblage which played an equally portant role in pelagic food chains. It is also implied from the gut analysis of e historical fish sample that three prey groups i.e. cyclopoids, diaptomids and adocerans were together the key dietary items and contributions from upplementary sources such as rotifers, nauplii, chaoborid and chironomid rvae/pupae and ostracods seem to have been proportionately lower. The dietary portance of the three key prey items is confirmed by their respective mean dry eights (Fig. 12b) i. e. cyclopoids 47.1%, diaptomids 23.6%, and Cladocerans 4.1% and therefore together accounting for 95% of the diet . In comparision to he modern diet, cyclopoids contribute (69.9%), diaptomids (2.8%) and cladocera 1.3%) of the total mean dry weight (see Figure 11b), together accounting for 74% of the diet requirements.

4.4.3. Ontogenetic changes in the diet

Size - dependent variation in the proportions of major dietary elements of *R. argentea* from the present study (Figure 13) point to different levels of utilisation by fish in different size classes. Clearly, cyclopoid copepods (copepodids and adults) constitute the primary prey item, utilised to the greatest extent by all fish across a size range of 10 - 60 mm sl. In all five size classes, the relative contribution of cyclopoids did not fall below 70% of the total number of prey items ingested. The diaptomid copepods contribution was generally low (0.5-3.7%) across all fish size classes. Notably, fish less than 20 mm sl hardly ingested diaptomids. On the other hand, among fish between 20 and 60 mm sl,

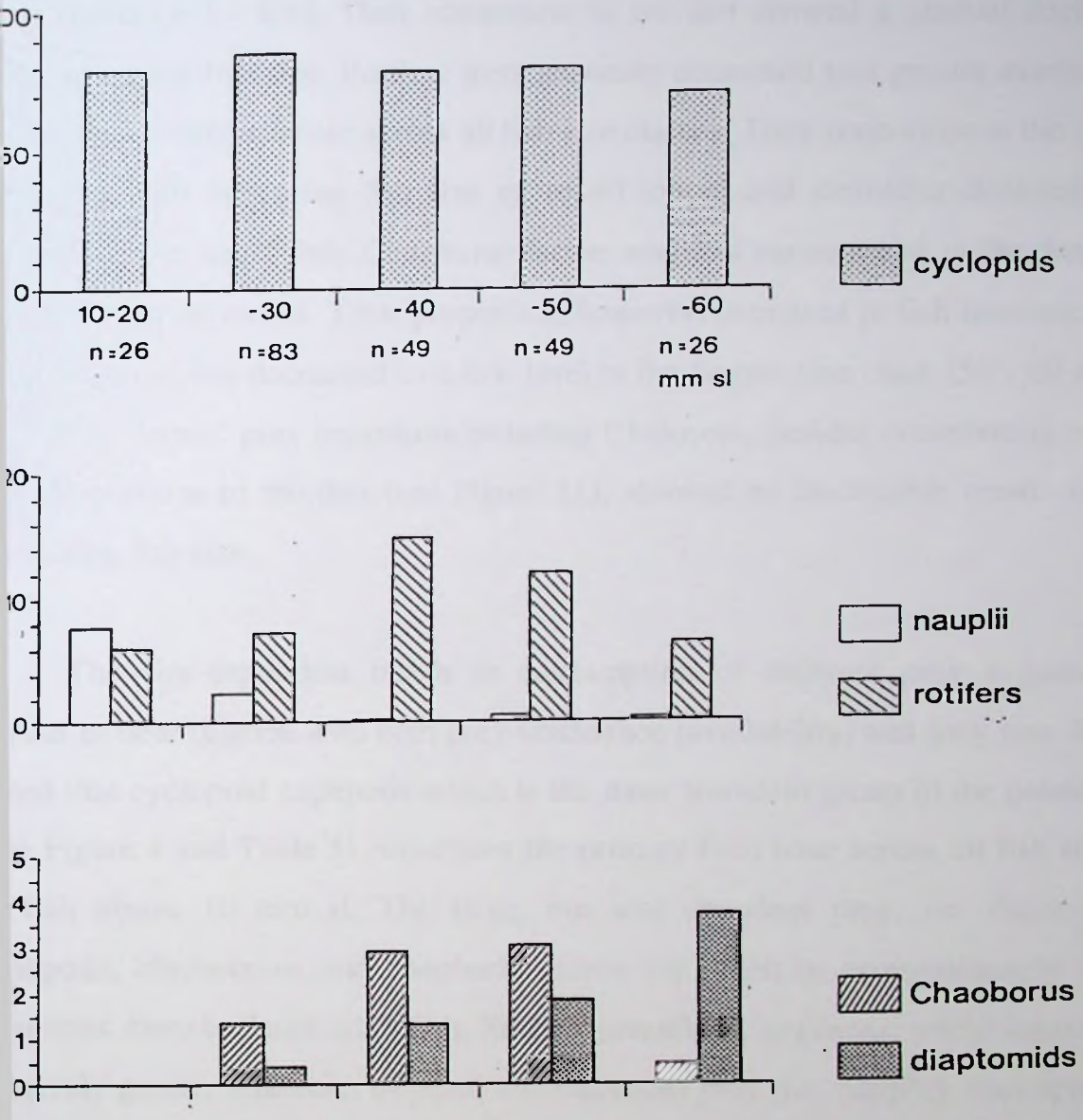


Figure 13. Diet composition (percentage numerical) of *R. argentea* with increasing fish size. Data pooled by sampling dates, sites, time of day and vertcal positions of fish capture.

the proportion of diaptomids increased steadily with increasing fish size. Nauplius larvae were ingested by fish in all size classes, but in consistently very low proportions (> 1 - 8%). Their component in the diet showed a gradual decline with increasing fish size. Rotifers were generally consumed to a greater extent (6 -14%) than nauplius larvae across all fish size classes. Their proportion in the diet increased with increasing fish size up to 40 mm sl and thereafter declined to lower levels in larger fish. *Chaoborus* larvae were not encountered in the diet of fish less than 20 mm sl. Their proportion, however, increased in fish between 20 and 50 mm sl, but decreased to a low level in the largest size class (55 - 60 mm sl). Other 'minor' prey organisms including Cladocera, besides contributing very low proportions to the diet (see Figure 11), showed no discernible trends with increasing fish size.

The size-dependent trends in consumption of different prey organisms appear to bear relation with both prey abundance (availability) and prey size. It is noted that cyclopoid copepods which is the most abundant group in the plankton (see Figure 4 and Table 5) constitutes the primary food base across all fish sizes of fish above 10 mm sl. The large, but less abundant prey, i.e. diaptomid copepods, cladocerans and chaoborid larvae are taken in proportionately less quantities even by large adult fish. Smaller juvenile *R. argentea*, while ingesting relatively greater quantities of small and numerous prey (i.e. nauplii), also appear to take advantage of cyclopoids, which, besides their superabundance in the environment, offer a wide choice in terms of species diversity (see Table 1) and body sizes (see Figure 4). The limited consumption or apparent avoidance of large prey items by juvenile fish may also be related to possible capture and handling constraints.

4.4. Diet composition: inshore vs offshore samples

The food composition in fish samples from two inshore sites (MSE, NG) d offshore station (BG) during December 1995 showed some clear similarities well as striking differences (Figure 14a). Cyclopoid copepods were the most ominent food item in all samples from the three sites. However, fish from the fshore station had higher numerical component of cyclopoids (98%) than shore stations (78% and 53% respectively). The only other food item of portance in the diet of the offshore fish population was chaoborid larvae .8%), while all other items ranked very low. At NG station rotifers (16%) were cond to cyclopoid copepods, in numerical importance in the diet while aptomids, nauplii, cladocerans, chaoborid larvae and insects together nstituted the remaining proportion (6%). Owing to the small sample size (n = 8) mostly large adult fish (> 50 mm sl) from MSE station, all of which originated om night samples, the insect component in the gut contents was quite high 2%).

Diaptomid copepods, which have been shown to occur with increasing portance in large adult fish (see Figure 13), showed a relatively high presentation (6 %) in fish from MSE station. The corresponding dry weight data ig. 14b) confirm the importance of cyclopoid copepods in the diet of fish from th inshore and offshore habitats (NG and BG respectively). The strikingly low oportion of cyclopoid prey in fish from MSE may partly be due to the small mple size and narrow size range of fish examined from this station. Despite the ortcomings in the MSE data, large mature fish at this shallow inshore habitat early ingested high quantities of adult insects that were probably abundant at ght on this particular sampling date. The data also seem to suggest diminishing oportions of this prey item in the fish diet, with increasing distance from the

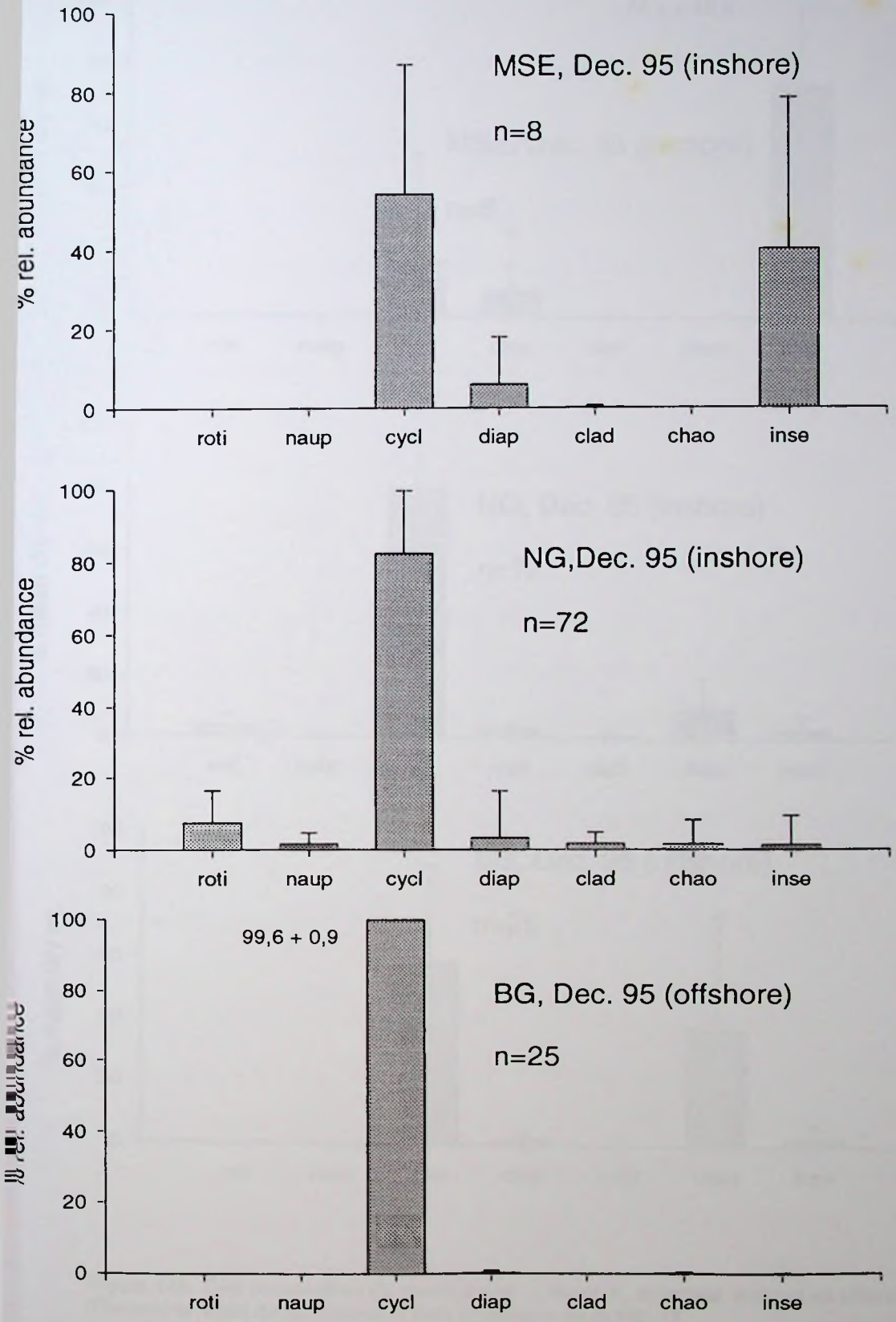


Figure 14a. Diet composition (% rel. abundance ± sd) of *R. argentea*: inshore vs offshore (December 1995 data). Names of prey organisms as in Fig. 11.

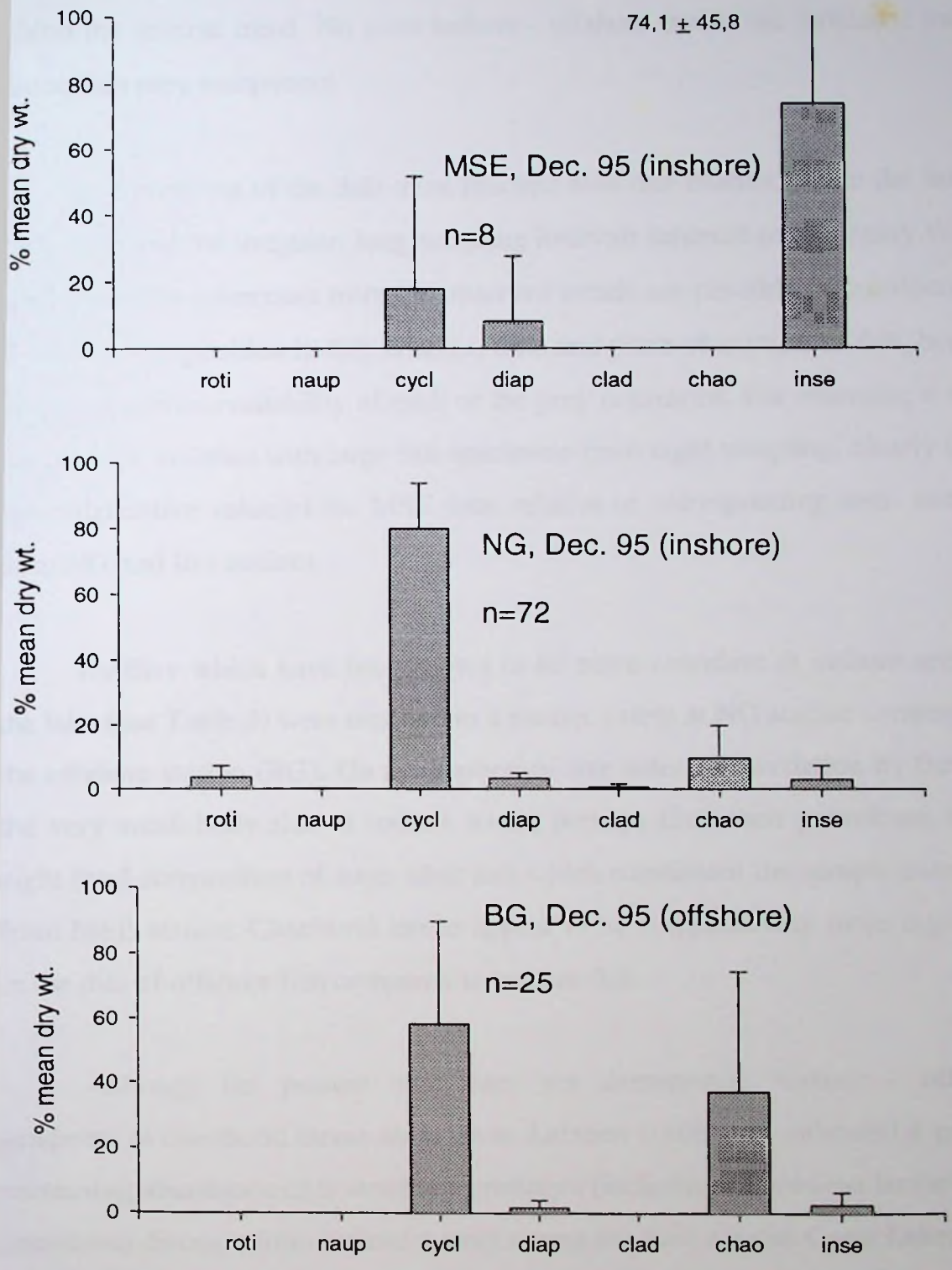


Figure 14b. Diet composition (% mean dry wt. ± sd) of *R. argentea*: inshore vs offshore (December 1995 data). Names of prey organisms as in Fig. 11.

shore. Diaptomid copepods and rotifers follow a similar pattern, while chaoborids exhibit the reverse trend. No clear inshore - offshore trends are indicated for the cladoceran prey component.

Interpretation of the data must proceed with due caution, given the limited study time and the irregular, long sampling intervals inherent in this study. Within limits, therefore inferences from the observed trends are possible in consideration of the size composition in fish samples, time and place of capture of fish, besides size and relative availability of each of the prey organisms. For example, a small sample size, coupled with large fish specimens from night sampling, clearly limits the comparative value of the MSE data, relative to corresponding data samples from NG and BG stations.

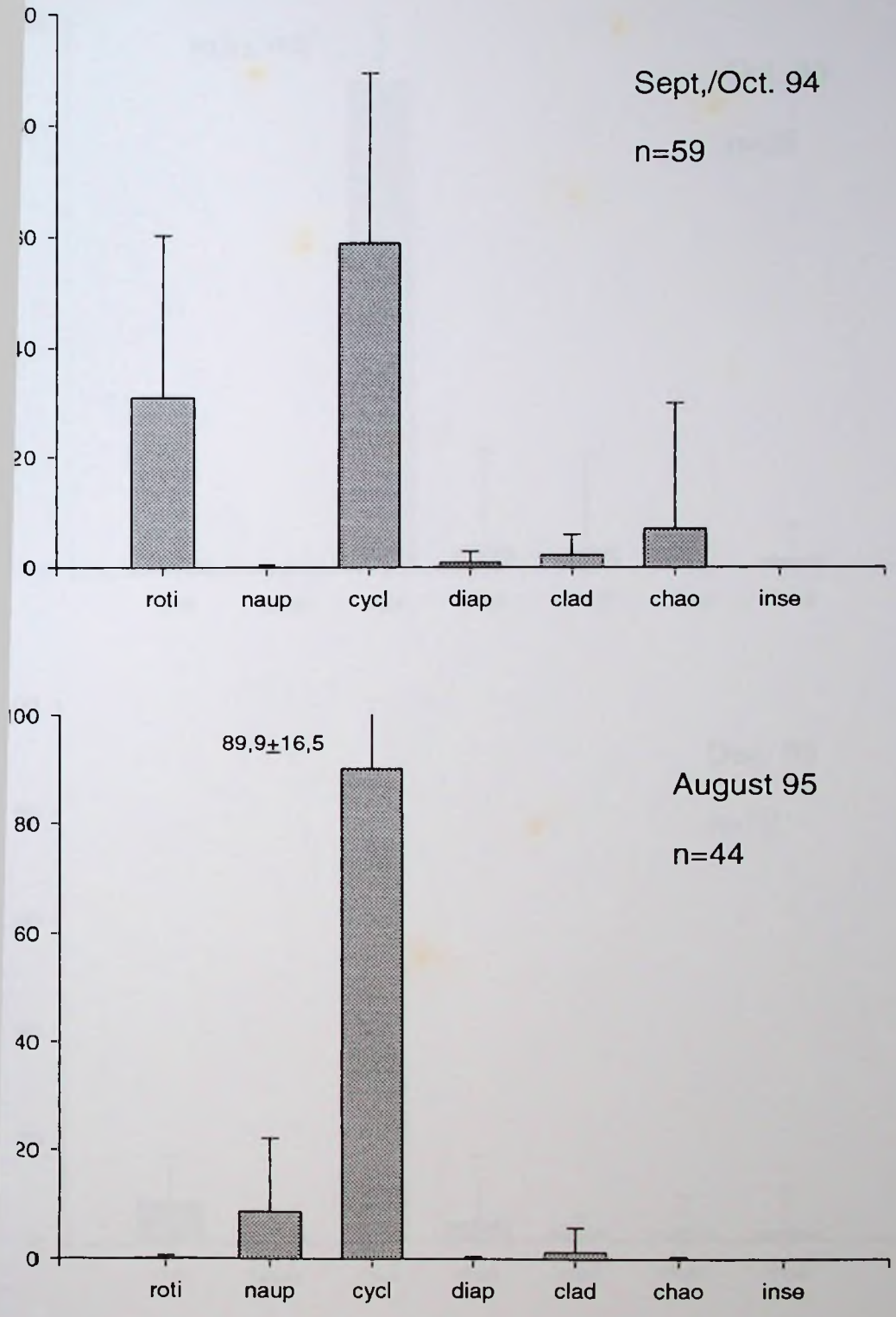
Rotifers which have been shown to be more abundant in inshore areas of the lake (see Table 5) were ingested to a greater extent at NG station compared to the offshore station (BG). On assumption of size selective predation by the fish, the very small body size of rotifers would perhaps limit their prevalence in the night food composition of large adult fish which constituted the sample examined from MSE station. Chaoborid larvae appear to be comparatively more important in the diet of offshore fish compared to inshore fish.

Although the present data does not demonstrate inshore - offshore gradients in chaoborid larvae abundance, Lehman (1996) has indicated a general increasing abundance of invertebrate predators (including *Chaoborus* larvae) with increasing distance from inshore waters among the East African Great Lakes. The relative prominence, therefore, of chaoborid larvae in the diet of offshore (BG) *R. argentea* may in part, reflect such potential inshore - offshore gradient in chaoborid abundance in Lake Victoria.

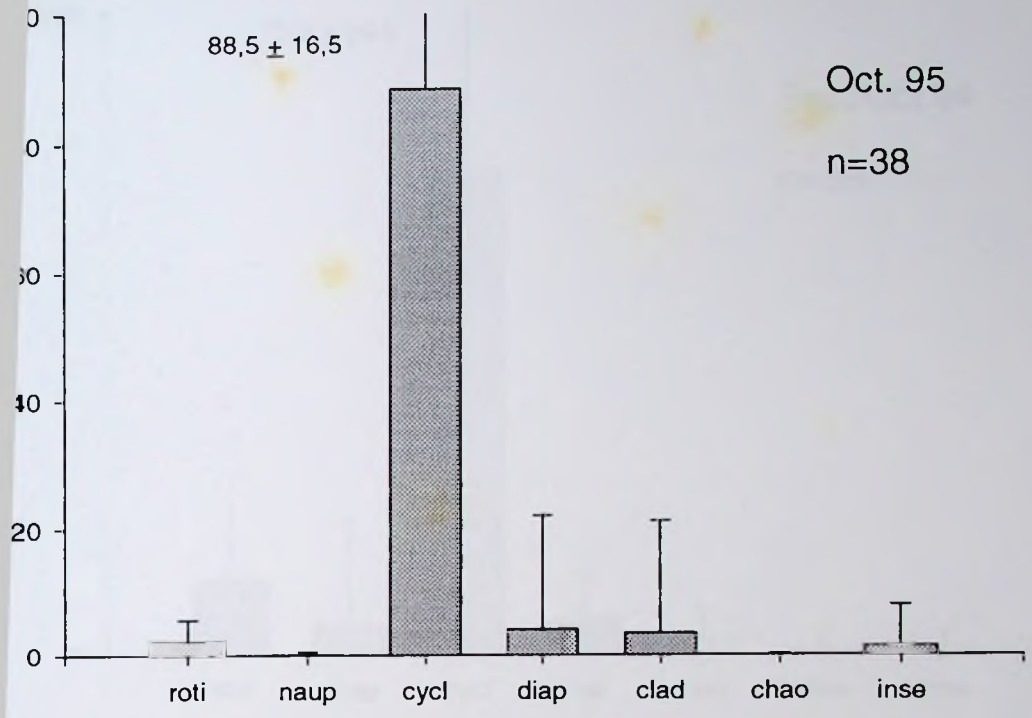
4.5. Seasonal changes in the diet

Relative abundances (numerical) of various prey organisms in guts of *R. gentea* for different sampling dates (September-October 1994 to December 995) at NG station (Figure 15a) indicated no marked seasonal changes in diet mposition. Cylopoid copepods remained the sole dominant food component in l fish samples, contributing between 64% and 92% of the diet. Most other prey ganisms appeared regularly in the diet, but generally in low proportions. otifers, however, were a notable exception. They attained relatively higher merical proportions among ingested prey organisms in September - October 994 (29%) and December 1995 (18%). It is however not clear if such increase rotifers in the diet is linked to their annual cycle of abundance in the plankton, owing peak densities in September (see Table 4).The corresponding mean dry eight data (Figure 15b) show similar seasonal patterns, with cyclopoid pepods as the principal prey item at all times. Mean dry weight of chaoborid rvae were relatively high in September-October (1994), October and December 995) fish samples. In contrast, chaoborids were hardly encountered in the ugust (1995) gut contents sample.

These temporal trends of the chaoborid component in the diet, however, em to relate more to the size composition of fish captured on different sampling tes, than to actual seasonality in their consumption by the fish. The August fish mple was dominated by small immature fish (< 35mm sl) which have been own to ingest generally low proportions of chaoborid larvae compared to larger lult fish (see Fig. 13). The same trend appears to hold for other larger prey items well e.g. diaptomids and insects, all of which contributed negligible mean dry eights in the August fish diet, but showed higher proportions in larger fish from her sampling dates. Cladoceran mean dry weights were very low and nearly



a. Diet composition (% rel. abundance ± sd) of *R. argentea* on different sampling dates at
h (September/October 1994 and August 1995 data). Names of prey organisms as in Fig. 11.



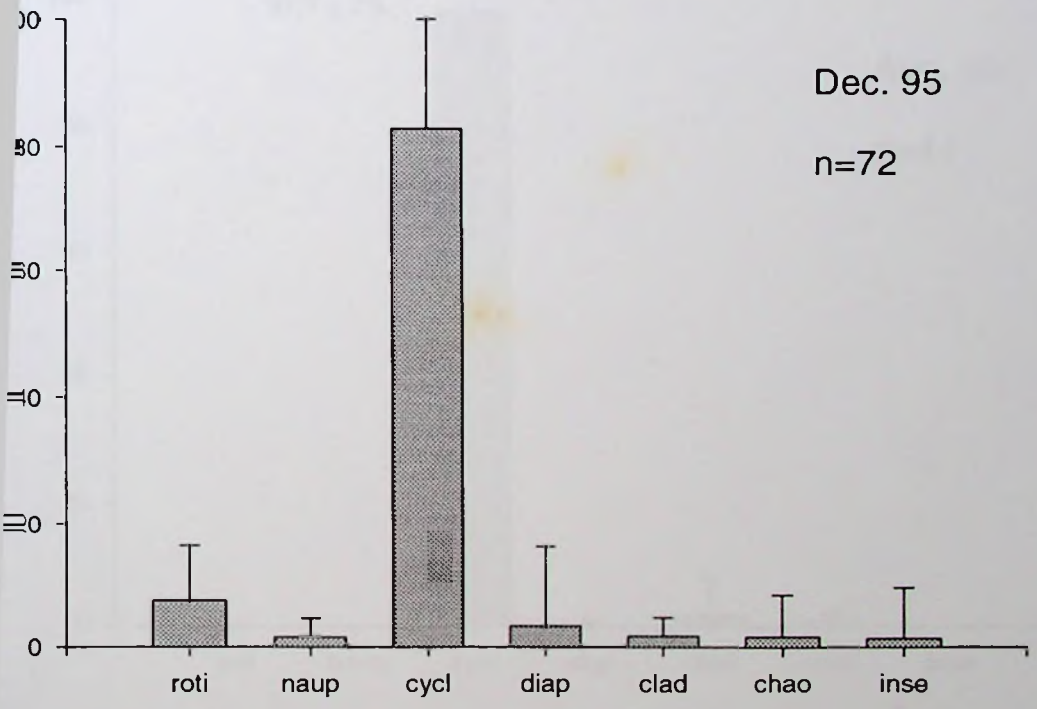
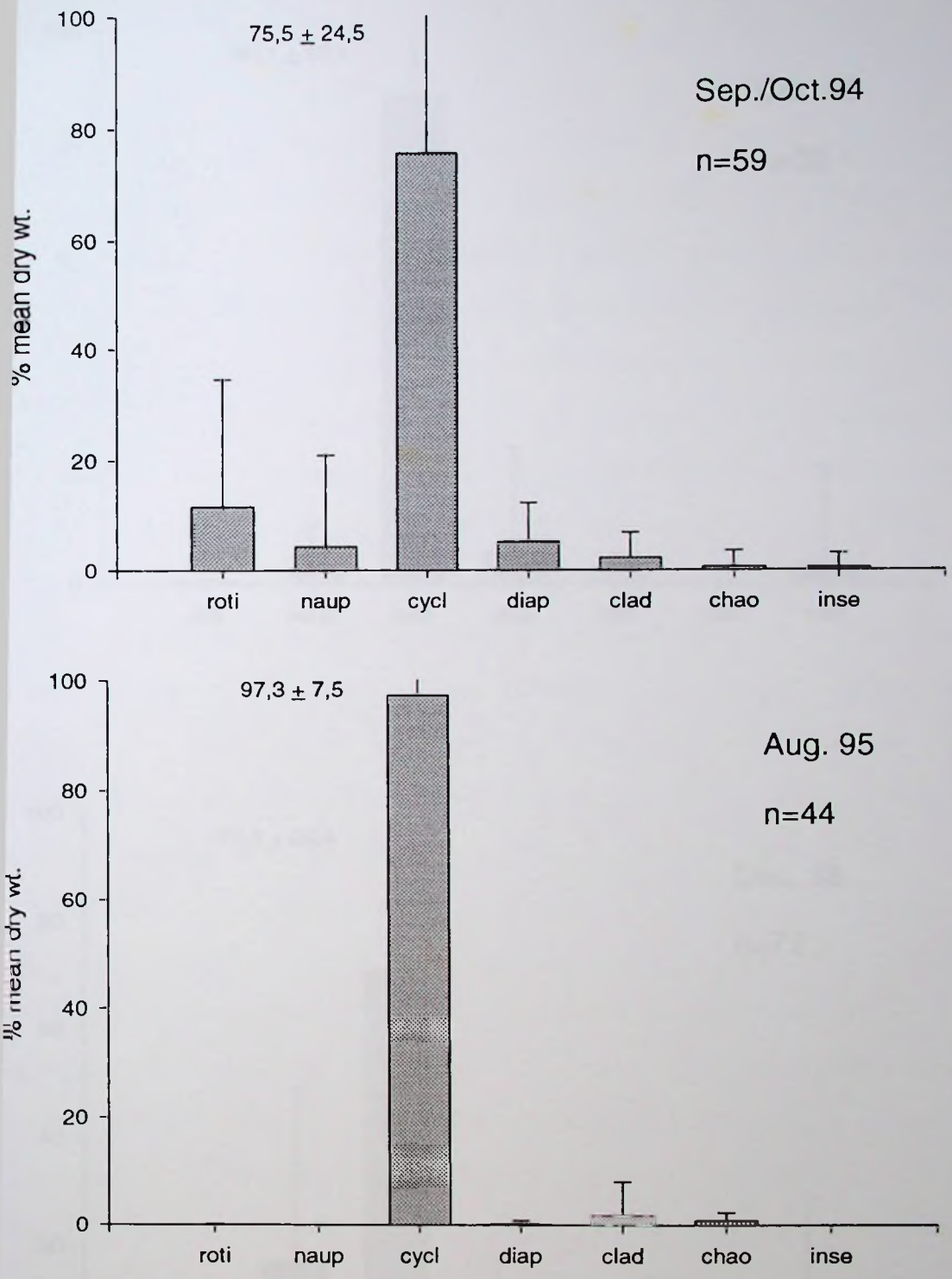
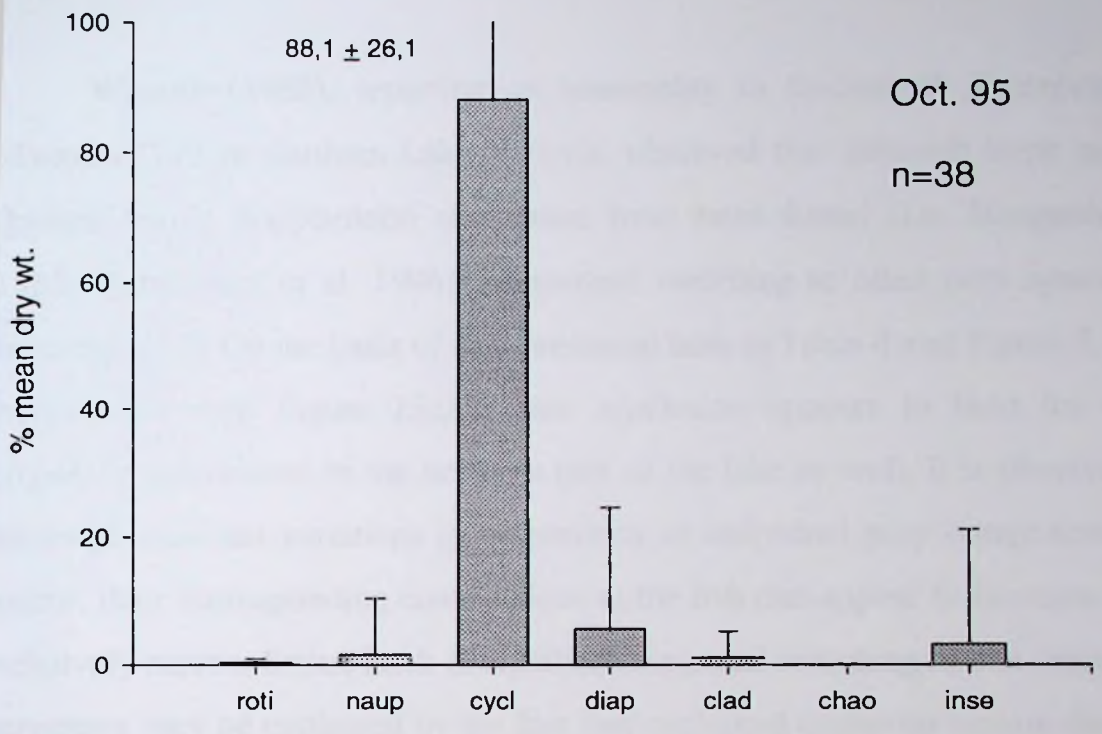


Figure 15a. continued (October and December 1995 data)



gure 15b. Diet composition (% mean dry wt. ± sd) of *R. argentea* on different sampling dates at
a station (September/October 1994 and August 1995 data). Names of prey organisms as in Fig. 11.



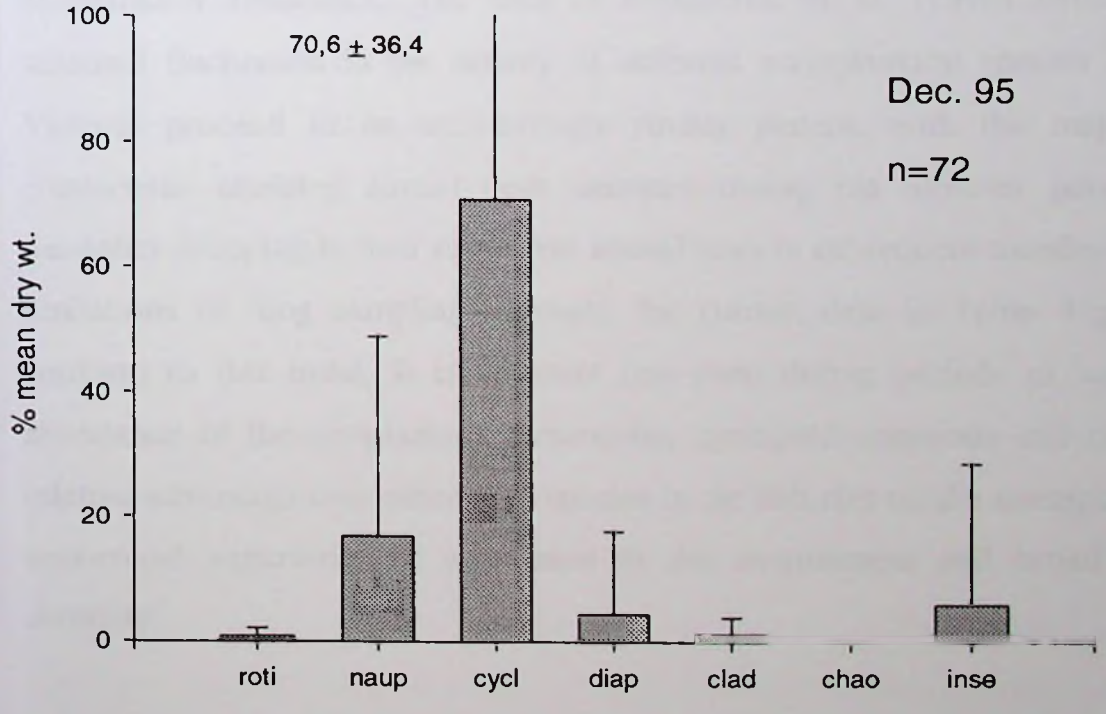


Figure 15b. continued (October and December 1995 data)

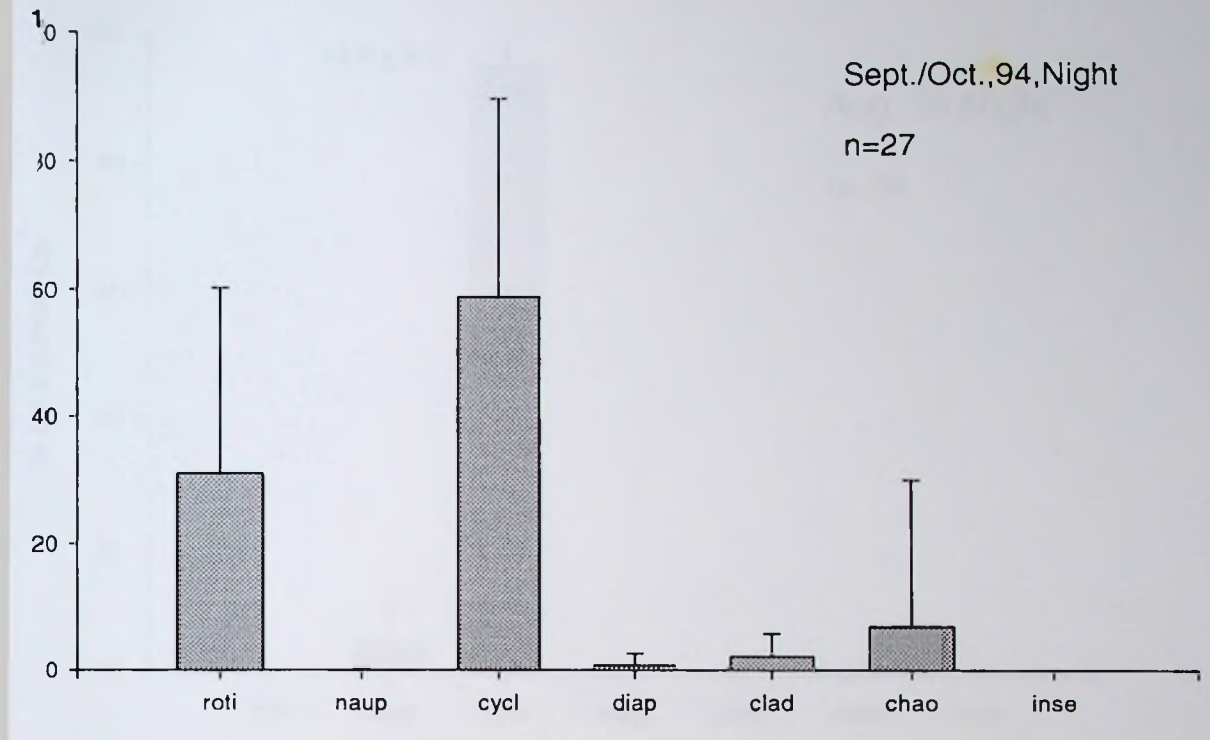
onstant in all fish samples.

Wanink (1988), reporting on seasonality in feeding of *R. argentea* in Mwanza Gulf in southern Lake Victoria, observed that although large seasonal fluctuations in zooplankton abundance have been found (i.e. Hoogenboezem 1985; Branstrator et al. 1996), no marked switching to other prey species has been reported. On the basis of data presented here in Table 4 and Figure 5, and in conjunction with Figure 15a&b, this conclusion appears to hold for the *R. argentea* populations in the northern part of the lake as well. It is observed that although seasonal variations in proportions of individual prey components may occur, their corresponding contributions to the fish diet appear to fluctuate within relatively narrow limits. Lack of significant seasonal switching in diet items by *R. argentea* may be explained by the fact that cyclopoid copepods remain the major element of the pelagic zooplankton community throughout the year and is evidently the main driving force of the observed seasonal cycle of total zooplankton abundance. The data of Branstrator et al. (1996) indicate that seasonal fluctuation in the density of different zoooplankton species in Lake Victoria proceed in an astonishingly similar pattern, with the majority of crustaceans attaining annual peak densities during the turnover period, and thereafter dropping to their respective annual lows in subsequent months. Despite limitations of long sampling intervals, the current data in Table 4 generally conform to this trend. It is apparent that even during periods of waning in abundance of the zooplankton community, cyclopoid copepods still command relative advantage over other prey species in the fish diet on the strength of their year-round superiority of abundance in the environment and broad species diversity.

.4.6. Diet composition in day and night samples

Separate analysis of gut contents (numerical) in samples of fish captured during day and night times (Figure 16a) at NG station showed no indication of major differences in the proportions of the various prey organisms ingested with respect to time of day. Cyclopoid copepods were consistently the dominant food item at all times in both day and night fish gut samples, supplemented by various other prey items. Corresponding mean dry weight data (Fig. 16b), however, revealed relatively higher night time consumption of insects and chaoborid larvae (September - October 1994; December 1995), probably during nights when these large prey organisms became abundant in the environment. Chaoborid larvae spend most of the day time in bottom sediments but ascend into the water column at night to feed on some planktonic elements such as rotifers, nauplii and copepodids. These macroplankton are therefore available to pelagic fish predators mostly at night time and this may explain their higher frequency and abundance in the diet of fish caught at night.

Earlier observations by Hoogenboezem (1985) in the Mwanza Gulf suggests a reduction in feeding intensity at night time and consumption of proportionately greater amounts of larger prey organisms such as lake flies, which at times of mass emergence become abundant at the water surface. This observation has been substantiated by Wanink (1988) with further data from the Mwanza Gulf and by Wandera (1991) with data from the nothern part of the lake. Based on these independent accounts and observations from the present study, the importance of insects in the night feeding activities of *R. argentea* in the lake is confirmed. The paucity of lake flies in night fish gut samples from NG station may have resulted from the timing of fishing activities relative to the emergence periodicity of lake flies. Both Hoogenboezem (1985) and Wanink (1988) pointed



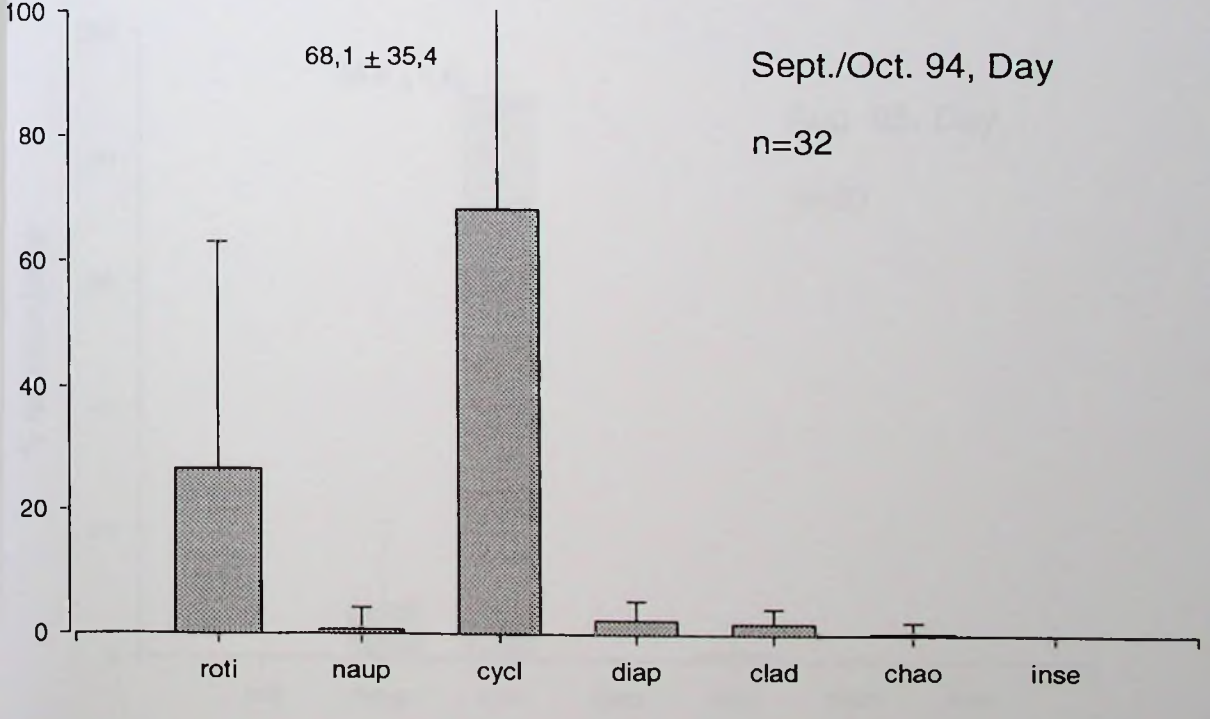
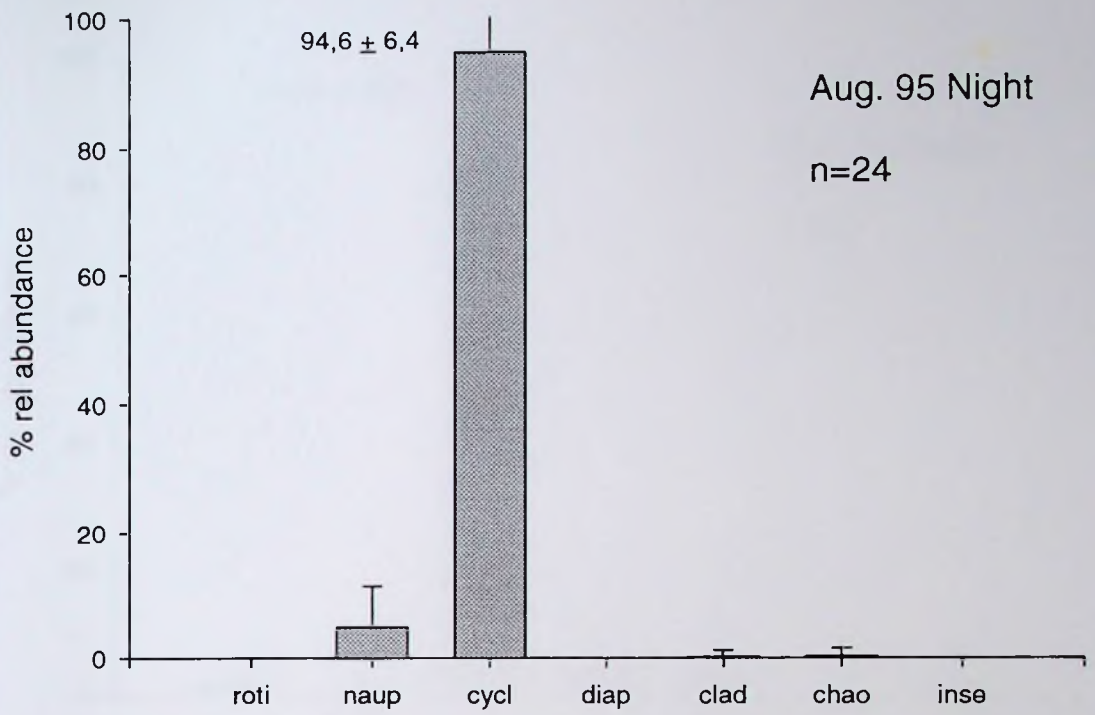


Figure 16a. Diet composition (% rel. abudance ± sd) of *R. argentea* at NG station: day vs night samples. Names of prey organisms as in Fig. 11.



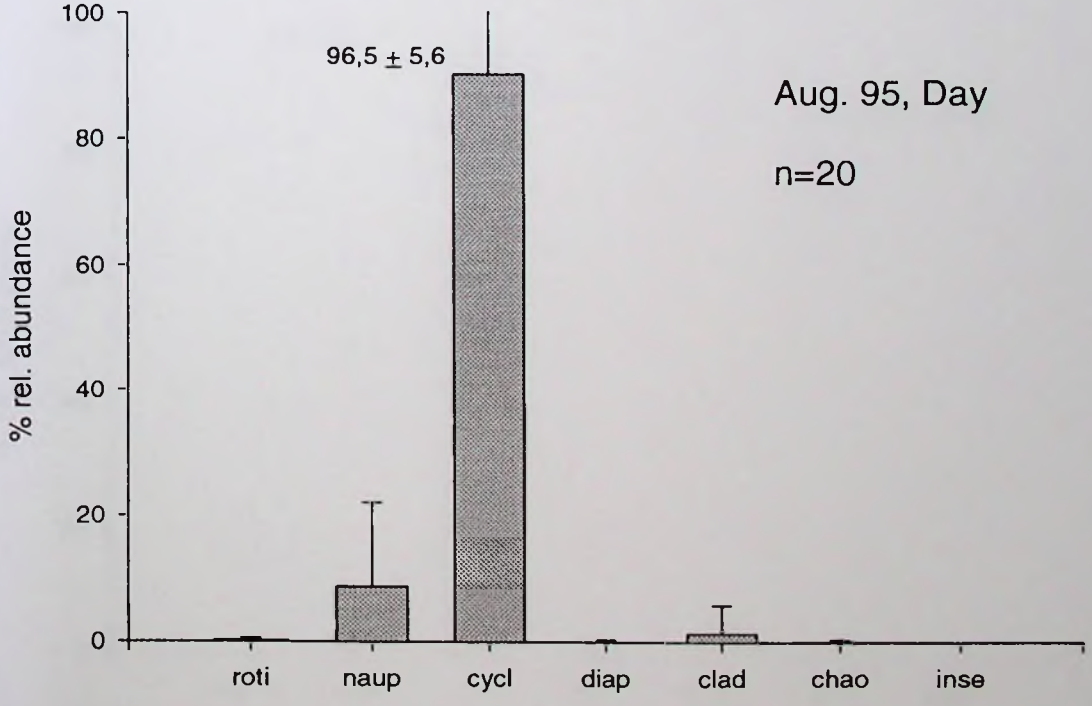


Figure 16a. continued (August 1995)

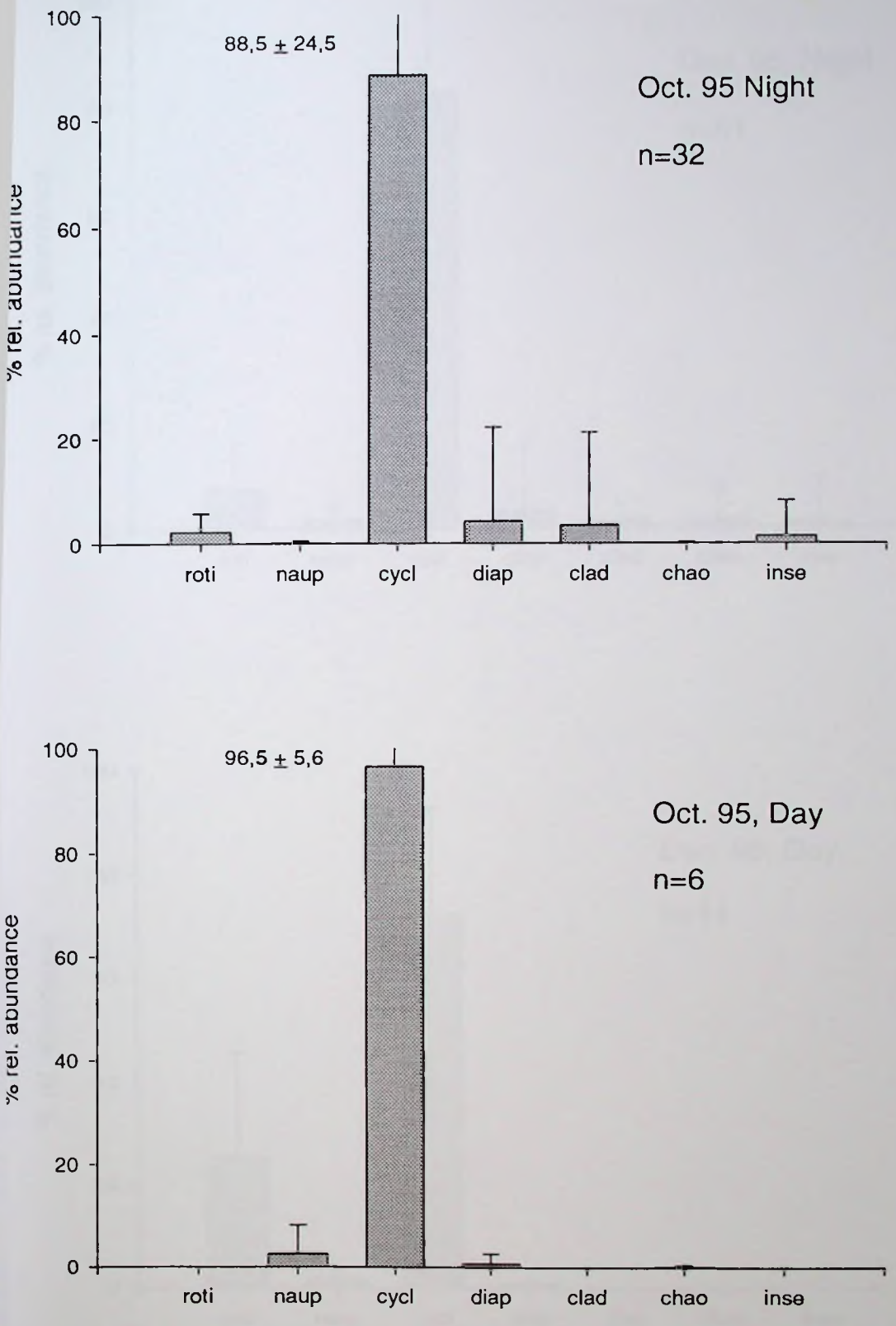
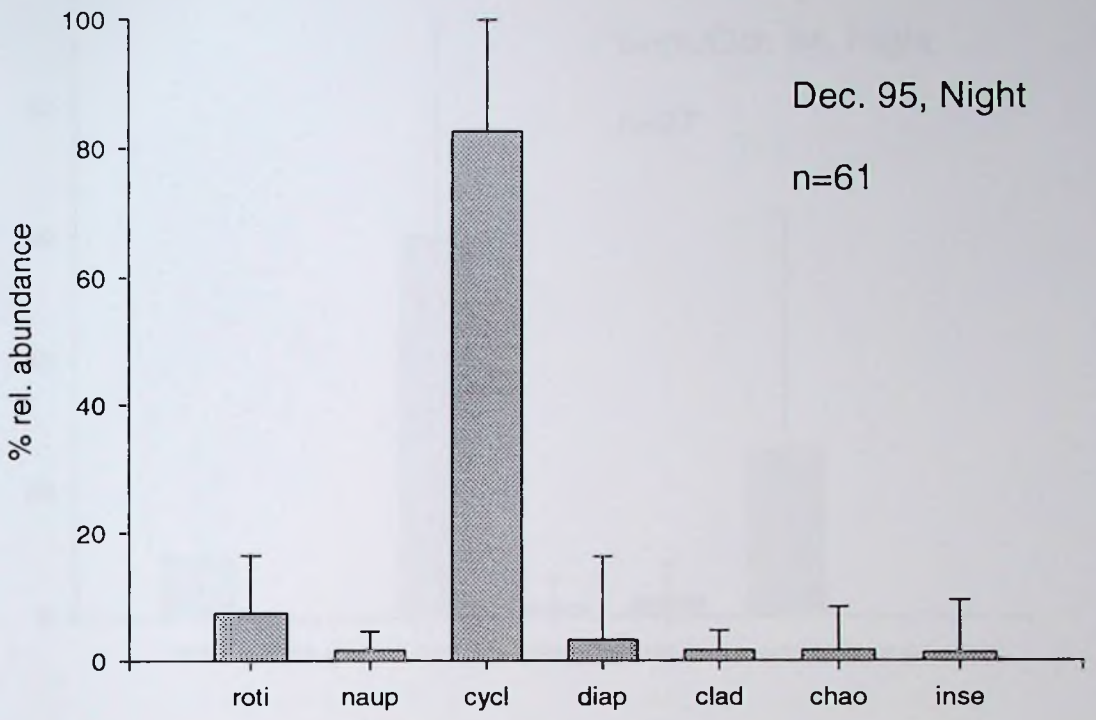


Figure 16a. continued (October 1995)



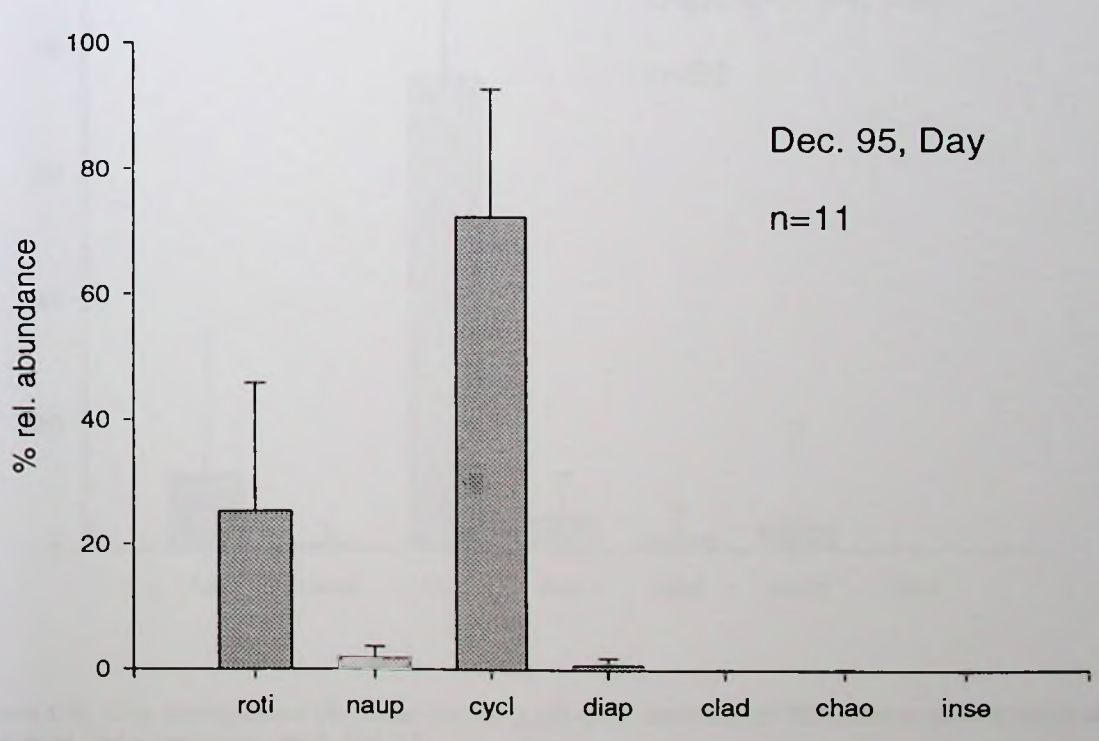


Figure 16a. continued (December 1995)

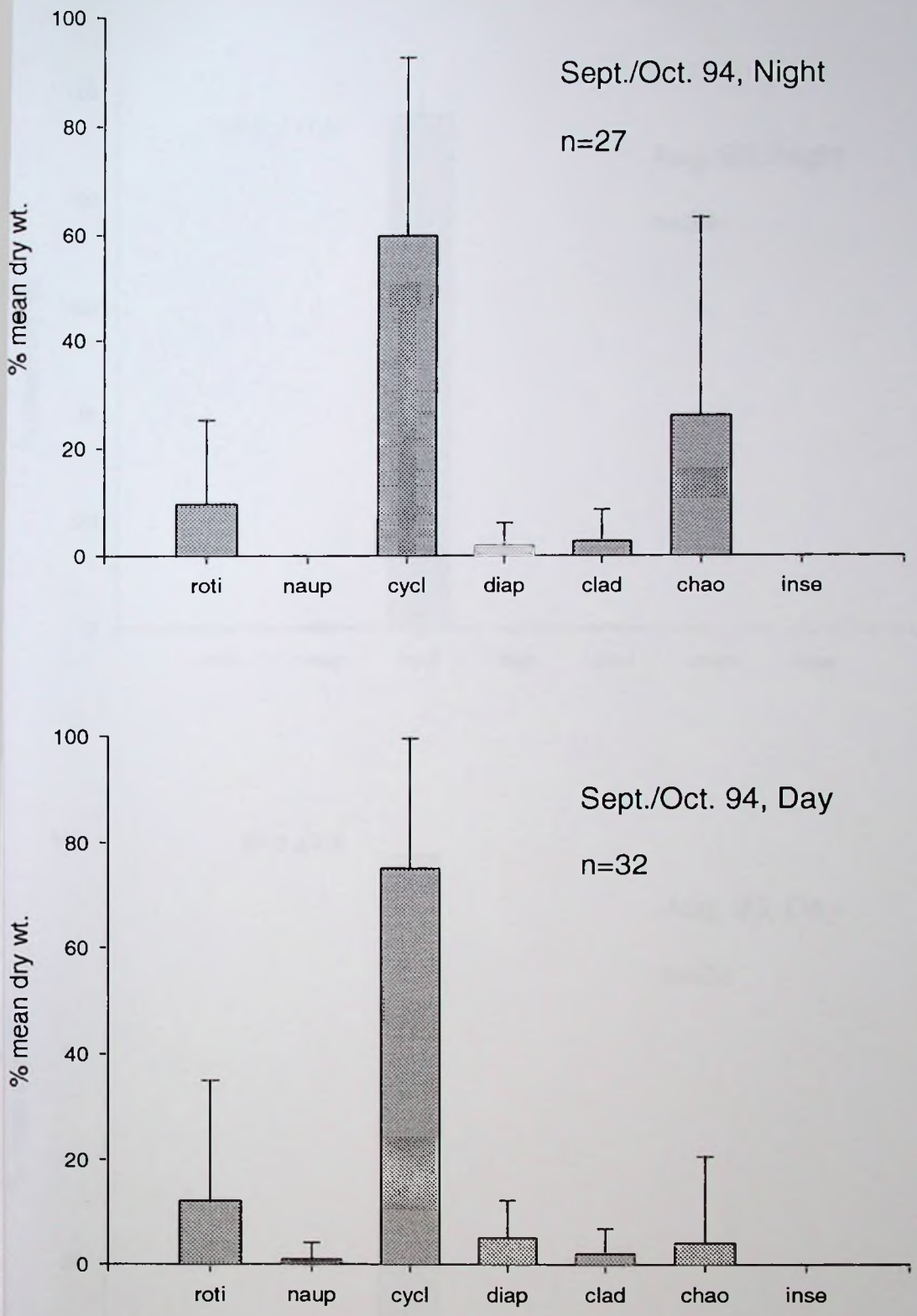
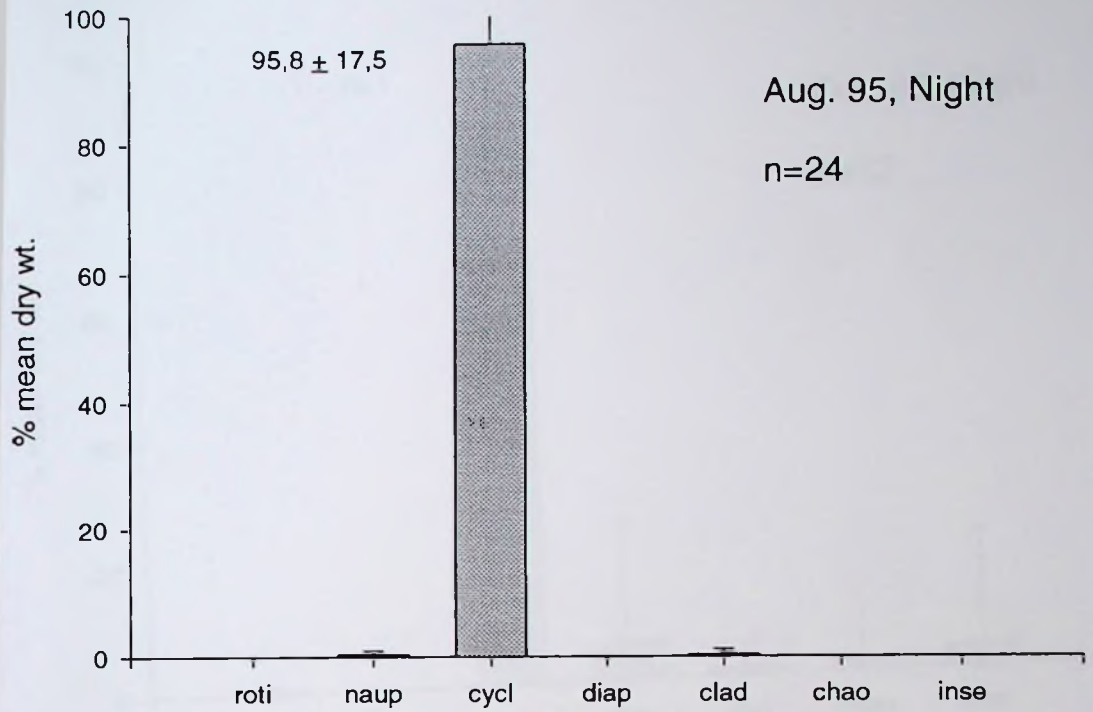


Figure 16b. Diet composition (% mean dry wt. ± sd) of *R. argentea* at NG station: day vs night samples. Names of prey organisms as in Fig. 11.



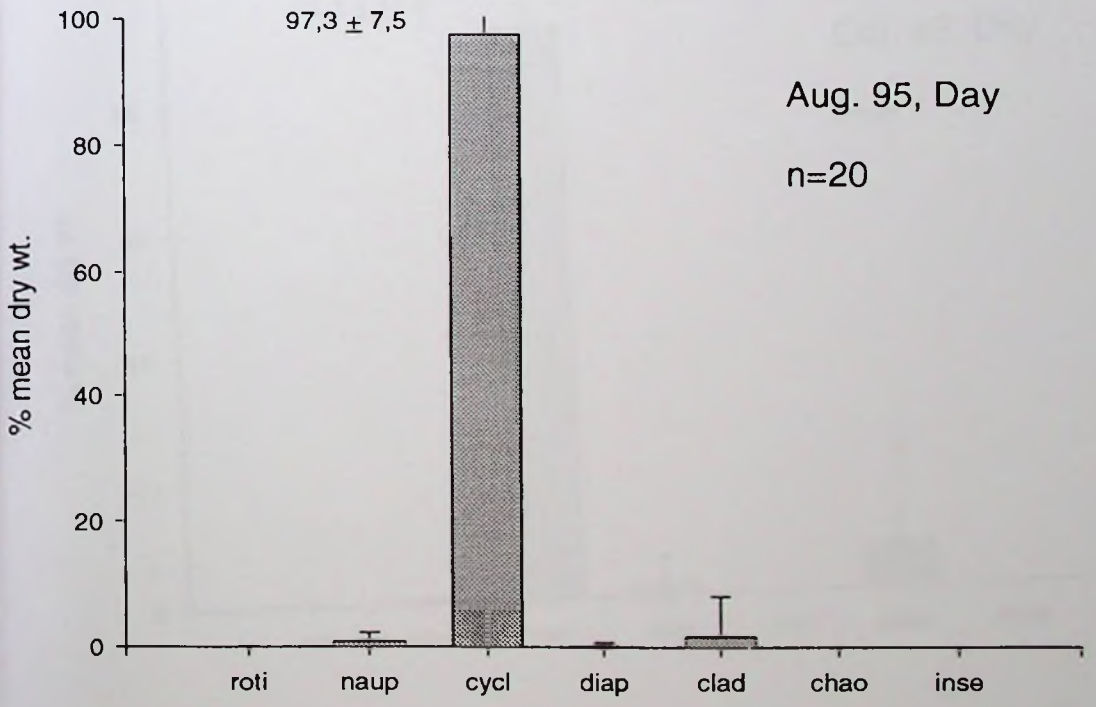


Figure 16b continued (August 1995)

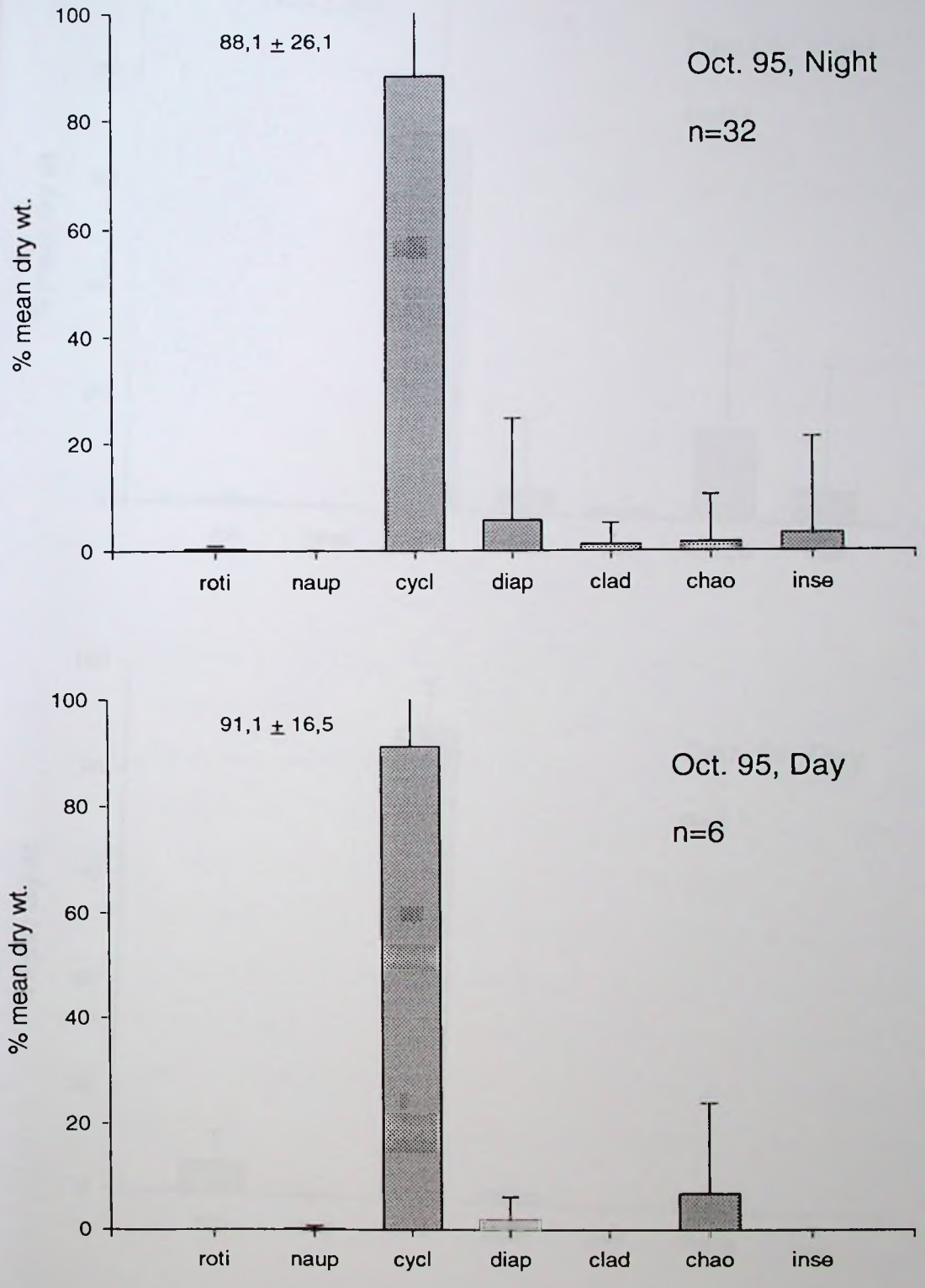


Figure 16b. continued (October 1995)

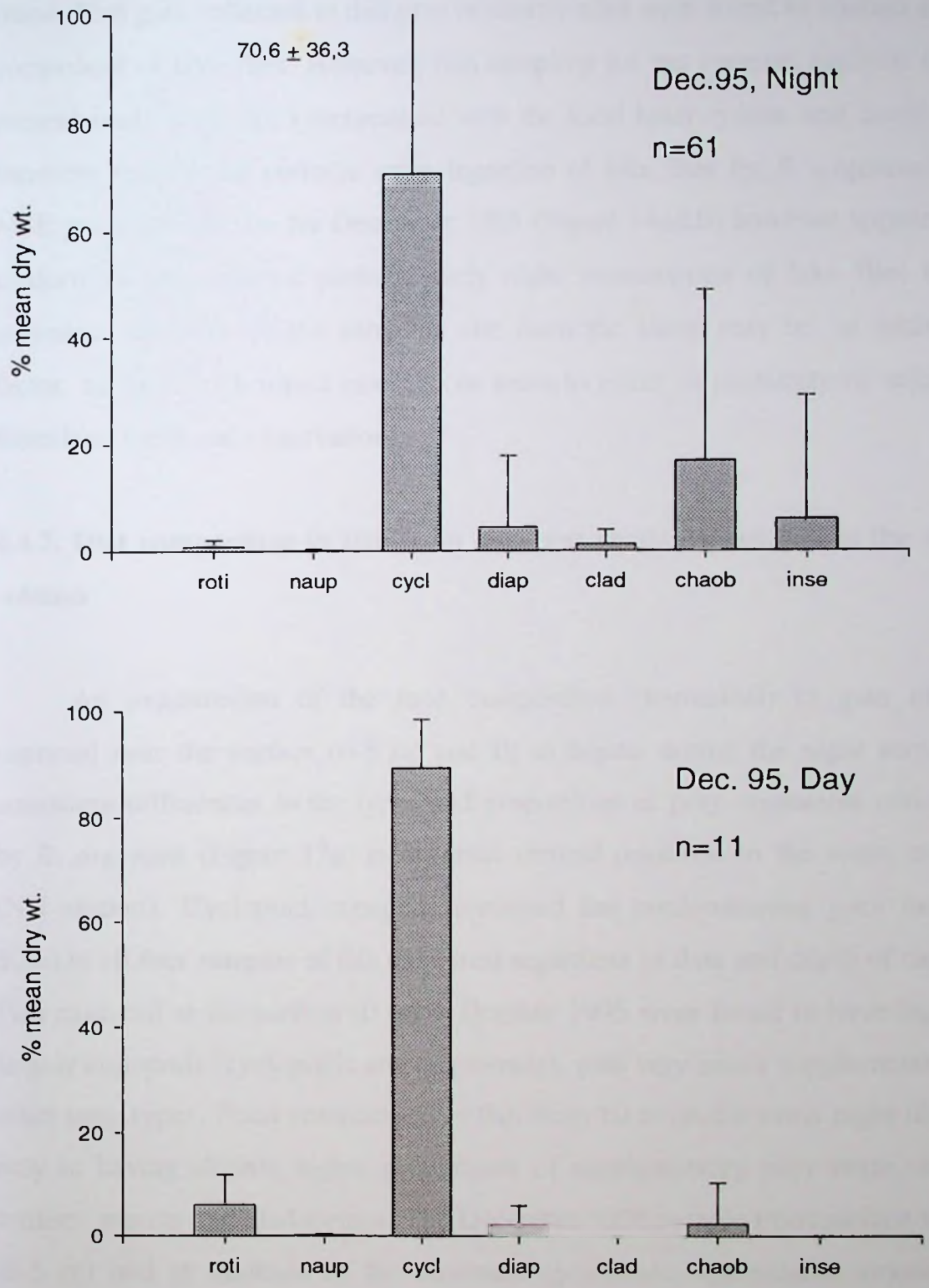
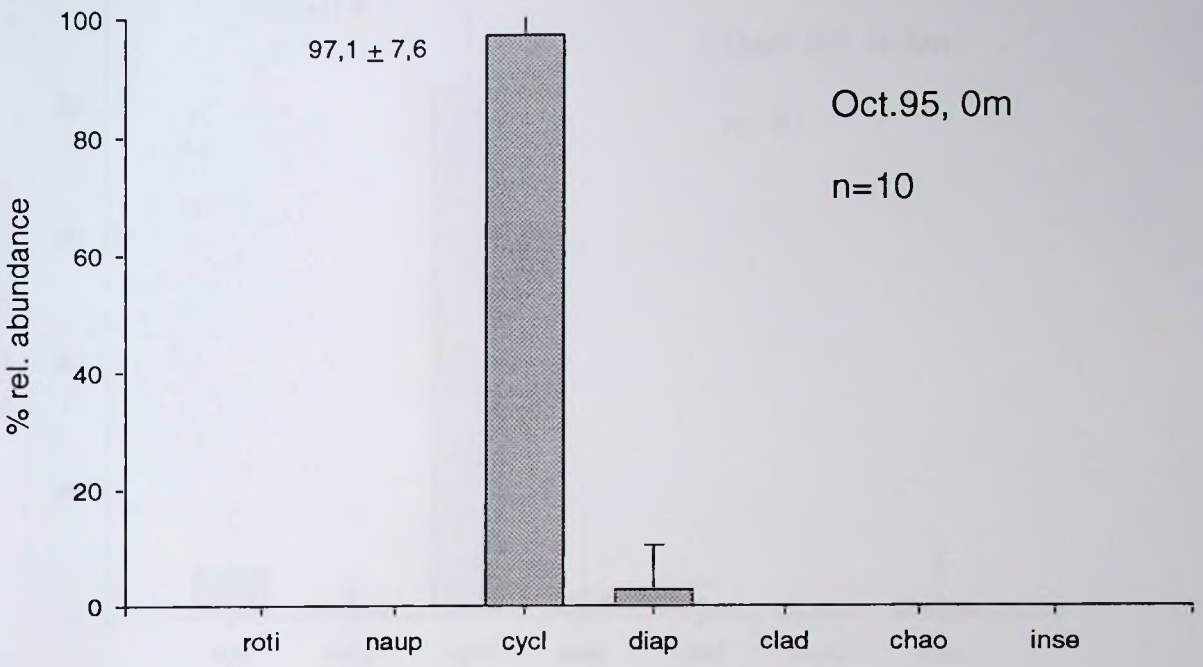


Figure 16b. continued (December 1995)

out that periodic mass emergence of lake flies occurs around dusk during new moon. Fish guts collected at this time or shortly after were found to contain a high component of lake flies. However, fish sampling for gut contents analysis in the present study were not synchronised with the local lunar rythms and could have therefore missed the periodic mass ingestion of lake flies by *R. argentea*. The MSE gut contents data for December 1995 (Figure 14a&b) however appeared to conform to the reported periodic early night consumption of lake flies by *R. argentea*. Distance of the sampling site from the shore may be an additional factor, as most such insect emergences seem to occur in proximity to adjoining hinterland (personal observation).

4.4.7. Diet composition in fish from different vertical positions in the water column

An examination of the food composition (numerical) in guts of fish captured near the surface (0-5 m) and 10 m depths during the night shows no consistent differences in the types and proportions of prey organisms consumed by *R. argentea* (Figure 17a) at different vertical positions in the water column (NG station). Cyclopoid copepods remained the predominating prey item (> 80%) in all four samples of fish examined regardless of date and depth of capture. Fish captured at the surface (0 m) in October 1995 were found to have ingested largely copepods (cyclopoids and diaptomids), with very minor supplements from other prey types. Food composition of fish from 10 m on the same night differed only in having slightly higher proportions of supplementary prey items, mainly rotifers, insects and cladocerans. The December 1995 sample from surface waters (0-5 m) had in addition to the dominant cyclopoids, appreciable amounts of chaoborid larvae, rotifers, diaptomids, cladocerans and insects. A nearly similar prey composition was observed in guts of fish captured at 10 metres on the same



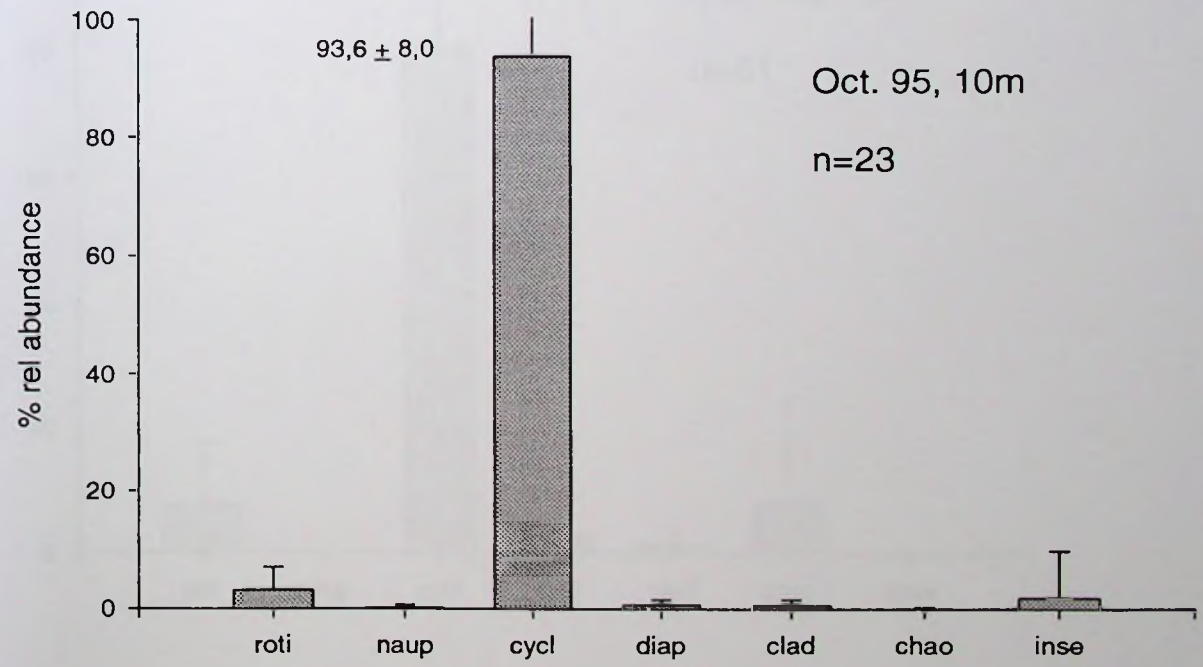
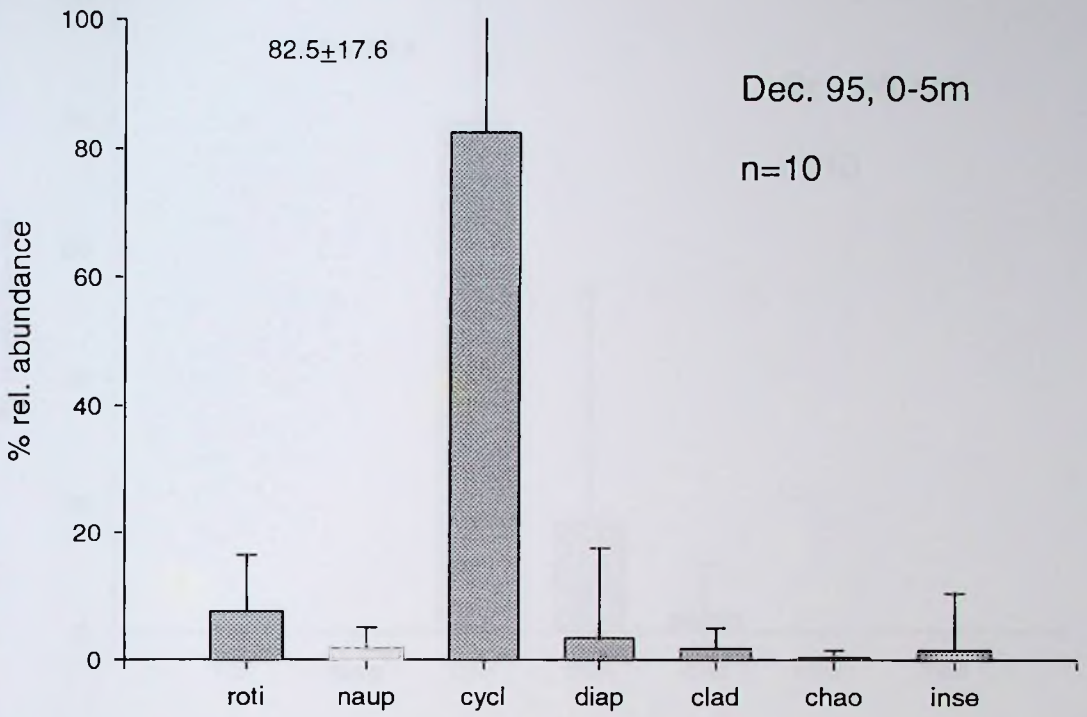


Figure 17a. Diet composition (% rel. abundance ± sd) of *R. argentea* taken at different vertical positions during the night at NG station (October 1995 data). Names of prey organisms as in Fig. 11.



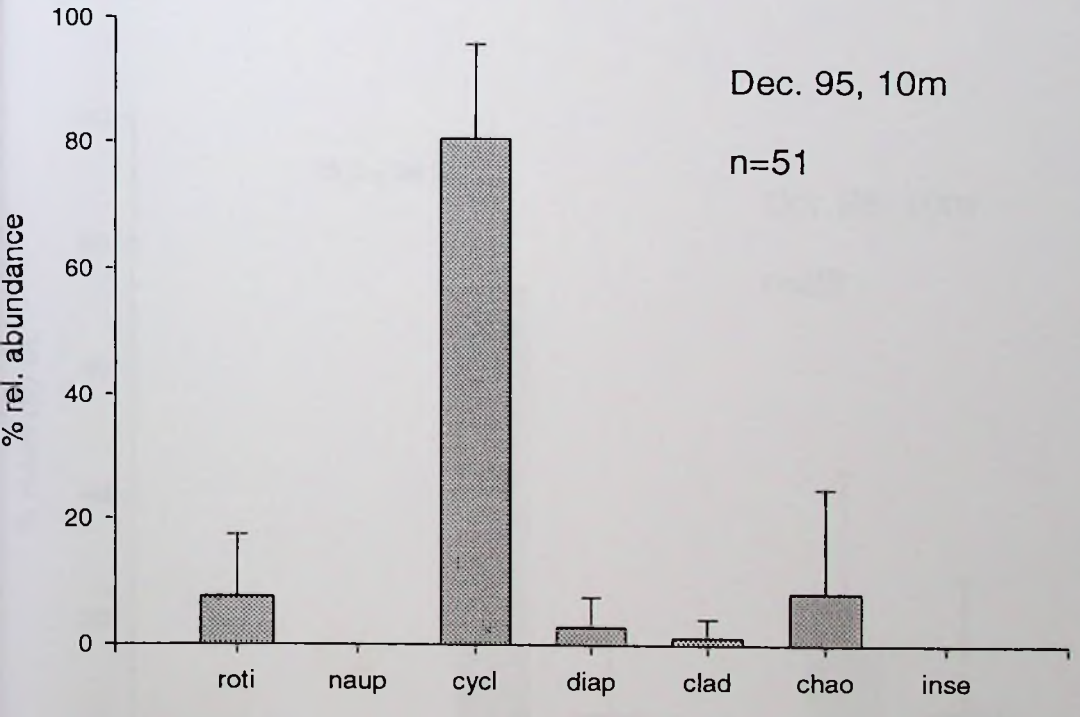


Figure 17a. continued (December 1995 data)

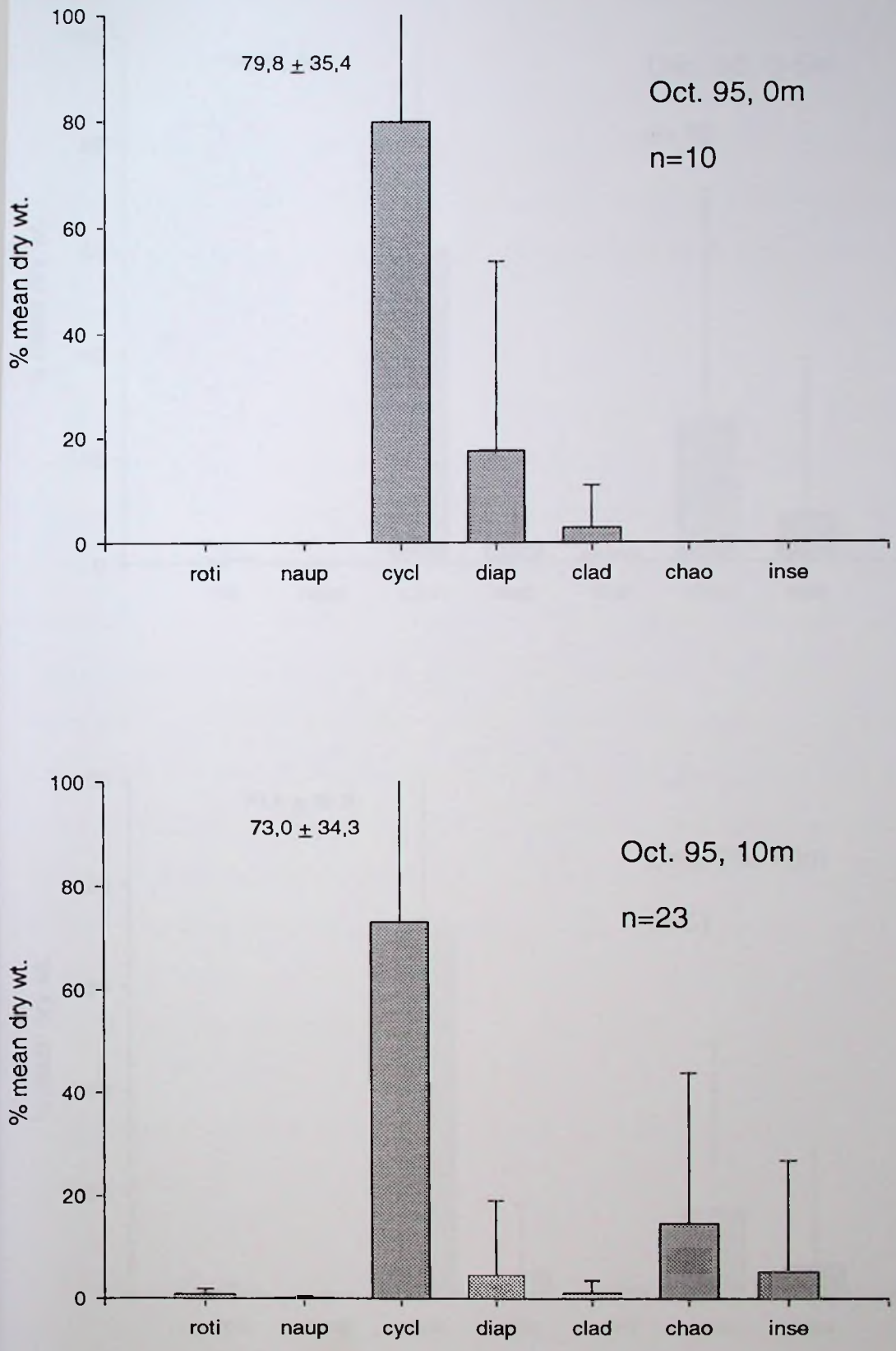
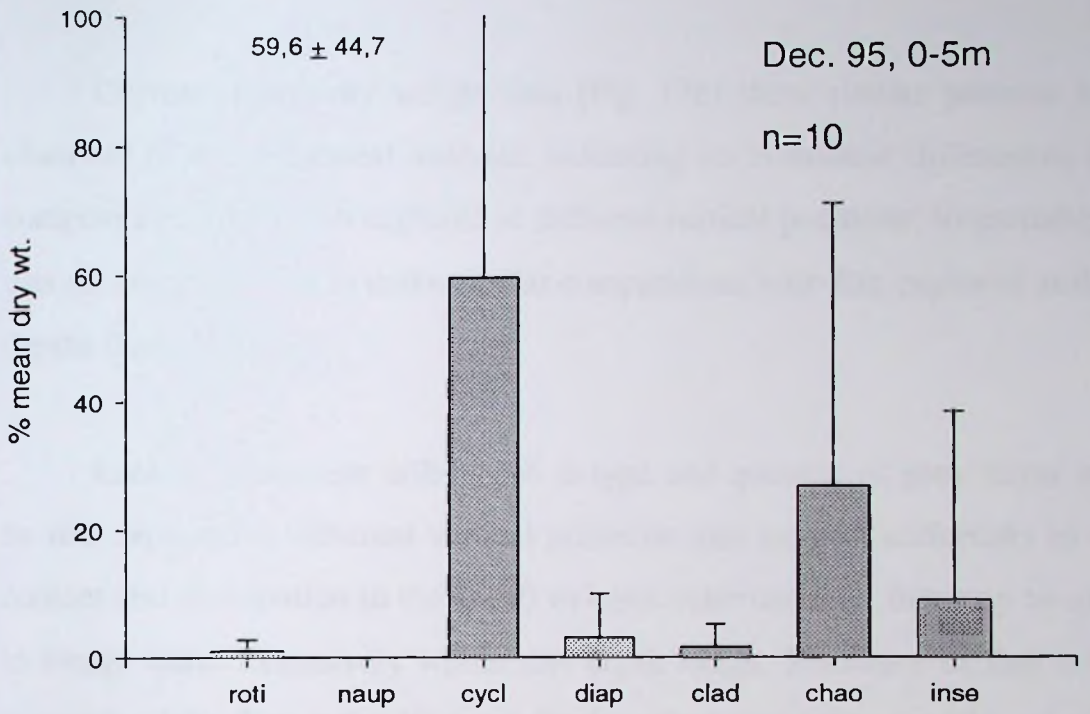


Figure 17b. Diet composition (% mean dry wt. ± sd) of *R. argentea* taken at different vertical postions during the night at NG station (October 1995 data). Names of prey organisms as in Fig.11.



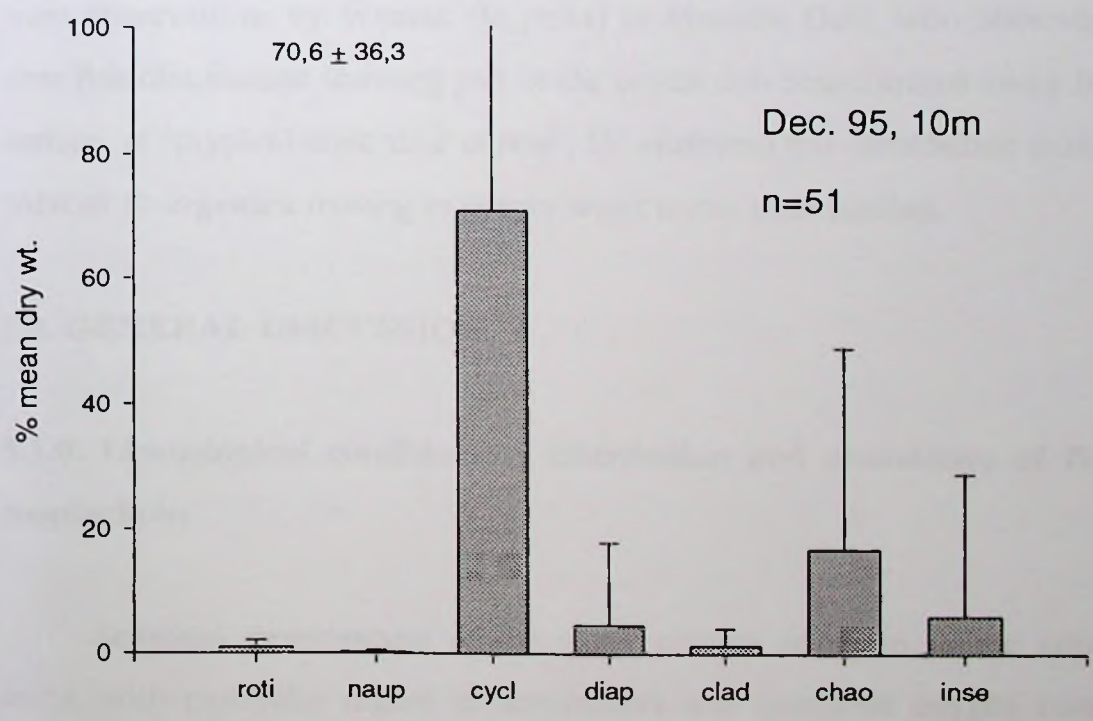


Figure 17b. continued (Dec. 1995 data).

night.

Corresponding dry weight data (Fig. 17b) show similar patterns to those observed in the numerical analysis, indicating no consistent differences in food composition among fish captured at different vertical positions. Regrettably, there was no adequate data to make similar comparisions with fish captured at different depths during the day.

Lack of consistent differences in type and quantity of prey items ingested by fish captured at different vertical positions may suggest uniformity in species content and distribution in the 0 - 10 m layer. Alternatively, fish may be assumed to forage quite extensively within this depth range. Recovery of fish with guts containing lake flies at the 10 metre depth renders support to the idea of extensive foraging behaviour, in that adult insects are presumed to have been caught at the water surface. Further credence to the suggestion of extensive foraging comes from observations by Wanink (in press) in Mwanza Gulf, who observed night time fish distribution showing part of the population concentrated away from the surface, at 'atypical night time depths'. He attributed this distribution pattern to a habit of *R. argentea* moving to deeper water layers after feeding.

5.0. GENERAL DISCUSSION

5.1.0. Limnological conditions vs distribution and abundance of fish and zooplankton

Seasonal development of the water column structure in the sub-littoral areas, with particular regard to temperature and dissolved oxygen conditions, indicate substantial oxygen depletion (up to < 1.0 mg O_2 l^{-1}) in the hypolimnetic

water mass, which accounts for 20-30% of the water column at the height of stratification in December (Figure 12b). Conditions of thermal stratification prevail from October through March (Figure 2a &b), not only in in the deep open waters of the lake (Hecky et al. 1994; Ochumba 1996), but also in the sub-littoral areas. These modern conditions contrast sharply with historical record showing deoxygenation infrequent throughout the year and occurring only near the bottom 60 metres (Talling 1966).

Assuming limited tolerance of most aquatic organisms to low oxygen conditions, severe oxygen-poor conditions in the hypolimnion will most likely lead to a general spatial displacement of bottom and/or near-bottom dwelling organisms to intermediate and surface water layers. Evidence of poor adaptation to low oxygen conditions amongst most demersal fishes in Lake Victoria is manifested in periodic fish kills, associated with upwelling of hypoxic water (Kitaka 1972; Ochumba 1990). Critical oxygen concentrations for *R. argentea* have been estimated at 2.5 mg O_2 l^{-1} (Wanink et al. in press). Clearly, hypolimnetic oxygen concentrations at NG station often fall below this critical level during the stratification period (Figure 2a&b). The observed higher densities of both zooplankton and *R. argentea* in the 5-10 metre water layer (Table 5; Figure 4) during months of thermal stratification is an indication of such seasonal displacement of organisms from their deep-water daytime positions. This observation concurs with the idea of Kaufman and Ochumba (1993) that *R. argentea* is abundant near the oxycline during periods of stratification. In the Mwanza Gulf, Goudswaard et al. (in ms) observed similar displacement of the Nile perch between December and May due to deoxygenation of the lower part of the water column. A potential alternative response would probably involve horizontal displacement of fish from the deeper waters to adjacent shallower (littoral) areas where the tendency to protracted thermal structuring can be

minimised by slight wind action. This possibility was not sufficiently examined during the present study due to limited fish catch data from the littoral MSE sampling station.

The implications of 'forced' seasonal shifts in the vertical distribution patterns of organisms include the possibility of spatial overlap between potential predator and prey organisms involving both fish and plankton. The ensuing trophic interaction can be viewed in terms of a general qualitative and quantitative improvement in the food environment for *R. argentea*, from which day-near-surface-dwelling juveniles (Wanink, in press; Wandera 1992; personal observations) can boost their somatic growth, while day-near-bottom-dwelling (Wanink 1988; Wandera 1992) adults may benefit from enhanced energy supply for gonadal development.

5.2.0. Zooplankton composition, community structure and seasonality

The zooplankton species composition of Lake Victoria represents an example of a tropical assemblage, with relatively few species among most groups and domination of the community by small-bodied species (Fernando 1980). The dominant cyclopoid copepods (Table 4) fall in a size range of 300-800 µm, compared to the rarer, larger diaptomids at 900-1400 µm (Figure 4). Compared to the historical community (1961), cyclopoids appear to have maintained their dominant position inspite of the profound ecological changes that have occurred in the lake food web structure (Ligtvoet et al. 1988). There are, however, indications of quantitative changes involving shifts in relative abundance of groups such as cladocerans and diaptomids (Mwebaza-Ndawula 1994). This view is supported by data from the historical zooplankton sample showing that these groups were much more abundant in the plankton as recently as the 1960s

(Figure 4). The zooplankton faunal list (Table 3) reveals a general similarity in species composition among modern (inshore and offsore) and historical collections and suggests relative stability of the zooplankton community inspite of long term changes in the trophic state of the lake (Ligtvoet et al. 1988).

Seasonal changes in relative abundance are also evident in the modern community, with cladocerans and some large-bodied cyclopoids (i.e. *Mesocyclops* spp.) becoming more abundant at certain times of the year, as was the case during July 1996 at NG station (Figure 4). Such seasonal variations in abundance may be linked to parallel changes in predation pressure by planktivorous fishes, and in availability of quality algal food resources for the different taxa.

Branstrator et al. (1996) reported finding of a large-sized, non-helmeted daphnid, *Daphnia lumholtzi* var. *monacha* in zooplankton samples from the deep offshore station BG, while the smaller form was more frequent in samples from the shallow inshore areas of the lake. The apparent size structuring of the zooplankton community along an inshore - offshore gradient bears relation to the corresponding gradients in planktivorous fish stock abundance as observed in the present study (Figure 10) and as reported in Lake Albert by Green (1967). A comparative examination of the zooplankton community at the inshore (NG) and offshore (BG) sites revealed no marked difference in species composition, other than an apparent higher species diversity and abundance of rotifers inshore. Higher relative abundance of diaptomid copepods offshore was also indicated (Table 5). The rotifer community in inshore areas is composed of all species listed in Table 3, while only a few brachionids and *Keratella* spp. were infrequently encountered in the offshore community.

These horizontal gradients in zoopolankton species composition and abundance are likely due to differential predation via size-dependent consumption by planktivorous fishes and, to some extent, by invertebrate predators including *Chaoborus* larvae. Invertebrate predators in general have been suggested to increase in abundance from inshore towards offshore waters (Lehman 1996). Higher fish stocks in littoral and sub-littoral areas (Kudhongania & Cordone 1974) coupled with the use of inshore habitats by most fishes as spawning and nursery grounds, may explain the implied higher levels of planktivory inshore and associated lower abundance of large-bodied diaptomid copepods. Notably, the general dearth of cladocerans in the modern zooplankton community in both inshore and offshore habitats (Table 5) can not, however, be fully explained on the basis of differential predation per se. This is because, between the 1960s and 1990s, the relative importance of the cladoceran component in the community has declined as a whole regardless of size and species. Such whole-sale decline of a multi-species and multi-size group, such as Cladocera suggests possible involvement of an environmentally-based factor such as change in quality and quantity of suitable food resources, probably in combination with changing levels of predation pressure as the fish fauna has undergone fundamental alterations (Ogutu-Ohwayo 1990) over the same period of time. Besides exhibiting relatively poor escape response when attacked by predators (Lazzaro 1987), cladocerans are known to be largely filter-feeders and are therefore likely to be more susceptible to changes in food particle (phytoplankton) composition than the raptorial feeders which make up the bulk of the cyclopoid species group. The phytoplankton community has changed from domination by relatively small-sized diatoms such as *Aulocosira* (*Melosira*) to the present community dominated by large-celled, cyanobacteria such as *Cylindrospermopsis* and *Planktolyngbya* (Hecky 1993; Kling et al 1997).

5.3.0. Fish size structure, distribution and abundance patterns

Bimodality in the length frequency distribution of *R. argentea* (Figures 6 &7) is a common feature of the fish population around inshore waters of the lake. The two modal groups represent juvenile (< 35 mm sl.) and maturing-to-adult (> 35 mm sl.) components of the population. Unimodal size structure occasionally observed at other times is possibly related to diurnal horizontal and/or seasonal age-specific movements of fish; an area which was not adequately addressed in the present study. Such age-specific diurnal and seasonal movements are common in fishes (Bohl 1980; Bauman & Kitchell 1974). Seasonal size-dependent mortality of fish resulting from the fishery and predation impacts from the Nile perch and bird predators (Wanink et al.1993; Goudswaard & Wanink 1993; Wanink 1996) may also contribute to this observation. Size frequency data from the deep offshore waters, indicating a unimodal population structure, skewed towards small-sized fish (> 30mm sl) are inadequate to draw any conclusions. Only two sampling trips, in December 1995 and October 1996 were undertaken to the deep offshore water station BG during the study. Witte and van Densen (1995) have reported increasing mean size of *R. argentea* with increasing distance from the shore up to 30 metres in the Mwanza Gulf area; but no size frequency data for fish in the deeper offshore region of the lake is available.

Due to the intermittent spread of the present size frequency data (Figures 6 & 7), modal progression of the broods representing the two reported peak annual breeding periods (Wandera 1992; Wanink 1988) could not be adequately traced with time. Fish growth studies based on modal progression to track year classes often become inconclusive due to possible obliteration of size class modes by effects of continuous, year-round breeding behaviour which characterise most tropical fish species.

An attempt to determine fish growth on the basis of a temperature model (Mooij et al. 1992) was hampered by insufficient data from few, widely spaced sampling dates. However, variations in two factors considered to be of paramount importance in the growth processes i.e. water temperature and food supply, were examined. Mean water column temperature at NG station increased from 25.6°C in December 1995 to 26.7°C by March 1996. According to available literature, (Wandera 1992; Wanink 1988) the period December-January represents one of the spawning peaks in the bi-annual peak breeding regime of *R. argentea* in Lake Victoria; the second one occurring between June and September. The two spawning peaks occur at the end of cool rainy seasons and the beginning of hot dry conditions in the region. In both cases the spawning peaks are preceeded by high phytobiomass, with a major peak of chlorophyll-a in October - December and a minor one in May (Mugidde 1993). High phytobiomass in turn enhances zooplankton production and therefore ensures ample food supply for larval *R. argentea* in subsequent months.

Based on these observations and on the assumption of a significant relation between fish growth and temperature, an increase of ca 1°C in mean water column temperature between December and March constitutes a positive factor favouring somatic growth and survival of the larval and juvenile fish. On the other hand, a mean temperature reduction of ca 2°C during the annual cool season, March (26.7°C) to July (24.5°C) is potentially likely to curtail fish growth rate at this time of the year. However, the cool season coincides with a significant build-up of zooplankton populations (Table 4; Branstrator et al. 1996; IDRC Technical Report 1993/94) culminating into the annual peak abundance during the turnover period. It is not certain if the hefty improvement in food supply may compensate for the cooler water temperature to sustain relatively high growth rates of juvenile fish. Rising mean column temperature from July (24.5°C) through September

(25.2°C) and October (25.8°C) is likely to favour growth of juvenile fish including the brood from the June-September breeding season, so long as there is no food limitation.

5.4.0. Planktivory by *R. argentea*

Prey composition of *R. argentea* shows an overwhelming dominance by cyclopoid copepods (numerically and gravimetrically) regardless of habitat, time and position in the water column, in fish above 10 mm sl (Figures 11-17). Major supplements include diaptomid copepods, chaoborid larvae and adult insects.The preponderance of cyclopoids in the diet is related to their dominant position in the zooplankton community throughout the year, compared to the larger crustacean prey which remain continuously at low levels of abundance (Mavuti & Litterick 1991; Branstrator et al. 1996; Mwebaza-Ndawula 1994). Sustained prominence of cyclopoids both in the plankton and diet of fish may result from high productivity under warm tropical conditions, where a prey taxon may be maintained at high concentrations despite heavy predation. This hypothesis, however, requires verification through studies in the biology of the various cyclopoid species including aspects of their reproductive potentials and life history strategies vis-a-vis heavy predation by *R. argentea* and other crustacean predators.

From the analysis of both historic zooplankton and fish samples (Figures 4 & 5 and 11a & b), there are clear indications that diaptomids and cladocerans historically comprised larger proportions in the zooplankton and diet of *R. argentea* than they do in the modern situation. Whether these groups have declined due to changes in food supply (qualitative and quantitative changes in the phytoplankton food) or to modified levels of predation pressure as the fish

community has undergone spectacular alterations over the years (Ogutu-Ohwayo 1990) is a question that remains to be investigated. An interplay of both factors has probably created certain interspecific interactions in which some taxa may have gained competitive advantage over others in the course of time. Potential effects of strong planktivory on prey communities have been widely shown to take the form of changed species composition (Hrbacek 1962; Brooks & Dodson 1965) via size selective predation. Although Branstrator et al. (1996) conclude that the relative composition of the various taxa has remained largely unchanged, there is evidence from the present study to suggest that certain cladoceran species such as *Bosmina longirostris* and others which were conspicuous in both zooplankton and fish diet about 30 years ago have now been reduced to nearly trace levels in the modern community.

Another common impact of planktivory is often manifested in its influence on the seasonal regime of zooplankton abundance. Seasonality in abundance both in fish (Figures 9 and 10) and zooplankton (Figure 4) is evident in Lake Victoria. Branstrator et al. (op. cit.) have suggested that planktivory together with seasonality in quality and quantity of the phytoplankton food are possible factors which may drive the observed seasonal fluctuations in zooplankton abundance. In the present study, highest fish abundance with respect to *R. argentea* and juvenile cichlid species, occurred in December 1995 at NG station (Figure 9); well after the annual zooplankton peak abundance during the turnover period. Lowest fish abundance on the other hand, was recorded in July 1996, coinciding with the highest zooplankton abundance (Table 4). Therefore, there appears to be a clear quantitative relationship between zooplankton and their fish predators, at least in the inshore parts of the lake.

5.5.0. The fisheries and sustainability of *R. argentea* in Lake Victoria

Discussion and evaluation of the sustainability of *R. argentea* in the current Lake Victoria ecosystem must take into account its distribution and abundance patterns along vertical and horizontal scales, in relation to those of its major food organisms (zooplankton) as well as those of its major predators such as the Nile perch. Wanink et al. (in press) have demonstrated horizontal differentiation in biomass distribution of the three major commercial fish species (the Nile tilapia *Oreochromis niloticus*), the Nile perch, *Lates niloticus* and *R. argentea*) in the Mwanza Gulf. Nile tilapia biomass is concentrated in the littoral zone (0-6 metres), that of *R. argentea* in the sub-littoral (6-20 metres) and the Nile perch, further out in deeper waters (> 20 metres). These patterns can be extrapolated to the rest of the lake, as reports from the northern portion (Kenya and Uganda waters) corroborate the horizontal trends in biomass distribution observed in the southern part. The apparent spatial segregation of the fish species in effect affords separation of potential predator and prey species, since both the Nile tilapia and *R. argentea* form part of the diet of the Nile perch (Ogutu-Ohwayo 1985; Ogari 1985). The horizontal separation has a stabilizing effect on the respective fish populations and the food web structure in general through mitigation of predation pressure on prey stocks.

On the vertical scale, however, the seasonal development of hypoxic conditions in the lower part of the water column in sub-littoral and pelagic zones has the undesirable effect of displacing both the predaceous, demersal Nile perch and the day-near-bottom-dwelling *R. argentea* into intermediate and surface water layers. The likelihood of spatial displacement and subsequent overlap in vertical distribution patterns of the two fish species is strengthened by their comparable sensitivity to low oxygen conditions (i. e. 2.5 mg O_2 l^{-1}) as estimated

by Wanink et al. (in press). In absence of the threat of low oxygen conditions, the major food resource of juvenile and sub-adult *Lates niloticus* is the day-bottom-dwelling atyid prawn, *Caridina nilotica*. The latter is known to thrive even in poorly oxygenated regions of the lake (Lehman 1996). Thus, populations of *Lates niloticus* diplaced from their demersal habitats and food resources thereof, will be inclined to seasonally inflict greater predation pressure on *R. argentea* in the mid-waters; a development which can upset the existing predator-prey balance. It is not known to what extent stocks of *R. argentea* can withstand increased, triple exploitation i.e. from the displaced Nile perch, the artisanal fishery and from the avian predators as reported by Goudswaard and Wanink (1993); Wanink et al. (1993) and Wanink (1996). It has been urgued that predation dynamics targeting mainly the adult population of *R. argentea* can maintain a certain measure of equilibrium between the predator and prey populations by ensuring greater survivorship and recruitment of most juvenile prey fish into the reproductive population (Wanink et al. in press). However, unlimited increase in adult fish mortality has the potential danger of undercutting the reproductive capacity of prey species ultimately to unviable population levels.

Another aspect of direct relevance to the sustainability of *R. argentea* relates to food supply. Cyclopoid copepod populations which constitute the major food source for juvenile and adult fish (Figures 11 - 17) appear to exhibit considerable resilience by sustaining high relative abundance inspite of heavy predation by *R, argentea* and other pelagic zooplanktivores in the lake. The strength of cyclopoids in the plankton community is derived from, among other factors, ample algal food supply. Lehman and Branstrator (1993) demonstrated that zooplankton grazing has no significant effect on the phytoplankton abundance. In this regard, there appears to be no immediate threat of food limitation to both zooplankton and *R. argentea* populations in the lake. The

demonstrated foraging flexibility and the ability to opportunistically supplement the diet with sporadically abundant, and more beneficial prey such as lake flies and atyid prawns (Wanink, in press; this study) are both ecological attributes favourable to the sustatinability of *R. argentea* in the lake.

Since the early 1990s, a new factor has been added to the ecological dynamics of the Lake Victoria ecosystem in form of an intrusion by an alien water weed, *Eichhornia craccipes* (Mart) Solms (common name: water hyacinth) which is believed to have entered the lake in the Kagera region (Njuguna 1991). The most favoured areas for settlement and proliferation of the weed are known to include shallow bays and gulfs (Twongo et al. 1992; personal observation). These areas coincide with two key habitats, the littoral and sub-littoral zones, where the Nile tilapia and *R. argentea* stocks abound (Wanink et al. in press; personal observation) and where their respective fisheries are based. Extensive dense mats of the weed are a common sight for prolonged periods and are obstructive to both fishing activities and water-borne transportation. Preliminary field observations have indicated very low dissolved oxygen levels and pH, high Secchi transparencies and a drastic reduction of biodiversity and biomass of most forms of aquatic fauna in the water mass beneath resident mats of the water hyacinth (Twongo et al.1992). The impact of the weed on the quality of the water environment and the associated fisheries appear to aggravate a situation already experiencing negative effects from eutrophication (Hecky 1993). This, together with other factors, present a threat to the long-term viability and sustainability of the fisheries in question (Willoughby.et al. 1993).

There are reports of rampant use small-meshed (5 mm stretched mesh) lampara nets in the Ugandan waters (Wandera 1992) and probably elsewhere around the lake. These fishing gears have been shown to harvest a substantial

portion of juvenile (< 30 mm sl) *R. argentea* (Wandera 1991;Ogutu-Ohwayo et al. 1989). Sustained and extensive use of these nets is bound to undercut the recruitment potential of *R. argentea* as well as that of other species such as the cichlids and the Nile perch which utilise the shallow inshore areas of the lake as breeding and nursery areas.

6.0. REFERENCES

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ABSTRACT

The pelagic cyprinid, *Rastrineobola argentea* (Pellegrin) has in the last decade become ecologically and economically important in Lake Victoria. Selectivity of its three major prey organisms (cyclopoid and diaptomid copepods and cladocerans) was investigated in fish and zooplankton samples collected from NG station (Napoleon Gulf) in the nothern part of the lake during December 1995. Fish were sampled with a small mid-water trawl net of 5 mm stretch mesh size; from the water surface, mid-waters and near-bottom vertical positions in the water column and immediately preserved in 10% formalin. Concomitant zooplankton samples were collected from similar water column positions with a Schindler trap, concentrated with a 60 µm Nitex mesh and preserved in sugar-4% formalin. Nearly equal proportions of cyclopoids were found in the fish guts and the environment; while diaptomids were higher and cladocerans were lower in the environment. Mean body length of cyclopoids was higher, while that of diaptomids was lower in the fish diet. Mean prey size of copepods in fish guts increased with increasing fish size but was generally lower than the corresponding mean size in the environment. The highly abundant cyclopoids were positively selected to varying extents by fish in all size categories, suggesting general preference for this prey type by *R. argentea*. In contrast, the rarer diaptomids and cladocerans were negatively selected by all fish size categories, more so by the smallest fish (< 20 mm sl.). Copepods in the size range of 500 to 700 µm were positively selected in all fish size categories, while the smallest (< 400 µm) and largest (> 1000 µm) copepods were negatively selected in all fish sizes. This suggested size selective predation in favour of medium-sized copepods. Strong preference

for the more abundant cyclopoids and negative selection for the rarer and more evasive diaptomids indicated that relative abundance and prey behaviour could have been decisive factors in prey selection. Negative selection for the much less evasive cladocerans can be ascribed to their very low abundance in the environment.

PREY SELECTION BY *RASTRINEOBOLA ARGENTEA* IN LAKE VICTORIA

1. INTRODUCTION

Fishery ecology investigations on Lake Victoria and other African inland water bodies have, among other studies, addressed the food and feeding habits of commercially important fish species (Corbet 1961; Hamblyn 1966; Okedi 1971; Hughes 1986; de Iongh et al. 1983; Moghraby & Rahman 1984; Ogutu-Ohwayo 1984; Ogari 1985; Hoogenboezem 1985; Hickley & Bailey 1987; Wanink 1988 etc). Food supply, in the broad sence of available food quality and quantity, is considered to be a vital environmental variable which, in early life history of fishes relates directly to growth and survival of larval and juvenile fish and recruitment into fishable stocks. In adult fish, food supply is linked to reproductive potential and ultimately to fishery yield. Field data and related information on the food of fishes is, therefore, of important applied value, particularly with regard to interpretation of field data on fish production.

In Uganda the cyprinid species, *Rastrineobola argentea* occurs in Lakes Victoria, Kyoga and Nabugabo (Greenwood 1966,) where it supports impotrant pelagic fisheries. In Lake Victoria, *R. argentea* has assumed greater importance during the 1980s when it increased threefold in abundance following the virtual extinction of formerly dominant haplochromine cichlid species (Wanink 1991; Witte et al. 1992). In an apparent response to the species ecological success, and parallel increasing

demand for fish food in the East African region, large commercial fishing villages sprang up mostly around shallow bays of the lake in all three riparian states: Uganda, Kenya and Tanzania. In view of the current intensive lakewide exploitation of the species, it is important to obtain a clear insight into aspects of its biology and ecology as a first step towards formulation of scientifically sound managerial strategies to ensure sustainable development and utilisation of the fishery. To this end, research investigations have been undertaken to cover areas such as habitats, population dynamics, food, growth and other related fishery aspects (Hoogenboezem 1985; Wanink 1988; Wandera 1991; 1992; Wandera & Wanink 1995; Wanink 1996).

With respect to the food and feeding habits, *R. argentea* has been shown to be largely planktivorous (Graham 1929; Corbet 1961; Greenwood 1966; Hoogenboezem 1985; Wanink 1988;Wandera 1991; 1992; Mwebaza-Ndawula: this study), but aspects of prey selectivity, the potential effects which planktivory may have on the zooplankton community and probable responses of the latter to predation have remained relatively unassessed and consequently poorly understood. It is necessary to understand prey selectivity patterns of the species in order to interprete trends in the community structure and population dynamics of the zooplankton food resource and to assess the possible implications such trends may have on the *R. argentea* fishery production.

In this study, the primary objective was to examine aspects of prey selection by *R.argentea* under natural field conditions. Specifically, numerical proportions and size distributions of potentially available prey in

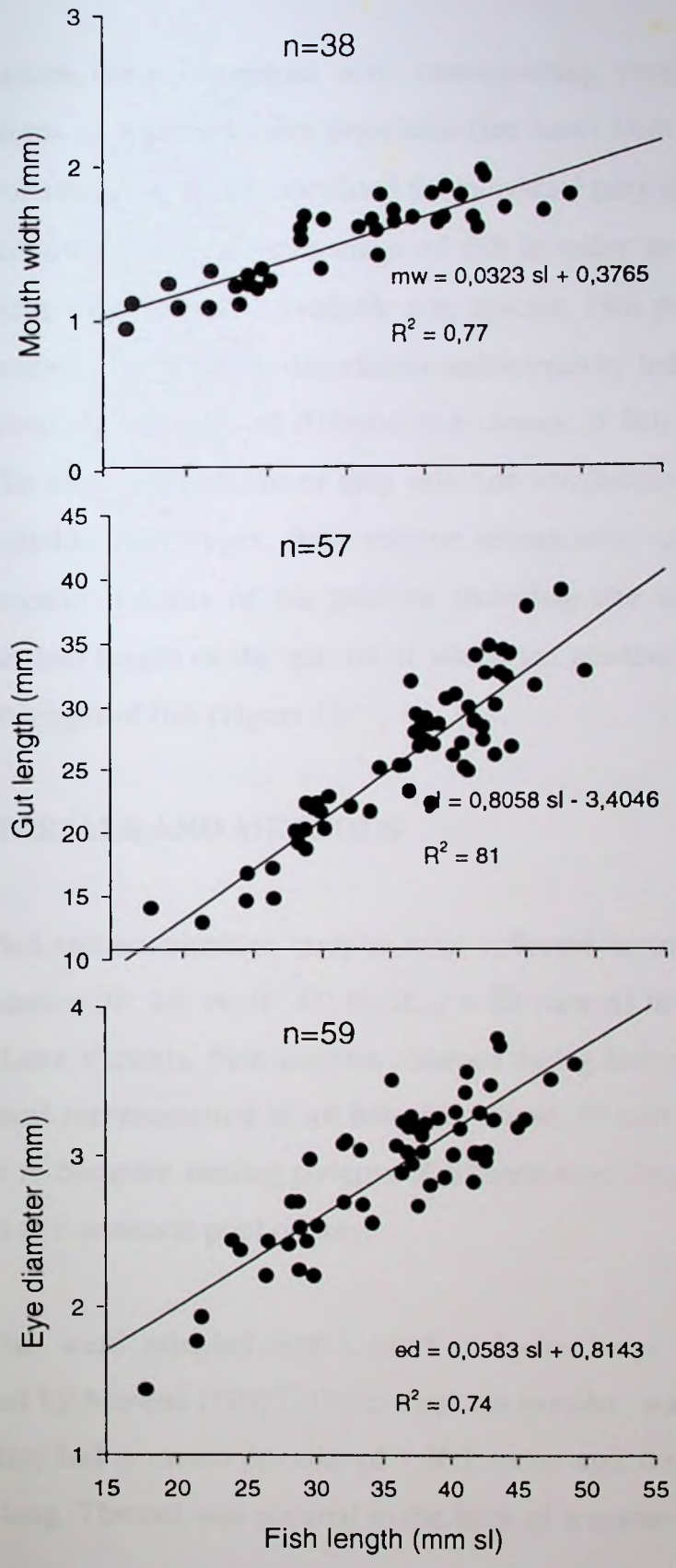

Figure 1. Relationship between standard length of *R. argentea* and mouth width (mw), gut length (gl) and eye diameter (ed).

the plankton were compared with corresponding proportions and size distributions of 'restored' prey organisms (see later) from fish gut contents. Indices of selectivity were calculated for individual prey species/groups and compared over the entire size range of fish in order to assess the fish's preferences with respect to available prey species. Fish and prey organisms were grouped into arbitrary size classes and selectivity indices calculated so as to reveal the affinities of different size classes of fish for different prey sizes. The observed patterns of prey selection are discussed in conjunction with available prey types, their relative abundances, size structure, and morphometric features of the predator including size of the mouth, eye diameter, and length of the gut, all of which are positively correlated with standard length of fish (Figure 1).

2. MATERIALS AND METHODS

Fish and zooplankton samples were collected during December 1995 at NG station (0° 24' N; 0° 33' E , Z_{max} = 22 metres) in the north western part of Lake Victoria. Fish samples obtained during December comprised a well mixed representation of all fish sizes above 10 mm sl. which made it possible to compare feeding patterns of different size classes of *R. argentea* exposed to a common pool of prey.

Fish were sampled with a small midwater trawl net of the design described by Matena (1995). The conical net sampler, was of 5 mm stretch mesh size, had a mouth opening of 1 X 1 metre and was approximately 6 metres long. The net was secured to the back of a canoe and towed though

the water, at a desired depth, with a 25 HP outboard motor. Fish samples were preserved in 10% formalin soon after capture.

In the laboratory, biometric data including standard length (mm sl: measured from the snout to the base of the hypeural bones), mouth width and eye diameter were measured to the nearest 0.01 millimetre with an electronic digital caliper. Each fish was dissected, its entire length removed and laid out on a petri dish, and its length measured. The gut was opened up by longitudinal incision with a pair of scisors and a preparation of the entire contents mounted on to a glass slide (plus coverslip) in gelvatol gel for subsequent microscopic examination. Identification and enumeration of planktonic prey items were carried out under a stereo compound microscope (x 40). Where gut contents were in an advanced state of digestion, resistant parts of the body were identified (i.e. furcal rami for copepods and mandibular structure for cladocerans) and were used as enumeration units in subsequent data analysis. For copepods which together constitute the principal dietary items of *R. argentea* (Mwebaza-Ndawula: this study), randomly selected furcal rami were measured (using a calibrated Camera Lucida fitted to a compound microscope), for subsequent use in furcal rami - total length regressions to 'restore' the original body lengths from digested individuals (see below).

Zooplankton were sampled with a 5-litre Schindler trap from the same water column depths as the fish samples in an attempt to accurately represent the prey spectrum encountered by the fish. Samples were concentrated by filtration through a 60 µm Nitex mesh net and preserved in sugar-4% formalin solution.

In the laboratory, each zooplankton sample was diluted with tap water to a convenient volume (depending on the concentration of the sample) in a glass beaker and stained overnight with Bengal Rosa dye prior to examination and counting. A series of 10 ml subsamples were taken with a calibrated bulb pipette, immediately after manual agitation of the sample, each placed into a counting chamber and left to settle for at least thirty minutes before commencement of counting under an inverted microscope (x100). Organisms were assigned to broad taxonomic groups i.e. cyclopoids diaptomids (copepod instars C1 to C6), and Cladocera. Body lengths, (excluding antennae and posterior terminal setae and spines) of randomly selected individuals (ca 50 individuals) were measured with the aid of a calibrated Camera Lucida fitted to a compound microscope. For cyclopoid and diaptomid copepods, furcal rami lengths were in addition measured and regression relationships between total length and furcal rami established (Figure 2). These regressions were used to calculate 'restored' body lengths of copepod prey items from fish guts.

Indices of prey selectivity by *R. argentea* for the various food items and sizes were calculated on the basis of Jacobs' (1974) modification of the Forage Ratio, (FR) (Edmondson & Winberg 1971). and Ivlev's Electivity Index (Ivlev 1961). Jacobs modified index is considerered superior as a means of quantifying prey selection mainly because of the advantage of being independent of the relative abundance of the prey types available to the predator and besides, it relates directly to differential mortality rates of different prey organisms in the environment (Jacobs op. cit.).

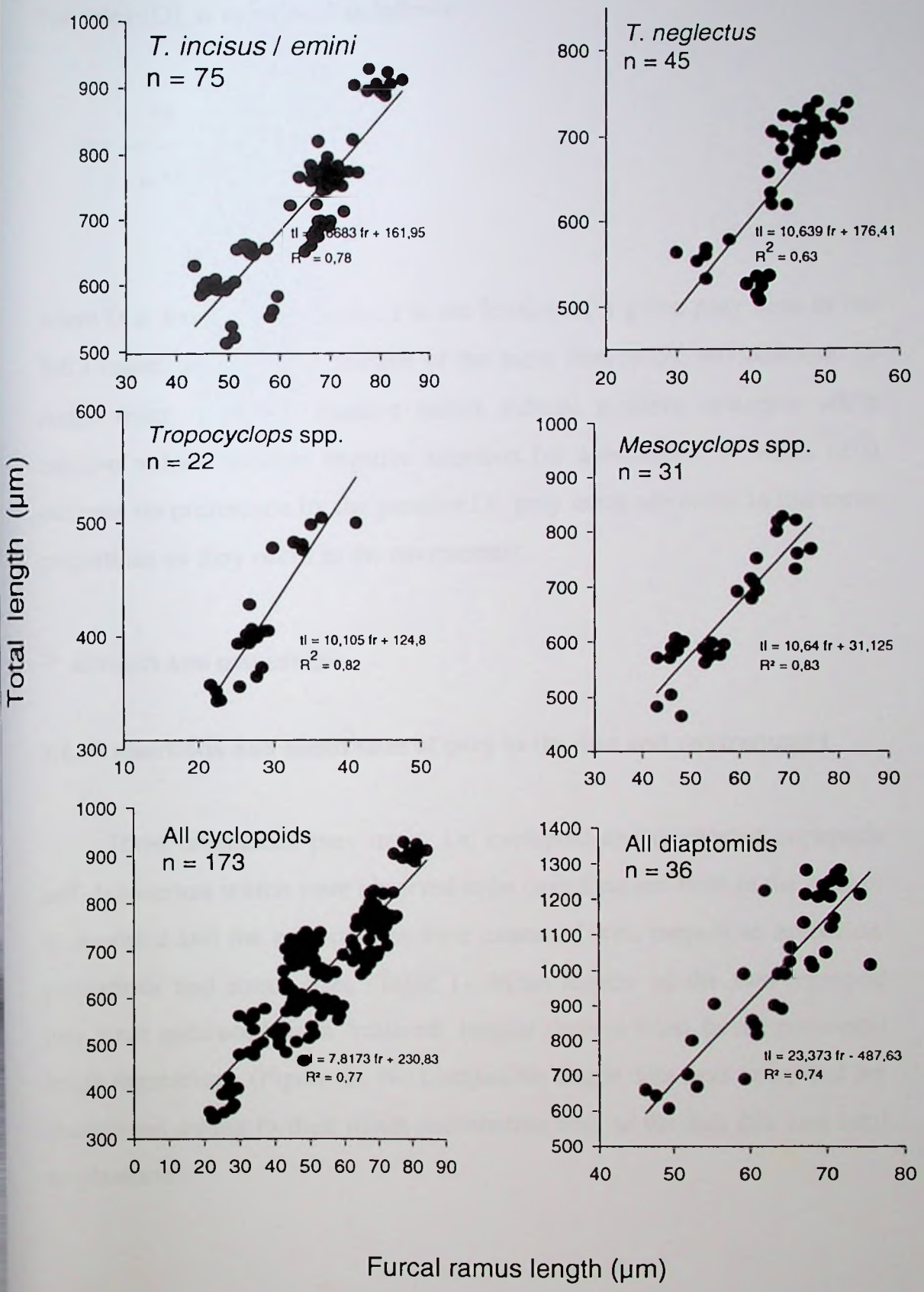

Figure 2. Furcal ramus - total length regressions for cyclopoid and diaptomid copepods.

The index (D), is expressed as follows:

$$D = \frac{r-p}{r+5-2rp}$$

where D is the electivity index, r is the fraction of a given prey item in the fish's ration, and p is the fraction of the same item in the environment. D ranges from -1 to +1. Positive values indicate positive selection while negative values indicate negative selection (or avoidance). A value of 0 indicates no preference by the predator i.e. prey items are eaten in the same proportions as they occur in the environment.

3. RESULTS AND DISCUSSION

3.1. Proportions and mean sizes of prey in the diet and environment

Three crustacean prey items, i.e. cyclopoid and diaptomid copepods and cladocerans which were observed to be most frequent both in the guts of *R. argentea* and the environment were examined with respect to numerical proportions and mean sizes (Table 1). Mean lengths of the two copepod prey were estimated from 'restored' lengths derived from furcal rami-total length regressions (Figure 2). No comparable length data was compiled for cladocerans owing to their minor contribution both to the fish diet and total zooplankton.

Table 1. Relative proportions and mean sizes (mean + SE) of major prey groups in the diet of *R. argentea* and the environment

	Numerical proportion in environment	Numerical proportion in the diet	Mean length (µm) in environment	Mean length (µm) in the diet
Prey items:				
Cyclopoids	0.9582	0.9741	508.1 ± 45.5	554.4 ± 9.7
Diaptomids	0.0387	0.0176	1001.3 ± 118.6	875.8 ± 160.8
Cladocerans	0.0031	0.0083	500.4 ± 83.8	

Comparision of respective mean proportions of the three prey items indicated differences in the diet and the environment. Proportions of cyclopoid copepods and cladocerans in the fish guts were significantly higher than those in the environment (Mann-Whitney U-test; $P < 0.05$). On the other hand, the proportions of diaptomid copepods were significantly lower in the diet compared to the environment (Mann-Whitney U-test; $P < 0.05$). Mean length of ingested cyclopoids was significantly higher than that in the environment (Student's t-test; $P < 0.05$). In contrast, *R. argentea* ingested a significantly smaller mean size of diaptomids than the corresponding mean size in the environment (Student's t-test; $P < 0.05$).

The observed differences in the proportions and mean sizes of ingested prey relative to those in the environment suggest that during its feeding activities, *R. argentea* employs selective foraging behaviour in form of preference with respect to prey types as well as prey sizes.

3.2. Prey size frequency distribution in the diet and the environment

Copepod size distribution in guts of fish ranged between 400 and 1300 µm (Figure 3). Modal size of ingested prey was at 500 µm in fish ranging between 10 and 50 mm sl., but a slight shift to 600-700 µm, in the largest fish above 50 mm sl. was apparent. Fish below 50 mm sl. ingested decreasing proportions of successively larger prey beyond the common modal prey size class of 500 µm. The proportions of large copepod prey ($\geq$ 600 µm) ingested by fish in different size categories were not significantly different across fish size categories (ANOVA; $P > 0.05$). A significant difference, however, existed in the proportions of such large prey

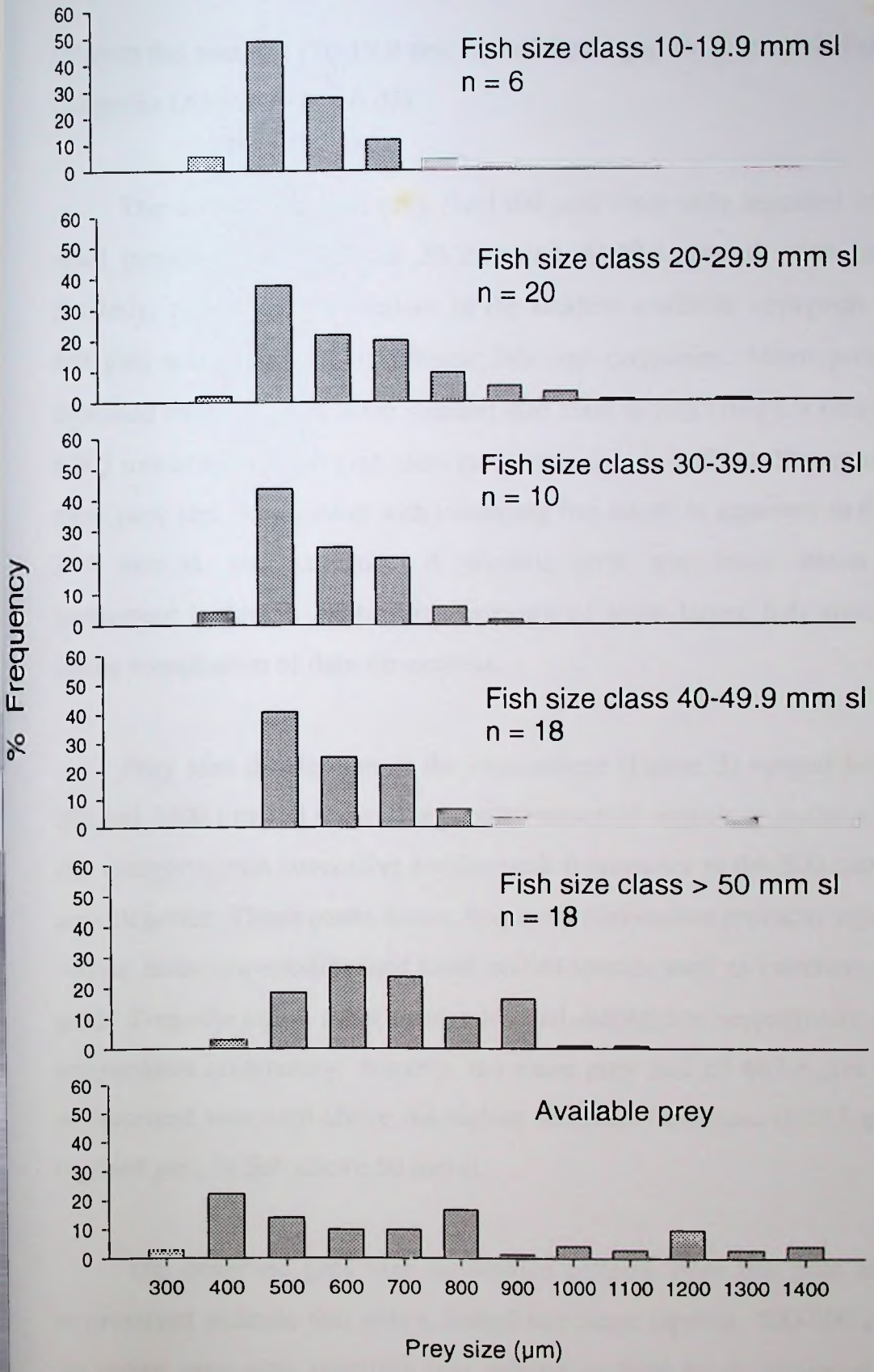

Figure 3. Size frequency distributions of copepod prey in guts of *R. argentea* and available prey.

between the smallest (10-19.9 mm sl) and the largest (> 50 mm sl) fish size categories (ANOVA; $P < 0.05$).

The largest copepod prey (i.e.1400 µm) were only ingested in very small proportions by fish in 20-29.9 and 40-49.9 mm sl. size classes. Similarly, rather low proportions of the smallest available copepods (300-400 µm) were ingested in different fish size categories. Mean prey size increased from 517 µm in the smallest size class of fish (10-19.9 mm sl.) to 629.3 µm in the largest size class (> 50 mm sl.). A baffling discrepancy in mean prey size progression with increasing fish length is apparent in the 20-29.9 mm sl. size category. A possible error may have arisen from inadvertent inclusion in this size category of some larger fish specimens during compilation of data for analysis.

Prey size distribution in the environment (Figure 3) ranged between 300 and 1400 µm and showed highest frequency of organisms in the 400 µm size category, with successive smaller peak frequencies in the 800 and 1200 µm categories. These peaks in size frequency distribution probably represent various instar copepodids (and small-bodied species such as members of the genus *Tropocyclops*), adult cyclopoids and diaptomids respectively in the zooplankton community. Notably, the mean prey size of 667.6 µm in the environment was well above the highest recorded mean size (629.3 µm) of ingested prey in fish above 50 mm sl.

The observed prey size distribution patterns from fish guts and the environment indicate that only a limited size range (approx. 500-900 µm) of the entire prey size spectrum was utilised as food by *R. argentea*. Prey

organisms from both extreme ends on the size scale, appear to have been underutilised as forage items. It is striking that the most frequent prey sizes in the environment were not necessarily the ones most ingested by the fish.

3.3. Selectivity of different prey types

A comparision of estimates of Jacobs mean Electivity Indices (D) pertaining to each of the three major crustacean prey (cyclopoids, diaptomids and cladocerans) showed consistent positive selection for cyclopoid copepods and negative selection for both diaptomids copepods and cladocerans across the entire size range of fish (Figure 4). Among cyclopoids, minimum and maximum mean electivities, +0.73 and +0.19 were obtained obtained in 30-39.9 mm sl. and >50 mm sl. fish size categories respectively. Marked variability in selectivity indices for cyclopoids was observed across the size range of fish. However, a general decreasing trend of selectivity with increasing fish size was apparent, such that the largest fishes (> 50mm sl.) tended to ingest cyclopoids more or less randomly as implied by the very low positive index (D = +0.19).

Diaptomid copepods were strongly negatively selected among small immature and maturing fishes (10-40 mm sl.). However, the level of negative selection decreased considerably in large mature fishes above 40 mm sl. such that, the biggest fishes (> 50 mm sl.) appeared to ingest diaptomids almost randomly (D = -0.19). Similar to cyclopoid copepods, strong variability in the selectivity data was evident across fish size classes. The selectivity for cladocerans relative to increasing fish size followed a comparable pattern to that of diaptomids, with the smallest fishes (10 -

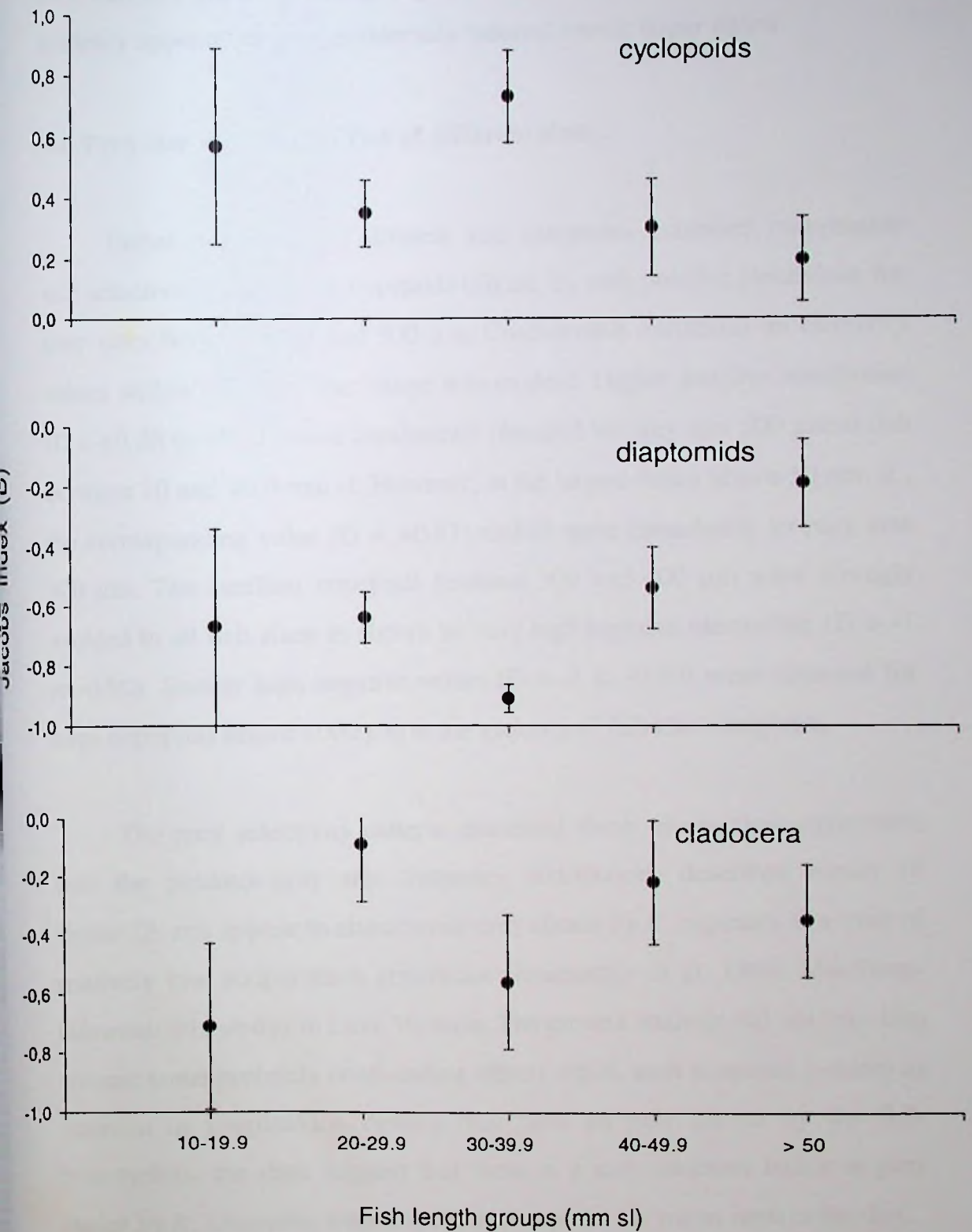

Figure 4. Jacobs Index of selection (mean + SE) for different prey species in relation to fish length.

19.9 mm sl.) showing strong negative selection (D = - 0.71), while this tendency appeared to be considerably reduced among larger fishes.

3.4. Prey size selection by fish of different sizes

Fishes belonging to different size categories exhibited comparable size selectivity patterns for copepods (Figure 5), with positive electivities for prey sizes between 500 and 900 µm. Considerable variability in electivity values within this prey size range was evident. Higher positive electivities (D = +0.58 to +0.71) were consistently obtained for prey size 500 µm in fish between 10 and 49.9 mm sl. However, in the largest fishes above 50 mm sl., the corresponding value (D = +0.87) shifted quite remarkably to prey size 900 µm. The smallest copepods between 300 and 400 µm were strongly avoided in all fish sizes as shown by very high negative electivities (D = -1 to -0.80). Similar high negative values (D = -1 to -0.60) were obtained for large copepods above 1000 µm in the majority of fish size categories.

The prey selectivity patterns described above are in close agreement with the predator-prey size frequency distributions described earlier in Figure 2A and appear to characterise prey choice by *R. argentea* at a time of relatively low zooplankton abundance (Branstrator et al. 1996; Mwebaza-Ndawula: this study) in Lake Victoria. The present analysis did not take into account some probably confounding effects which such temporal patterns as variation in zooplankton density may have on prey choice by the fish. Nonetheless, the data suggest that there is a size selection factor in prey choice by *R. argentea*, with respect to copepods, the major item in the diet.

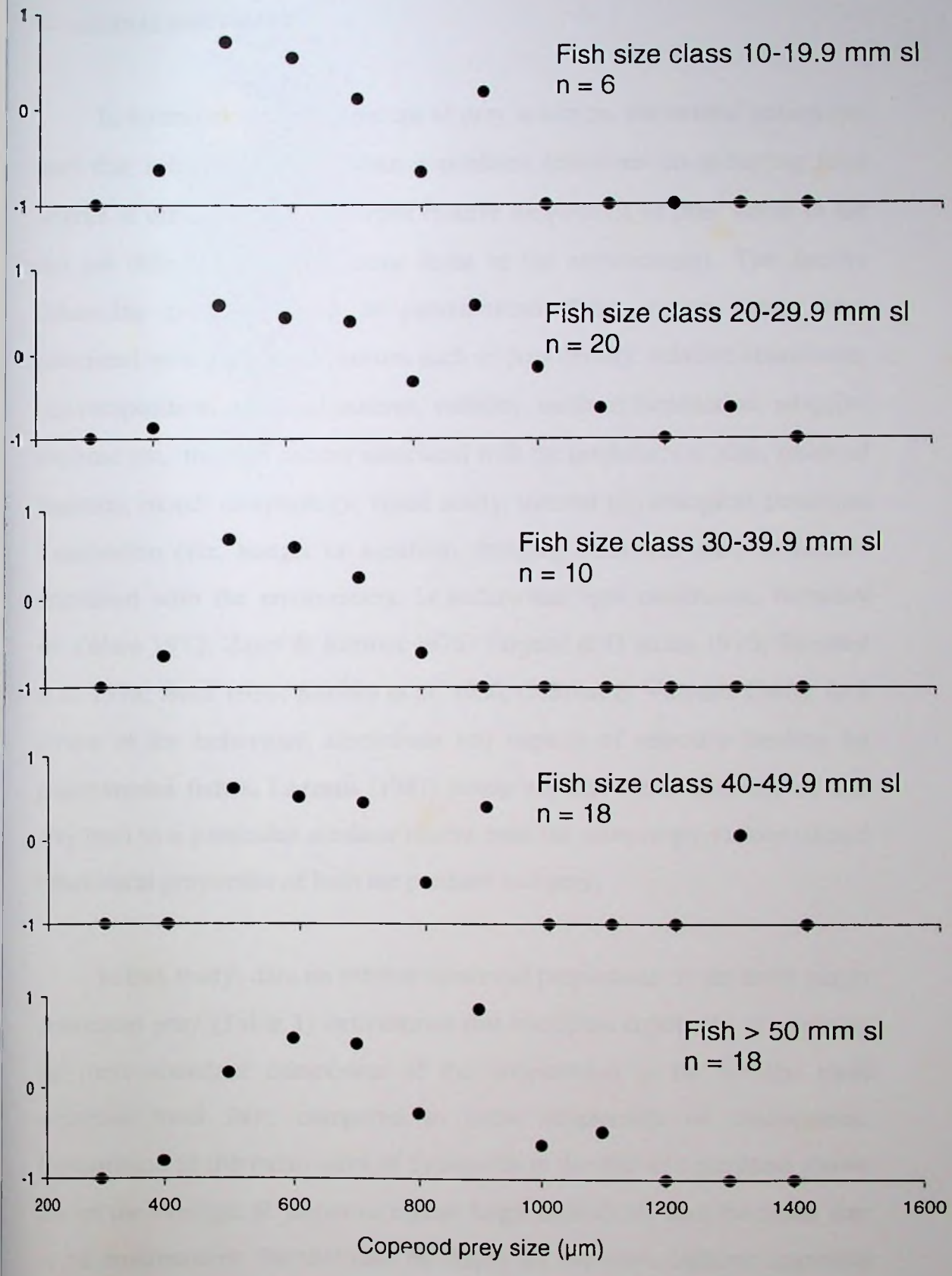

Figure 5. Selectivity patterns for different copepod sizes in different size groups of fish.

4. GENERAL DISCUSSION

In formulation of the concept of prey selection, the central notion has been that selection occurs when a predator consumes co-occurring food sources at different rates (i.e.when relative frequencies of prey items in the diet are different from the same items in the environment). The factors influencing prey selection in planktivorous fishes range from those associated with the prey organisms such as prey density, relative abundance, size composition, dispersal patterns, visibility, mode of locomotion, adaptive response etc,. through factors associated with the predator: i.e. size, mode of ingestion, mouth morphology, visual acuity, internal physiological condition / motivation (viz. hunger or satiation), foraging behaviour etc., to factors associated with the environment: i.e.underwater light conditions, turbidity etc. (Ware 1972; Zaret & Kerfoot 1975; Vinyard & O'Brien 1976; Drenner et al. 1978; Bohl 1980; Kerfoot et al. 1980, O'Brien & Vinyard 1980). In a review of the behaviour, mecanisms and impacts of selective feeding by planktivorous fishes, Lazzaro (1987) points out that the availability of one prey item to a particular predator results from the relative physiological and behavioural properties of both the predator and prey.

In this study, data on relative numerical proportions of the three major crustacean prey (Table 1) demonstrate that cyclopoid copepods, comprising the most abundant component of the zooplankton is by far the most important food item compared to either diaptomids or cladocerans. Comparision of the mean sizes of cyclopoids in the diet and plankton shows that on the average, *R. argentea* ingests larger individuals than the mean size in the environment. Parallel data on diaptomid copepods indicate ingestion

of smaller sizes than the mean size in the environment and generally, limited utilisation of these prey items in the diet despite their much larger mean body size and by implication, higher energy content. The same is true for cladoceran prey although their mean proportion in diet was higher compared to that in the environment.

These observations suggest that abundance of different food organisms in the environment is one of the key factors governing the choice of prey by *R. argentea*. Similar observations have been made elsewhere with respect to planktivorous fishes (Visser 1982; Rajasilta & Vuorinen 1983). Visser (1982) noted that concentration of the predator on the more abundant prey has a stabilizing effect on the zooplankton through density-dependent mortality. On the basis of the present data, and the assumption that *R.argentea* is currently the major zooplankivore in the lake, such planktivore-induced stability may apply to the Lake Victoria zooplankton community

In many instances, a predator changes its diet when prey density in the environment changes. In this regard, Murdoch (1969) suggested that the composition of a predator feeding on two (or more) prey types depends on their relative densties. However, there exists also cases where absolute density of the preferred prey has been found to be the main determinant of diet composition (Pyke et al. 1977; Visser 1982). Rajasilta and Vuorinen (1983) reported the consumption of large calanoid prey when their absolute abundance was high, but fish switched to small-bodied cladocerans at low calanoid abundance. Owing to the limitation of the present data to field observations, it is not clear which of the two factors: absolute or relative

abundance of prey is the more decisive factor in prey choice by *R. argentea*. What has emerged clearly elsewhere in this study, is the reduction in the relative contribution of cyclopoids to the diet on a diurnal basis associated with corresponding changes in availability of some alternative prey groups (i.e. adult insects, chaoborid larvae at night) in the environment.

Prey size frequency data computed from 'restored' copepod lengths (Figure 3) reveals that prey in the size range 500-900 µm represent the most vulnerable segment of the copepod community. This portion contains the most abundant, medium-sized zooplankters in the environment (Mwebaza-Ndawula: this study). From comparision of data by Ivlev (1955), Werner (1974), and Zaret (1980), Milkheev (1984) drew the conclusion that the range of prey size ingested depends, among other things, on the size of the mouth as well as the concentration and ratios of different size groups of prey in the environment. Mouth size is known to set the upper limit to the size of ingestable prey (Ivlev 1955; Wong & Ward 1972; Werner & Hall 1974). In the present study, the occurrence of large prey up to 1000 µm length over a wide range of fish sizes suggests that mouth dimentions may not hamper ingestion of prey of such size magnitude in fish above 10 mm sl. Increasing mean prey size with fish size (Figure 3) implies an increasing capacity of fish to handle larger prey as they grow bigger. Such capacity is supported by increasing mouth width (hence gape), eye diameter and gut length relative to fish size (Figure 1). In conjunction with the Optimal Foraging Theory (OFT) Li Kao et al. (1985) contended that enhanced visual resolution in older fish should lead to increased specialisation on larger prey. Additionally, increasing gut length relative to body length should result in greater

assimilation efficiencies which confer further advantage to bigger fish to utilise larger prey.

Visually feeding fish show a tendency to consume zooplankton that are on the average larger than the mean size present in the environment (Ivlev 1961; O'Brien 1979; Zaret 1980; Li et al. 1985). This does not appear to be the case with respect to the combined mean length data for cyclopoid and diaptomid prey shown in Figure 3. Large copepods $\geq$ 1000 µm (mostly diaptomids), although potentially available in the environment, (Figure 3) were hardly ingested by *R. argentea* of any size. Non-consumption of such large and energetically valuable prey by a vertebrate predator, would seem to contradict the basic tenets of Optimal Foraging Models (OFM). In this case, however, two factors seem to explain the apparent 'atypical' foraging behaviourof *R. argentea*:

1. Field sampling in the present study coincided with the season of low zooplankton densities in Lake Victoria (Branstrator et al. 1996; Mwebaza-Ndawula: this study). It has been emphasised in literature that during periods of low zooplankton densities fish generally tend to feed randomly on prey organisms as they are encountered in the environment (Ivlev 1961;O'Brien et al. 1976; Werner & Hall 1974; Gardner 1981). Given the much lower relative abundance of diaptomids in the environment (Table 1), fish would be inclined to ingest proportionately greater quantities of the more abundant but smaller cyclopoid prey. Selective patterns at the time of the annual zooplankton peak densities (July/August) were not investigated during this study due to very small sample sizes of fish. Among sticklebacks, Visser (1982) found selection for the more preferred prey (*Daphnia*) to increase as

total prey density increased. On the other hand, some predators are reported to select rare prey types at high prey densties (Horsley 1979).

2. A fair body of evidence exists from experimental studies suggesting that diaptomid copepods are more evasive prey when faced with imminent predation than cylopoids (Drenner et al. 1978; Drenner & MacCommas 1980). This behavioural attribute, coupled with low diaptomid relative abundance in the environment, may to some extent, explain the minimal ingestion of the large-bodied diaptomid copepods by *R. argentea*.

Patterns of electivity for three major prey species by different fish sizes (Figure 4) provide further proof for preference of cyclopoid prey by *R. argentea* while both diaptomids and cladocerans appear largely underutilised. Both latter organisms were strongly avoided by small fish under 20 mm sl. (i.e. high negative electivities) but were more or less randomly consumed among larger fish over 40 mm sl. (i.e. D values close to 0). Non-consumption of large-sized prey among juvenile fish, may to some extent be explained by morphological limitation especially with respect to mouth gape size. It may also be understandable for juvenile fish to avoid large evassive prey such as diaptomids. It is however surprising that cladocerans, commonly known to exhibit very poor escape response (Kerfoot et al 1980; Winfield et al 1983; Unger & Lewis 1983) were not positively selected even among large fish categories. In this case, it appears that an interplay of selective factors involving relative abundance, body size and ability to escape may have favoured selection of cyclopoids. Besides, the preference for cyclopoids may be viewed as a mechanism to minimise costs of prey capture, (i.e. energy and time) by choosing the most abundant prey as has been noted in other similar cases (Ponton & Müller 1990).

Prey size selection patterns for different fish size groups (Figure 5) show consistent strong negative selection for both the smallest and largest prey groups (< 500 and > 1000 µm respectively) while intermediate prey sizes were positively selected, albeit to varying degrees in different fish size categories. Although a size selection factor in prey choice clearly exists, evidence of increasing preference for large prey with increasing fish size is not as strong as observed elsewhere in planktivorous fishes (i.e. Wong & Ward 1972; Baird & Hopkins 1981; Mittelbach 1981; Hansen & Wahl 1981). In terms of energetic benefits, small prey below a critical body size can theoretically be presumed to be relatively unattractive to a foraging predator; as shown by high negative electivities (i.e. Figure 5, copepods less than 500m µm). Large prey such as diaptomids may be avoided by larval and juvenile fishes largely due to morphological contraints. However, the strong negative selection of large copepods observed among large fish seems to be related more to the prevailing low standing stocks of zooplankton at this time of the year, (Branstrator et al. 1996), in combination with very low relative abundance and higher escape abilities of this taxon, than to deliberate avoidance by the fish. Baird & Hopkins (1981) concluded from their study on *Valenciennellus tripunctulatus* that, prey size may not always be the overriding factor in prey choice and as pointed out by Lazzaro (1987) electivity measures are generally highly influenced by relative abundance of prey types in the environment.

According to the pioneering classic studies by Hrbacek (1962) and Brooks & Dodson (1965), effects of planktivory by fish may be manifested through changes in species composition and size structure of zooplankton

communities. Such effects are a direct result of selective feeding behaviour through disproportionate consumption of preferred prey types and sizes. Both features of prey selection have been vital in the development of theories relating to optimal foraging (Werner & Hall 1974; O'Brien 1976; Eggers 1977; Krebs 1978; Pyke 1984). These theories provide a useful basis to interprete differences in feeding patterns of fishes under varying environmental conditions as well as assessing impacts which predation may exert on prey communities. There is evidence that Lake Victoria zooplankton community has undergone changes in relative abundance involving the major zooplankton groups, from domination by diaptomids and to some extent cladocerans (Worthington 1931), to the present community dominated by relatively small-bodied cyclopoid copepods (Mwebaza-Ndawula 1994). Recent analysis and comparision of relative abundances of the various taxa between historical (1961) and modern (1994-95) zooplankton samples (Mwebaza-Ndawula: this study) has provided further support for such changes following drastic transformations of the fish fauna in recent decades (Ligtvoet 1988; Witte et al 1992; Kaufman 1992). The role of planktivory in these changes is presumed to be important probably in combination with other factors such as eutrophication of the lake and the parallel changes in the phytoplankton community (Hecky 1993; Hecky et al. 1994).

Information on prey selectivity is important in predicting food chain stability and ultimately fish production. While studying feeding selectivity of *Alestes baremose* in Lake Chad, Gras and Saint Jean (1983) concluded that decrease in the useful fraction of zooplankton could play a role in growth deceleration and stock decrease of the planktivore during the lowering of the

lake water level. Differences in growth rate of fishes have been shown to be related to food particle size both from field (Hall et al. 1970) and laboratory studies (Paloheimo & Dickie 1966). The tripling of stocks of *R. argentea* in Lake Victoria during the 1980s, following the collapse of formerly abundant haplochromine fishes (Wannk 1991; Witte et al. 1992), provided a positive, though indirect indication of the state of zooplankton as a food resource base for pelagic planktivorous fishes. Cyclopoid copepods, the preferred prey for *R. argentea* has to date exhibited considerable resilience to predation both in terms of sustained abundance and stability of species and size composition. Currently therefore, the zooplankton community of Lake Victoria as a whole appears to offer positive prospects for further sustainance of the pelagic fishery.

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MDIX 1.

erature and dissoved oxygen depth data

mber 1995

	Time: 17.20h Secchi depth: 1.45m MSE		Time:18.00h Secchi depth: 0.78m NG		Time: 16.00h Secchi depth: 1.48m BG	
(m)	°C	DO (mgl^{-1})	°C	DO (mgl^{-1})	°C	DO (mgl^{-1})
0	27,7	9,7	27,8	9,8	26,6	7,7
1	27,4	10,2	27,7	10,0	26,2	7,9
2	26,9	10,3	26,5	8,4	25,2	8,3
3	26,3	9,6	26,1	6,6	25,2	7,7
4	26,1	7,0	25,7	5,6	25,2	7,3
5	26,0	6,1	25,7	5,5	25,1	6,9
6	25,7	3,7	25,6	5,4	25,1	6,8
7	25,3	0,2	25,6	5,2	25,1	6,5
8	25,2	0,1	25,6	5,2	25,1	6,4
9			25,5	5,4	25,1	6,3
10			25,5	5,5	25,1	6,1
11			25,5	5,8	25,1	
12			25,0	0,2	25,0	6,1
13			24,8	0,4		
14			24,8	0,6		
15			24,7	0,4	25,0	5,6
16			24,7	0,3		
17			24,7	0,3		
18			24,7	0,3		
19						
20					25,0	1,4
25					24,4	1,3
30					24,3	1,4
35					24,3	1,3
40					24,3	1,3
50					24,3	0,9
60					24,3	0,9

Appendix 1. continued

ch 1996:
Time: 15.45h
Secchi depth: 1.3m
MSE

th (m)	°C	DO (mgl^{-1})
0	28,3	9,8
1	27,1	9,1
2	26,9	7,7
3	26,8	7,5
4	26,7	6,4
5	26,6	5,5
6	26,6	5,6
7	26,6	5,5
8	26,5	5,2
9		
10		
11		
12		
13		
14		
15		
16		
17		
18		

March 1996:
Time: 01.00h

NG

°C	DO (mgl^{-1})
26,8	11,8
26,8	9,7
26,8	9,6
26,8	9,5
26,8	9,4
26,8	9,3
26,8	8,9
26,8	8,1
26,7	7,9
26,7	7,7
26,7	7,6
26,7	7,6
26,7	7,4
26,7	7,0
26,7	6,8
26,7	7,0
26,7	7,0
26,7	6,8
26,6	5,2

July 1996:
Time: 11.45h
Secchi depth: 2.2m
NG

°C	DO (mgl^{-1})
24,7	10,6
24,7	7,6
24,6	7,3
24,6	6,9
24,5	6,9
24,5	6,4
24,5	6,1
24,5	6,2
24,5	6,2
24,5	6,4
24,5	6,3
24,5	6,6
24,5	6,0
24,5	6,0
24,5	6,2
24,5	6,0
24,5	6,2
24,5	5,3
24,5	2,5

Appendix 1. continued

Sep 96

Time: 12.10h
Secchi depth: 0.81m

MSE

Depth (m)	°C	DO (mgl^{-1})
0	27,1	10,2
1	26,6	10,1
2	25,8	9,7
3	25,5	8,5
4	25,4	7,2
5	25,2	5,7
6	25,1	5,0
7	25,0	3,1
8	24,9	2,5
9		
10		
11		
12		
13		
14		
15		
16		
17		
18		

Time: 15.30h

NG

°C	DO (mgl^{-1})
27,6	10,1
26,4	10,9
26,3	12,3
25,7	10,5
25,6	8,4
25,5	7,7
25,5	7,3
25,4	6,4
25,3	6,2
25,3	5,5
25,0	3,6
24,7	1,5
24,5	1,4
24,5	1,3
24,4	1,3
24,3	1,3
24,3	1,3
24,3	1,2
24,3	1,2

Appendix 1. continued

October 1996

	Time: 12.10h Secchi depth: 0.81m **MSE**		Time: 16.45h Secchi depth: 0.86m **NG**		Time: 10.00h Secchi depth: 1.64m **BG**	
Depth (m)	°C	DO (mgl^{-1})	°C	DO (mgl^{-1})	°C	DO (mgl^{-1})
0	27,7	8,5	28,6	12,5	25,7	9,7
1	26,5	8,4	28,2	11,2	25,8	8,7
2	26,2	7,1	26,3	10,2	25,7	8,7
3	26,0	5,7	26,1	9,0	25,6	8,3
4	26,0	5,4	26,0	7,2	25,6	8,2
5	26,0	5,4	25,9	7,2	25,6	8,0
6	25,9	5,2	25,9	7,0	25,6	7,9
7	25,9	5,0	25,9	6,8	25,6	7,8
8	25,9	4,7	25,9	6,5	25,3	6,5
9			25,8	5,1	24,6	5,4
10			25,8	5,1	24,6	5,4
11			25,7	4,9	24,5	5,3
12			25,4	1,9	24,5	5,5
13			25,3	1,4	24,5	5,2
14			25,2	1,1	24,5	5,3
15			25,2	1,1	24,5	5,1
16			25,1	1,0	24,4	4,8
17			25,0	1,0	24,4	4,7
18			25,0	1,0	24,4	4,5
19					24,4	4,2
20					24,4	4,1
25					24,3	3,7
30					24,2	3,4
35					24,8	4,0
40					24,1	3,1
50					24,1	1,8
60					24,0	1,7

Appendix 1. continued

August 1995:

Time:14.45h

Secchi depth:1.24m

	NG	
Depth (m)	°C	DO (mgl^{-1})
0	25,8	9,5
1	25,8	9,0
2	25,4	8,6
3	25,1	7,4
4	25,0	6,0
5	25,0	5,6
6	25,0	5,1
7	25,0	4,9
8	25,0	4,6
9	24,9	4,4
10	24,8	4,1
11	24,8	3,4
12	24,8	3,4
13	24,8	3,0
14	24,8	2,9
15	24,8	2,5
16	24,8	2,6
17	24,7	2,4
18	24,7	2,4

Sep 95

Time: 12.38h

Secchi depth: 1.16m

	NG	
	°C	DO (mgl^{-1})
	26,9	10,0
	25,9	9,6
	25,3	8,8
	25,2	8,3
	25,1	7,6
	25,0	7,2
	25,0	6,8
	24,9	6,3
	24,9	5,9
	24,9	5,4
	24,8	4,8
	24,8	4,7
	24,8	4,8
	24,8	5,2
	24,8	5,3
	24,8	5,3
	24,7	5,5
	24,7	4,6
	24,7	4,6

APPENDIX 2.

Mean biomass (µg dry wt.) of different zooplankton sizes for samples taken on different sampling dates. Names of organisms as in Fig. 11.

Mean biomass (µg/organism/ size class: (NG & BG Dec.95, NG July 96 and Historical)														
NG, Dec. 95, 5m, night	<100 µm	-200	-300	-400	-500	-600	-700	-800	-900	-1000	-1100	-1200	-1300	-1400
rotif														
naupl	0,024	0,075	0,179	0,549										
cyclop			0,371	0,526	1,172	1,734	2,491	3,335						
diapto					0,903			3,226	4,941	6,313	8,28	9,562	12,591	13,99
cladoc					0,535	1,437								
BG, Dec.95, 15m, day														
rotif														
naupl	0,022	0,062	0,241	0,459	0,557									
cyclop			0,355	0,547	1,073	1,741	2,202	3,372						
diapto							2,551	3,838	4,518	6,009	7,721		12,416	14,218
cladoc				0,487	0,596				3,735*					
NG, July 96, 5m, day														
rotif														
naupl	0,023	0,058	0,19	0,601		1,425								
cyclop				0,698	1,148	1,653	2,478	3,269	4,616					
diapto					1,192	1,541	2,636	3,741	4,836	6,283	7,197	9,721	12,183	
cladoc			0,158	0,442	0,711	1,287	1,94	2,67	3,502					
Historical (July 1961)														
rotif														
naupl	0,026	0,084	0,214	0,434										
cyclop				0,731	1,118	1,63	2,465	3,607	4,499	5,899	8,003	9,987		
diapto					1,11	1,933	2,29	3,411	4,435	6,03	8,529	9,675	11,22	14,56
cladoc		0,074	0,14	0,375	0,61	1,211	1,697	2,333	4,099			7,549		
Integrated mean biomasses (µg/organism/size class)														
	<100 µm	-200	-300	-400	-500	-600	-700	-800	-900	-1000	-1100	-1200	-1300	-1400
rotif														
naupl	0,02375	0,06975	0,206	0,51075	0,557									
cyclop			0,363	0,6255	1,12775	1,6895	2,409	3,39575	4,5575	5,899	8,003	9,987		
diapto					1,068333	1,737	2,492333	3,554	4,6825	6,15875	7,93175	9,652667	12.1025	14,255
cladoc		0,074	0,291	0,434667	0,613	1,311667	1,8185	2,5015	3,778667			7,549		

6. GENERAL SUMMARY

The Lake Victoria ecosystem has experienced profound ecological transformations over the past three decades involving changes in physical, chemical and biological characteristics which continue to alter the lake's character up to the present time. Resulting largely from the establishment in the lake of the introduced top predator, the Nile perch (*Lates nioloticus*), stocks of once superabundant and speciose haplochromine (Pisces: Cichlidae) species flock collapsed during the 1980s, as did most stocks of other non-cichlid fishes. Emerging from virtual ecological desecration, a small endemic pelagic cyprinid, *Rastrineobola argentea* (Pellegrin) increased three-fold in abundance over most of the 1980s, becoming a major commercial fish species around the lake in subsequent years. However, the ensuing accelerated lakewide exploitation of the species proceeded in near-absence of vital information on its biology and ecology to guide formulation and implementation of viable management regulations. Among areas of study requiring urgent research attention was the food and feeding behaviour of *R. argentea*. Such knowledge was considered to be a major tool towards understanding of the functional role of the species in the ecosystem food web especially with regard to fish production.

The study investigated the feeding ecology of *R. argentea* in the north-western part of Lake Victoria (Uganda waters) during the years 1994 to 1996. Study sites were selected so as to include areas in the shallow inshore waters as well as the deep and open waters of the lake. The major objective of the study was to investigate the dietary elements of the fish and to establish to what extent diet may be influenced by spatial and temporal

distribution and abundance patterns of both the fish and its food organisms (zooplankton). Dispersion patterns of *R. argentea* and zooplakton were investigated in conjunction with water column structure (i.e. temperature and dissolved oxygen depth profiles) and other pertinent limnological parameters including water transparency, light extinction coefficients and phytoplankton biomass.

Potential impacts of predation upon the prey community were examined by comparisions of community size and biomas structure of zooplankton between inshore areas where fish densities are high and the offshore areas with much lower fish abundance. Seasonal comparisions of zooplankton size structure were made between the December 1995 (low zooplankton densities; high fish densities) and July 1996 (high zooplankton densities; low fish densities) samples. Long term effects of planktivory were examined by comparisions between historical samples of zooplankton and fish collected during the 1960s (pre-Nile perch era; characterised by abundant cichlid planktivores) and modern samples collected during the present study (post-Nile perch era; with *R. argentea* as the main planktivore). Prey selectivity was investigated by comparisions of relative abundances and mean sizes of major prey items in guts of *R.argentea* and the environment and selectivity indices pertaining to different prey types and sizes in different sizes of fish.

Water column structure showed alternation of conditions of thermal stratification, with well developed thermoclines and oxyclines (October to March) and mixing (March to July) both in inshore and offshore areas of the lake. Substantial oxygen depletion (up to < 1.0 mg $O_2 l^{-1}$) was observed

particularly at the height of thermal stratification in December both in inshore and offshore areas. Vertical distributions of both zooplankton and *R. argentea* were shown to be influenced by the stratification-mixing regime. Concentration of organisms occurred above the anoxic hypolimnion during the period of thermal stratification, while nearly homogeneous distribution pattern was attained during the turnover period. The distribution patterns appeared to be explained by the sensitivity of *R. argentea* (and apparently zooplankton) to low oxygen conditions obtaining in the hypolimnion during thermal stratification and an improvement of oxygen conditions throughout the water column during the turnover.

The apparent general spatial displacement of bottom and/or near-bottom dwelling organisms to intermediate and surface layers during spells of thermal stratification raises the possibility of greater spatial overlap between *R. argentea* and both its food organisms as well as its natural predators, (the Nile perch). While the former appears to potentially lead to a general improvement of the food environment for *R. argentea*, populations of *L. niloticus* seasonally displaced from their demersal habitats and food resources thereof, are likely to inflict greater predation pressure on stocks of *R. argentea*; a development which may upset the existing predator-prey balance. It is not known to what extent stocks of *R. argentea* can withstand increased exploitation from the displaced Nile perch, the fishery and from avian predators reported elsewhere.

Zooplankton and fish densities, water transparency, light extinction coefficients and phytoplankton biomass (Chll-a) all exhibited inshore-offshore gradients. In October 1996, low water transparency inshore was

matched with high light extinction coefficient and the converse was true for the offshore waters. Chlorophyll-a level was nearly twice as high inshore compared to offshore areas during November/December 1995 and October 1996. A vertical gradient in Chll-a distribution showed biomass peaks between 1 and 10 m at both inshore and offshore study sites. A clear quantitative relationship existed between fish and zooplankton densities in inshore and offshore waters. Zooplankton densities were higher offshore where fish densities were much lower, relative to lower zooplankton densities inshore where fish densities were much higher. The zooplankton community was composed of cyclopoid copepods (3 genera: 8 species) diaptomid copepods (2 genera: 2 species), Cladocera (7 genera: 8 species), Rotifera (12 genera: 19 species), the atyid prawn (*Caridina nilotica*) aquatic dipteran larvae/pupae and acarid mites. All zooplankton groups occurred in both inshore and offshore waters, but some exhibited horizontal gradients in relative abundance. Rotifers were numerically more abundant and exhibited higher species diversity in inshore than in offshore waters. Large-sized diaptomids (900-1400 µm) were less abundant inshore compared to offshore waters, as were cyclopoids in the size range 500-700 µm. Although cyclopoids were numerically the most dominant group, the less abundant but larger diaptomids dominated the biomass composition.

Population size structure of *R. argentea* showed alternation of two modal length classes (10-35 and 40-60 mm sl.) in inshore waters on different sampling dates, while a unimodal distribution (modal length 20 mm sl.) comprising small-sized fish was obtained in offshore waters on the two sampling occasions. Seasonal development of fish population structure at NG station was evident with a single cohort of large fish (modal class

45 mm sl.) dominating in the December 1995 sample while a bimodal pattern with modal lengths at 10 & 50 and 15 & 30 mm sl. was observed in the March and September-October 1996 samples. The seasonal changes in population size structure appear to reflect the annual breeding cycle and growth of juvenile fish in inshore areas of the lake.

Different pelagic species (i.e. *R. argentea* and juveniles of cichlids and the Nile perch, *Lates niloticus* exhibited different seasonal patterns of abundance in inshore waters. *R. argentea* and cichlids were abundant in December 1995, (up to > 20 fish / 600m^3), declined in March through July (< 3 fish / 600m^3) 1996 before the former increased in September and October (up to 80 fish / 600m^3). Cichlids mantained low abundance through July to September 1996. Juvenile *Lates* became abundant in March 1996 through July(< 40 fish / 600m^3) and declined during September and October 1996 (< 10 fish / 600m^3). The offshore area was characterised by very low fish densities and ichthyomass on both occasions when it was sampled. The seasonal trend in biomass in inshore areas followed nearly a similar pattern as the that of fish densities. Observed seasonal patterns appeared to be related to the breeding seasonality in respective fishes, all of which utilise the shallow inshore areas as breeding and nursery grounds. *R. argentea* constituted the greatest pelagic fish densities and ichthyomass at all stations, on all sampling dates.

The diet of *R. argentea* in fish over a size range 10-60 mm sl.,was dominated by cyclopoid copepods, constituting > 75% and > 65% of the prey items by numbers and dry weight respectively. Other dietary items were diaptomids, cladocerans, rotifers, chaoborid larvae and adult

insects.The atyid prawns, *Caridina nilotica* which become very abundant in the water column at night were not encountered in fish guts, despite reports of ingestion of this prey in the Mwanza Gulf (southern part of the lake). This may have arisen from differences in methods of fishing used by different workers and timing of fish sampling for diet analysis.

Comparision of the diet in fish samples from offshore (BG) and inshore (MSE & NG) showed a higher numerical contribution of cyclopoids in offshore fish diet (ca 98%), compared to ca 78% and 53% in inshore fish. The second most important prey item in offshore fish was *Chaoborus* larvae (4.8%) while adult insects and rotifers contributed 42% and 16% (NG and MSE respectively) in inshore fish diet. Corresponding dry weight data confirmed the importance of cyclopoids regardless of area of capture of fish, while some items like *Chaoborus* larvae and adult insects were periodically important depending on place and time of fish capture.

Ontogenetic changes in the diet showed consumption of greater proportions of diaptomids with increasing fish size while the proportions of naupliar larvae showed the opposite trend. Historical data from fish caught in 1966 at Windy Bay Napoleon Gulf, (adjascent to NG and MSE study sites) showed cyclopoids still as the dominant dietary item, though with a markedly lower numerical abundance (just > 50%). Cladocerans and diaptomids, on the other hand, contributed much higher proportions (approx. 13% and 30% respectively) than their respective contributions (0.5 - 3.7%) in the modern *R. argentea* diet. The dietary importance of the three key prey items in the historical diet was further confirmed by their respective mean dry weights i.e. cyclopoids 47.1%, diaptomids 23.6% and cladocerans

24.1%; togehter accounting for ca. 95% of the diet then; compared to: cyclopoids 69.9%, diaptomids 2.8% and Cladocera 1.3%; together accounting for ca. 74% in the modern diet. No major seasonal variations in diet composition were observed in fish from NG station. Cyclopoids maintained a dominant position in the diet on all sampling dates. Rotifers, however, attained high numerical proportions in September-October 1994 and December 1995, although it could not be ascertained if such increase was linked their annual cycle of abundance in the plankton. Mean dry weight of chaoborid larvae in the diet were relatively high in September-October 1994, October and December 1995 while hardly any chaoborids occurred in the August 1995 diet. The temporal trends with respect to chaoborids, however, seemed to relate more to the size composition of the respective fish samples vis - a - vis size-dependent consumption of these macroplankters, than to actual seasonality in their consumption by the fish. No consistent differences in diet composition were observed in day-night comparisions and with respect to different vertical positions in the water column. Mean dry weight analysis however, showed relativel higher night time consumption of chaoborid larvae; an indication of enhanced availability of these prey in the water column due to their diurnal migration behaviour.

Dominance of the diet by cyclopoids in both the historical and modern fish samples seems to stem from their much greater pelagic abundance relative to other zooplankters, combined with the offer of a wide choice in terms of species diversity and size range of food particles. Sustained prominence of cyclopoids both in the plankton and fish diet may result from high productivity under warm tropical conditions where a prey taxon may be maintained at high concentrations despite heavy predation.

Analysis of mean sizes of major prey types in the environment and guts of fish in the December 1995 data from NG station revealed consumption of significantly larger cyclopoids than the mean size in the environment. In contrast, *R. argentea* consumed a smaller mean size of diaptomids than in the environment. Modal prey size of ingested copepods was 500 µm in fish less than 50 mm sl. but shifted to 600-700 µm in the largest fish above 50 mm sl. Mean sizes of ingested cyclopoids increased with increasing fish standard length. Jacobs electivity indices for diffrent prey types showed positive selection for cyclopoids by all fish size categories over a size range of 10 to 60 mm sl. Both diaptomids and cladocerans were strongly negatively selected by juvenile fish (< 20 mm sl.) but were more or less randomly consumed among larger fish categories. Fish in the size range 10 - 60 mm sl. showed relatively high positive selection (D = + 0.58 to + 0.71) for copepod prey of 500 µm, but the largest fish (> 50 mm sl.) exhibited even stronger positive selection (D = +0.87) for larger copepods in the 900 µm size category. The smallest and largest copepods (< 400 and > 1000 µm respectively) were strongly avoided by fish in all size categories.

Overwhelming positive selection for cyclopoids and negative selection for the rarer diaptomids and cladocerans indicate that relative prey abundance is one of the decisive factors in prey choice. Strong negative selection for the smallest available copepods and positive selection for larger copepods (500-700 µm) suggests size-dependent consumption of prey and appears to be in agreement with Optimal Foraging Theories(OFT). Negative selection for the largest copepods (diaptomids) seemed to relate to both their

low relative abundance in the environment and to their greater efficiency in evasion of predators.

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Makerere University, Kampala	1971-74	B.Sc. (Hons) (Diploma Ed.)
University of Dar es salaam, Tanzania	1981-85	M.Sc. (Fish. & Aquat Sci.)
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-Institute of Limnology, Mondsee, Austria	1991	Cert. Limnol.
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F. Collaboration in international research programs:

-I.D.R.C. Lake Productivity Project on Lakes Victoria, Kyoga and Albert (FWI, Canada)

-Lake Ecosystem and Biodiversity Research Program on Lake Victoria (Univ.Mich.USA)

-Regional Fisheries Research Program (EEC project) (KEMFRI, Kenya; TAFIRI, Tanzania)

- Lake Victoria Fisherie and Biodiversity Research Project (KEMFRI, Kenya; TAFIRI, Tanzania)

- Lake Victoria Eutrophication Project (KEMFRI, Kenya; TAFIRI, Tanzania)