Food partitioning within the species-rich benthic fish community of Lake Malawi, East Africa

F. Duponchelle, A.J. Ribbink, A. Msukwa, J. Mafuka, D. Mandere, and H. Bootsma

Abstract: Temporal diet patterns were studied for nine species of haplochromine cichlids in Lake Malawi, East Africa, using a combination of stable isotope and stomach content analyses. The results illustrate the complementarity of the two approaches in elucidating dietary differences. Evidence was found that benthic algal production contributed to the energy requirements of offshore fishes that occupy depths between 10 and 30 m. The importance of the lake fly *Chaoborus edulis* as a food source for demersal fishes was confirmed, supporting the recent hypothesis that deep demersal fish production is principally sustained through the pelagic food chain rather than from benthic detrital sources. Isotopic differences were observed among species with apparently similar diets, feeding behavior, and depth preferences, suggesting that important resource partitioning exists among Lake Malawi benthic haplochromine cichlids.

Résumé : Les variations temporelles de régime alimentaire de neuf espèces de cichlidés haplochromis du lac Malawi (Afrique de l'est) ont été étudiées grâce à l'utilisation combinée des contenus stomacaux et des analyses d'isotopes stables. Les résultats illustrent la complémentarité des deux approches pour élucider les différences d'alimentation entre espèces proches. Cette étude a mis en évidence la contribution de la production algale benthique aux besoins alimentaires des poissons entre 10 et 30 m de profondeur. L'importance de *Chaoborus edulis* comme source alimentaire pour les espèces démersales a été confirmée, ce qui renforce l'hypothèse récente selon laquelle la production de poissons démersaux repose principalement sur une chaîne alimentaire de type pélagique et non pas sur des sources de détritus benthiques. Des stratégies trophiques distinctes ont été observées entre espèces ayant apparemment des préférences bathymétriques, des régimes et des comportements alimentaires similaires, ce qui suggère l'existence d'un important partage des ressources au sein des cichlidés haplochromis benthiques du lac Malawi.

Introduction

The Cichlid fishes have evolved an astonishing diversity of feeding adaptations and behaviours that enable them to utilize a large variety of food types, including phytoplankton, epilithic and epiphytic algae, plants, detritus, zooplankton, molluscs, insects, benthic invertebrates, fish eggs, larvae, scales, and whole fish (reviews in Fryer and Iles 1972; Ribbink 1990; Yamaoka 1991). The role of the feeding apparatus and trophic specializations in the adaptive radiation of African cichlids has received much attention (Liem 1980, 1991; Ribbink et al. 1983). Many species appear to have diets that are nearly indistinguishable based on stomach content analyses (Greenwood 1981), raising uncertainties about the significance of neurocranial structure. McKaye and Marsh (1983) suggested that trophic partitioning might only be invoked when food resources are scarce. A number of studies in Lake Malawi (Reinthal 1990; Bootsma et al. 1996; Kuusipalo and Kakela 2000), Lake Tanganyika (Sturmbauer et al. 1992), and Lake Victoria (Bouton et al. 1997) have demonstrated the potential importance of trophic segregation, but mechanisms other than food resource partitioning may also allow for species coexistence (Genner et al. 1999*a*, 1999*b*, 1999*c*).

While diet, feeding behaviour, and trophic specializations in the nearshore rock-dwelling communities have received much attention, very little is known of the diverse offshore (sensu; Turner 1996) cichlid communities. Apart from the zooplanktivorous *utaka* group (*Copadichromis* spp.; Fryer and Iles 1972), the *chambo* group (*Oreochromis* spp.; Turner et al. 1991), and the pelagic species, whose feeding ecology was recently studied (Allison et al. 1996*a*; Ngatunga and

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Allison 1996), the only information available on the diet of offshore fishes comes from Eccles and Trewavas (1989) and Turner (1996). These studies resulted in useful new insights into fish-feeding habits, but they were limited by the relatively small numbers of observations and the narrow time span over which fish stomach contents could be monitored. More recent studies in Lake Malawi have used stable isotope analysis to disentangle the trophic behavior of inshore (Bootsma et al. 1996) and rock-dwelling species (Genner et al. 1999*a*).

Both stomach content and stable isotope analyses have advantages and disadvantages that make them complementary. Stomach content analysis provides information about ingested food items over a very short time period, generally a few hours. Nevertheless, monitoring stomach content over long periods of time can give insights into seasonal or temporal trends in feeding patterns that may not be evident in stable isotope signatures because they represent a spatio-temporal integration of the assimilated food over periods varying from months to years, depending on fish growth rates and tissue turnover times (Peterson and Fry 1987; Hesslein et al. 1993; Gannes et al. 1997). Stable isotope signatures are useful when stomach contents cannot be identified, or when there is uncertainty regarding the assimilation efficiency of various food items. Stable isotope analysis is also useful for deep-water species that often have everted stomachs when retrieved from trawls.

In comparison with the structurally complex inshore zones (Ribbink et al. 1983; Konings 1995), offshore benthic zones are often poorly structured in Lake Malawi, and the typical substratum variability ranges from sand to mud (Konings 1995; Turner 1996; Duponchelle et al. 2003). Nevertheless, there are a number of potential food resources for cichlid fishes that occupy offshore habitats, including benthic invertebrates, zooplankton, sedimented phytoplankton, and other fish. Most offshore species studied to date seem to have a mixed diet made of varying proportions of these potential food items (Eccles and Trawavas 1989; Turner 1996). As a consequence, one might expect that the general trend of interspecific resource overlap often observed in inshore zones (McKaye and Marsh 1983; Ribbink et al. 1983; Genner et al. 1999*c*) might also occur, possibly to a larger extent, in the poorly structured offshore zones. The present study tests this hypothesis by investigating the temporal trends of some demersal fish diets using both monthly stomach content analysis and stable isotope analysis of carbon and nitrogen composition.

Material and methods

Fish sampling

Temporal variability of diet was determined over 8 months (November 1998 – May 1999) for nine demersal fish species that were selected according to their relative abundance and importance in the fishery. Each of these nine species is a dominant component of the fish community in its respective depth range (Duponchelle et al. 2003): *Lethrinops gossei*, *Lethrinops argenteus* (= *L. longipinnis* orange head), *Diplotaxodon limnothrissa*, *Diplotaxodon macrops*, *Copadichromis virginalis*, *Mylochromis anaphyrmus*, *Alticorpus mentale*, *Alticorpus macrocleithrum*, and *Taeniolethrinops praeorbitalis*. Fish were collected from monthly trawl surveys in the south-west arm (SWA) of Lake Malawi at depths of 10, 30, 50, 75, 100, and 125 m (see Duponchelle and Ribbink (2000) and Duponchelle et al. (2003) for details).

Stomach content analysis

During each monthly sampling event, 20 specimens of each species were sampled from the main catch as soon as the total catch weight was estimated. A solution of 15% formalin was injected into the abdominal cavity of each fish to ensure the preservation of food items, and the fish were fixed in a solution of 10% formalin for later examination. A problem frequently encountered when trawling below 50 m was that fish stomachs were everted during hauling. Every specimen from the whole catch of *A. mentale* was checked for intact stomachs, since the stomachs of these fish were almost always empty. Even apparently intact stomachs usually contained very little amounts of food.

When enough stomachs containing food items were available, five specimens of each species were analysed each month for diet composition. The method used was the modified version of the point method (Hynes 1950; Genner et al. 1999*a*). The weight of the stomach plus contents and the stomach minus contents were determined to the nearest 0.001 g. Total weight of stomach contents was calculated as the difference between the two weights. The stomach content was then examined under binocular microscope (10×–40× magnification) following the procedure detailed in Genner et al. (1999*c*).

Stable isotope analysis

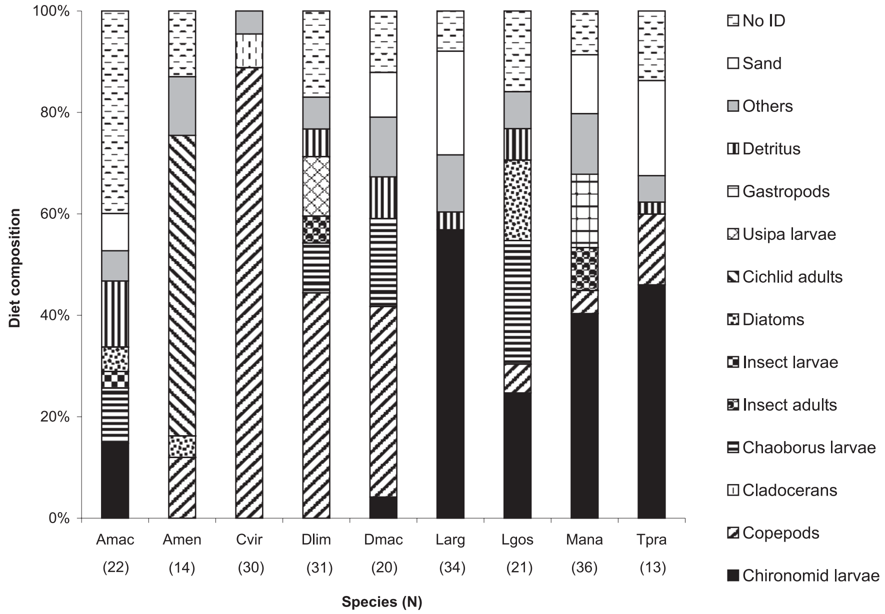
Fish samples for stable isotope analysis were collected by trawling during the January 1999 cruise. Approximately six specimens of each of the nine target species, three small ones and three large ones whenever possible, were collected. Dorsal muscle tissue was subsampled for analysis. Potential food sources were collected during the April 1999 cruise. Gastropods and other benthic invertebrates were sorted out from grab samples taken at depths of 10, 30, 50, 75, 100, and 125 m. Sediment samples were taken from the upper layer (3 cm) of grab samples at every depth. Zooplankton and mayfly larvae were collected by 125-m vertical tows with a 50-μm mesh zooplankton net.

Stable isotope analyses were carried out with an isochrome continuous flow stable isotope mass spectrometer (Micromass; Waters Corp., Milford, Mass.) coupled to a Carlo Erba elemental analyzer (CHNS-O EA1108; ThermoFinnigan Italia S.p.A., Milan, Italy). Results were corrected to nitrogen standards IAEA-N1 and IAEA-N2 (both ammonium sulphate) and carbon standards IAEA-CH6 (sugar), EIL-72 (cellulose), and EIL-32 (graphite). EIL-70b, a lipid-extracted – ball-milled fish material, was used as a monitoring standard (EIL denotes internal standards, with values calculated using international standards). The error for clean ball-milled standard material was ±0.2‰ for carbon and ±0.3‰ for nitrogen. Standards were placed throughout each run at a range of weights to allow for additional linearity corrections, when necessary, for instrument fluctuations or samples of varying signal peak areas.

Statistical analyses

Interspecific differences in stable isotope signatures were analysed with an analysis of variance (ANOVA) and Tukey

Fig. 1. Overall diet composition (% stomach content by weight) of nine demersal cichlid fishes in the SWA of Lake Malawi. Amac, *Alticorpus macrocleithrum*; Amen, *Alticorpus mentale*; Cvir, *Copadichromis virginalis*; Dlim, *Diplotaxodon limnothrissa*; Dmac, *D. macrops*; Larg, *Lethrinops argenteus*; Lgos, *L. gossei*; Mana, *Mylochromis anaphyrmus*; Tpra, *Taeniolethrinops praeorbitalis*. Items that made up less than 2% of the diet were lumped together and referred to as "Others". Unidentifiable materials were recorded as "No ID". "Detritus" refers to unidentifiable vegetal material and organic matter.



posthoc tests. Differences between small and large specimens within a species were assessed by regression analysis. All parametric tests were carried out after verifying the conditions of application.

The PRIMER 5 Package (Clarke and Warwick 1994) was used to analyse stomach content data following the procedure described in Genner et al. (1999*a*, 2003). A similarity matrix of the diet of the 221 individuals of the nine species was constructed using the Bray–Curtis similarity coefficient (Bray and Curtis 1957). Temporal differences of stomach content within and among species were analysed using the one-way ANOSIM (analysis of similarity) procedure on the similarity matrix. ANOSIM is a nonparametric test analogous to ANOVA. The test involves the calculation of a global test statistic R by contrasting the variance in similarity within groups with that between groups (Genner et al. 2003). Stomach content differences between small and large individuals (when small individuals with food in their stomach could be found (Appendix A)) were also tested with the one-way ANOSIM procedure.

Results and discussion

Diet analysis

There were significant differences in stomach content composition between every species pair except for *D. limnothrissa* and *D. macrops*, *L. argenteus* and *T. praeorbitalis*, and *M. anaphyrmus* and *T. praeorbitalis* (Fig. 1; Table 1). Except for *A. macrocleithrum*, *L. argenteus*, and *M. anaphyrmus*, there was significant intraspecific variability of either or both δ^{13}C and δ^{15}N for all species (Fig. 2). This was particularly striking for *A. mentale*, which covered δ^{13}C and δ^{15}N ranges of 3.75‰ and 3.05‰, respectively (Figs. 2*a* and 2*b*). For most of the species examined, this variability was mainly explained by size differences among individuals, confirming previous observations for the rock-dwelling species *Pseudotropheus callainos* (Genner et al. 2003). In general, smaller specimens had a lower δ^{15}N signature than larger ones, suggesting that they occupy a lower trophic level (Fig. 2*a*). However, *D. macrops*, *L. argenteus*, *L. gossei*, and *M. anaphyrmus* did not show significant variation of δ^{15}N with size, and *A. macrocleithrum* showed a decrease of δ^{15}N with size (Fig. 2*a*). Intraspecific variations of δ^{13}C also indicated that, for some species, small specimens fed on items that were different than the ones fed on by large ones (Fig. 2*b*). In *D. macrops*, *L. gossei*, and *T. praeorbitalis*, small specimens relied on food sources with heavier carbon signals than the ones relied on by larger specimens, whereas the opposite pattern was observed for *D. limnothrissa*. Small *L. argenteus* also tended to rely on food sources relatively enriched in carbon compared with those relied on by large specimens, but the differences were not significant. In *A. mentale*, *A. macrocleithrum*, *C. virginalis*, and *M. anaphyrmus*, there was no significant variation of δ^{13}C according to size. Because of these intraspecific variations in δ^{13}C and δ^{15}N ranges, small and large specimens of every species but *A. macrocleithrum*, *L. argenteus*, and *M. anaphyrmus* were subsequently separated in the interspecific analyses.

The average isotopic composition of the nine target species and their potential food sources are presented in Fig. 3. Owing to small sample size for most of the food sources, samples were analysed for δ^{13}C only, and few δ^{15}N measurements are available. The isotopic composition of adult mayflies is not displayed on this figure because, owing to their high mean δ^{15}N signature of 7.82, they are not likely to be a significant food source for these fish. The nine fish species displayed a total δ^{15}N range of 3.35‰. Although interspecific variance of δ^{15}N values may result from reliance on

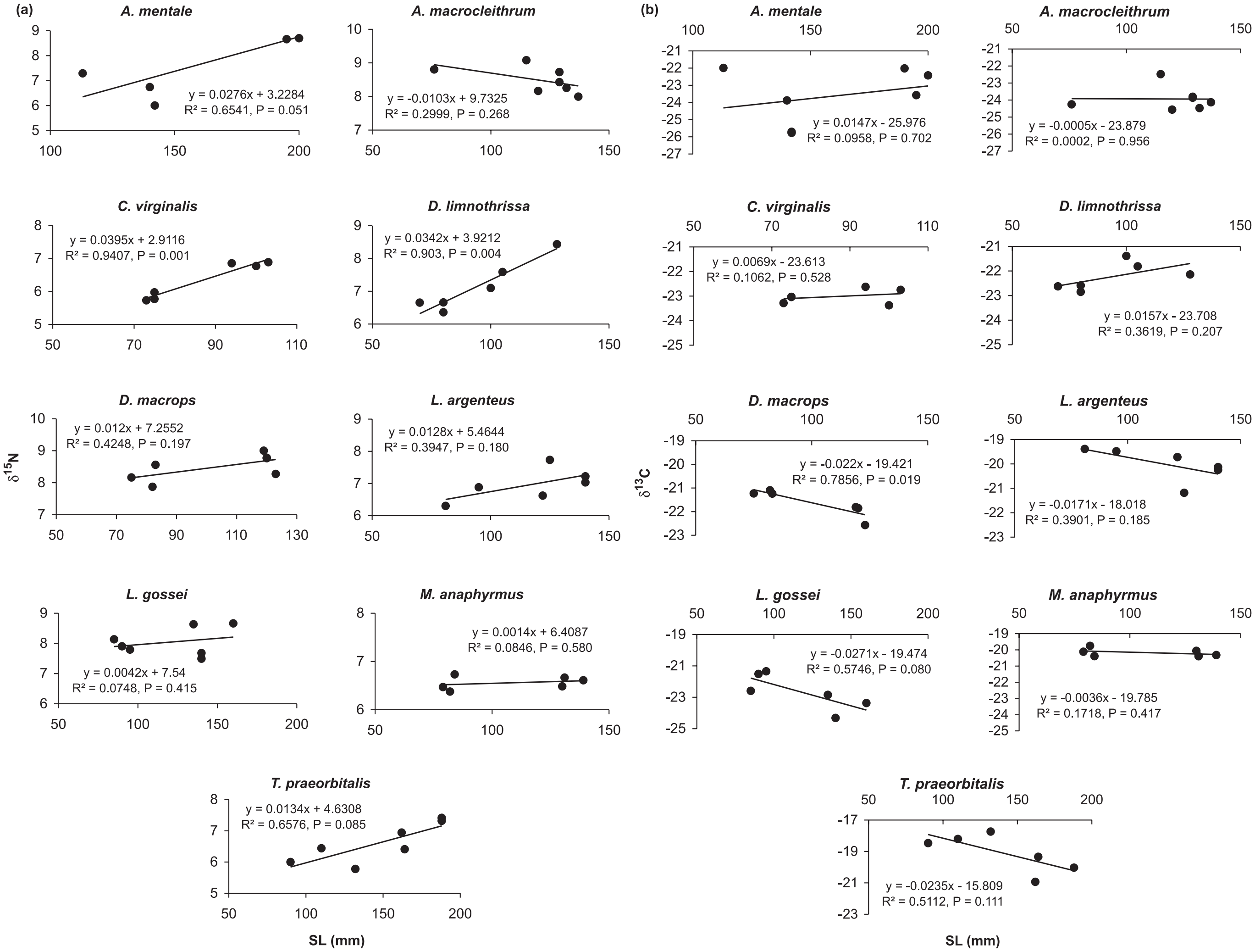
Table 1. Interspecific comparison of stomach content and stable isotope composition.

				Amen		Cvir		Dlim		Dmac			Lgos			Tpra	
			Amac	S	L	S	L	S	L	S	L	Larg	S	L	Mana	S	L
		$\delta^{13}C$															
Amen	S	$\delta^{13}C$															
		$\delta^{15}N$	**														
		St															
	L	$\delta^{13}C$	ns														
		$\delta^{15}N$	ns	**													
		St	**														
Cvir	S	$\delta^{13}C$															
		$\delta^{15}N$	**	ns	**												
		St															
	L	$\delta^{13}C$	ns		ns												
		$\delta^{15}N$	**	ns	**	ns											
		St	**		**												
Dlim	S	$\delta^{13}C$	ns		ns		ns										
		$\delta^{15}N$	**	ns	**	ns	ns										
		St															
	L	$\delta^{13}C$	**		ns		ns	ns									
		$\delta^{15}N$	ns	ns	ns	**	ns	*									
		St	**		**		**										
Dmac	S	$\delta^{13}C$	**		**		*	ns	ns								
		$\delta^{15}N$															
		St															
	L	$\delta^{13}C$	*		ns		ns	ns	ns	ns							
		$\delta^{15}N$	ns	**	ns	**	**	**	ns								
		St	**		**		**		ns								
Larg		$\delta^{13}C$	**		**		**	**	*	ns	**						
		$\delta^{15}N$	**	ns	**	*	ns	ns	ns		**						
		St	**		**		**		**		**						
Lgos	S	$\delta^{13}C$	**		ns		ns	ns	ns	ns	ns	*					
		$\delta^{15}N$															
		St															
	L	$\delta^{13}C$	ns		ns		ns	ns	ns	*	ns	**	ns				
		$\delta^{15}N$	ns	**	ns	**	**	**	ns		ns	**					
		St	*		**		**		**		**	**					
Mana		$\delta^{13}C$	**		**		**	**	ns	ns	*	ns	ns	**			
		$\delta^{15}N$	**	ns	**	ns	ns	ns	*		**	ns		**			
		St	**		**		**		**		**	**		**			
Tpra	S	$\delta^{13}C$	**		**		**	**	**	**	**	*	**	**	*		
		$\delta^{15}N$	**	ns	**	ns	ns	ns	**		**	ns		**	ns		
		St															
	L	$\delta^{13}C$	**		**		**	**	ns	ns	ns	ns	ns	**	ns	ns	
		$\delta^{15}N$	**	ns	**	*	ns	ns	ns		**	ns		**	ns	ns	
		St	*		**		**		**		**	ns		**	ns		

Note: An asterisk (*) indicates a significant difference (*, α = 5%; **, α = 1%) observed between two species for a given variable. When there was no significant difference between small (S) and large (L) individuals for either $\delta^{13}C$ or $\delta^{15}N$ in a species, results of interspecific comparisons are given for large individuals. Idem for stomach content comparisons. Amac, *Alticorpus macrocleithrum*; Amen, *Alticorpus mentale*; Cvir, *Copadichromis virginalis*; Dlim, *Diplotaxodon limnothrissa*; Dmac, *D. macrops*; Larg, *Lethrinops argenteus*; Lgos, *L. gossei*; Mana, *Mylochromis anaphyrmus*; Tpra, *Taeniolethrinops praeorbitalis*; ns, not significant; st, stomach content analysis.

different food webs with different basal $\delta^{15}N$ values (e.g., planktonic versus benthic), measurements of both planktonic and benthic algal $\delta^{15}N$ values indicate that the $\delta^{15}N$ of these two groups of autotrophs are generally within 1‰ of each other. Therefore, the observed range of 3.35‰ for fishes suggests that the species sampled represent a span of approximately one trophic level (3‰–5‰; Peterson and Fry 1987; Hesslein et al. 1991; Bootsma et al. 1996). Comparison of fish and potential food source isotopic composition may be complicated by temporal variations in food source isotopic enrichment. This has been observed in temperate lakes (e.g., Leggett et al. 1999, 2000), but few data are available for tropical systems. To determine the potential significance of temporal variation in Lake Malawi, we ex-

Fig. 2. Relationships between (*a*) standard length (SL) and $\delta^{15}N$ signatures and (*b*) SL and $\delta^{13}C$ signatures for each species in the SWA of Lake Malawi.



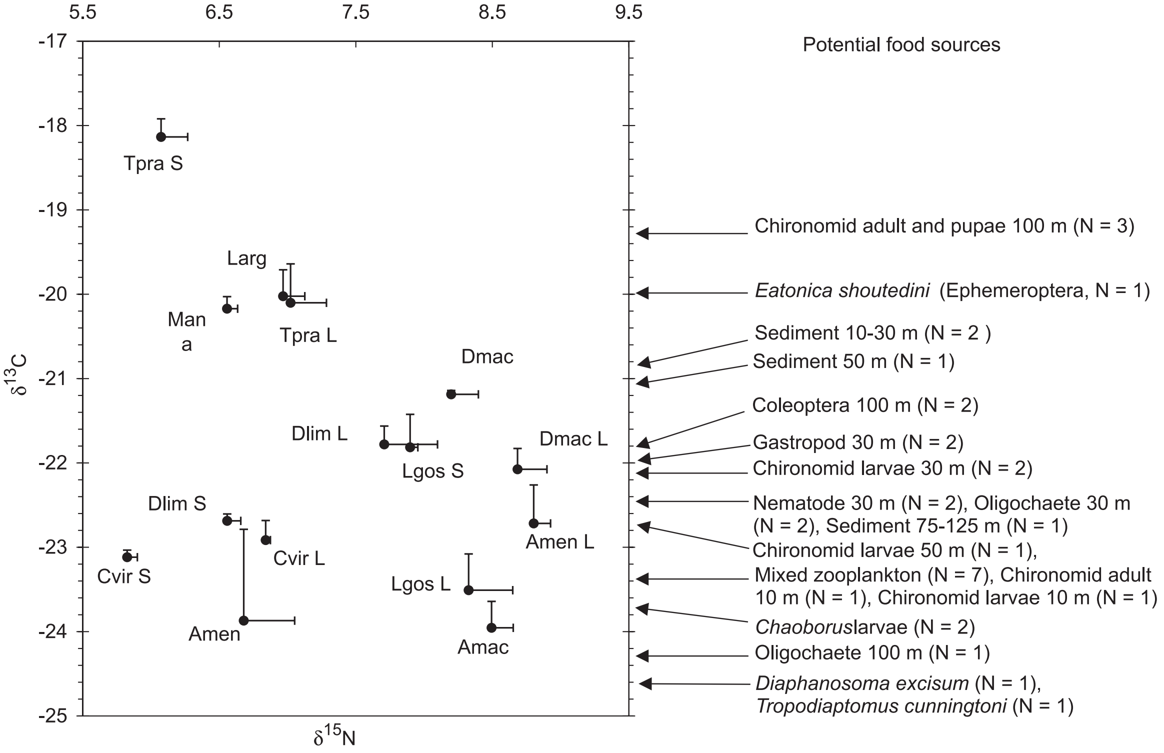
amined isotope data for samples that we previously collected in different seasons over several years. Samples included *Chaoborus edulis* adults, zooplankton collected from shallow and deep regions of the lake, the small clupeid *Engraulicypris sardella*, and periphytic algae collected from rocks at a depth of 10 m in the southwest arm of the lake. The mean $\delta^{13}C$ of all pelagic samples combined was –23.9, with a standard deviation of 1.1 (n = 28), indicating that there is little temporal variability of pelagic $\delta^{13}C$ values, regardless of organism. This is not surprising for a tropical lake in which phytoplankton growth rates are high throughout the year (Bootsma 1993). Variability of periphytic algal $\delta^{13}C$ was slightly greater (mean = –11.7, standard deviation = 1.9, n = 6). Standard deviations of $\delta^{15}N$ for *E. sardella*, *C. edulis*, zooplankton, and benthic algae were 1.0, 1.0, 1.2, and 0.9, respectively. Although these samples do not include some of the potential food organisms sampled during the present study, they provide an indication of the potential magnitude of isotopic variability in pelagic and benthic lower trophic level organisms. These magnitudes are similar to or smaller than the statistically significant differences observed within and between fish species in this study, suggesting that these differences result more from different feeding habits than from temporal fluctuations in the isotopic composition of food organisms. For most of the nine fish species, stable isotope results were consistent with stomach content analysis.

Alticorpus macrocleithrum

Alticorpus macrocleithrum is a deep-water species found between 75 and 125 m (Duponchelle et al. 2003). As for most of the deep-water species, stomachs were often everted during trawl hauling. Only 22 specimens with remaining items in their stomachs were caught between November 1998 and May 1999. The average weight of the stomach contents was 31.2 mg, ranging from 6.4 to 96.8 mg for fishes of 103- to 137-mm standard length (SL, 31–67 g).

Alticorpus macrocleithrum had one of the highest mean $\delta^{15}N$ signatures (8.50, Fig. 3), just below that of the piscivorous large *A. mentale*. Large specimens in general exhibited slightly lighter $\delta^{15}N$ and enriched $\delta^{13}C$ signatures than small ones did (Figs. 2*a*, 2*b*). However, only a single small specimen was analysed for stable isotopic composition. As inferred from its anatomy by Stauffer and McKaye (1985), *A. macrocleithrum* appears to be a benthic invertebrate feeder (Fig. 1). Overall, 51% of the diet was not identifiable,

Fig. 3. Mean isotopic composition (±SEM) of some demersal cichlid fish species and their potential food sources in the SWA of Lake Malawi. Amac, *Alticorpus macrocleithrum*; Amen, *Alticorpus mentale*; Cvir, *Copadichromis virginalis*; Dlim, *Diplotaxodon limnothrissa*; Dmac, *D. macrops*; Larg, *Lethrinops argenteus*; Lgos, *L. gossei*; Mana, *Mylochromis anaphyrmus*; Tpra, *Taeniolethrinops praeorbitalis*. S and L refer to small and large specimens of a given species, respectively. The numbers correspond to the depth at which the samples were collected. Adult insects refer to the averaged $\delta^{13}C$ values of Hemiptera ($N = 1$), Ephemeroptera ($N = 1$), Corixidae ($N = 2$), and Coleoptera ($N = 2$). Mixed zooplankton refers to the averaged $\delta^{13}C$ values of various crustacean copepod species with similar signatures (*Diaptomus vraepelini*, $N = 1$; *Diaptomus dimixtus,* $N = 1$; *Mesocyclops neglectus*, $N = 2$; *Mesocyclops leukarti,* $N = 1$). Other zooplankton species with lighter signatures (*Diaphanosoma excisum* and *Tropodiaptomus cunningtoni*) were separated.



recorded either as detritus or "no ID". The other 49% was made up of chironomid larvae, *Chaoborus* larvae, insect larvae, diatoms, sand, and other items (fish scales, adult insects, cladocerans, copepods, gastropods, oligochetes, macrophytes, and other algae). The most important food items were chironomid larvae and lake fly (*Chaoborus*) larvae. Its isotopic composition was consistent with these observations since it was intermediate between the lightest $\delta^{13}C$ signatures (zooplankton: *D. excisum*, *Tropodiaptomus cunningtoni*, and Oligochaetes at 100 m) and the heavier *Chaoborus* larvae, average zooplankton and sediment between 75 and 125 m (Fig. 3). Although the $\delta^{13}C$ of chironomid larvae at 100 m was not measured, it might be inferred from the chironomid larvae $\delta^{13}C$ values at 30 m and 50 m that it would have been close to that of *A. macrocleithrum*. Owing to its short gut and deep-water existence, Stauffer and McKaye suggested that *A. macrocleithrum* does not feed on algae. However, at every sampled month except February (0.3%, Appendix A), diatoms constituted between 1.4% and 10.5% of the diet and averaged 4.8%. Diatoms might be ingested incidentally with sediment and sand while foraging to catch invertebrates. However, diatoms accounted for 10.5% of the diet in November, when only a small quantity of sand had been ingested, and for 4.1% in March, when almost no sand was ingested (Appendix A). Therefore, the proportion of diatoms ingested appeared too high to be incidental.

Alticorpus mentale

Alticorpus mentale is also a deep-water species mostly abundant between 75 and 125 m (Duponchelle et al. 2003). Because stomachs were almost always empty, all specimens from the entire catch were checked for intact stomachs. Only 14 specimens had remaining items in their stomachs during the period November 1998 – May 1999. The average weight of the stomach contents was 1374.8 mg, ranging from 10.2 to 6549.2 mg for fishes of 110- to 245-mm SL (25–279 g).

As expected from its morphology, *A. mentale* is a piscivore. Overall, 60% of its diet consisted of adult cichlid fishes (Fig. 1), often *Aulonocara minutus*. However, the small specimens (110–117 mm) had a diet that was significantly different (60% copepods, $p < 0.001$) from that of the large ones (170–245 mm), which fed mainly on other cichlid fishes (70%, Appendix A). Carbon isotopic composition of small *A. mentale* matched these observations (Fig. 3), being intermediate between the different zooplankton species (enriched mixed zooplankton species and depleted *D. excisum* and *T. cunningtoni*). Other items in the *A. mentale* diet were cichlid fry, scales, eggs, chironomid larvae, *Chaoborus* larvae, insect pupae, crustacean zooplankton, nematodes, sand, macrophytes, and other algae. The large specimens (190- to 200-mm SL) of *A. mentale* had the highest δ^{15}N signature, as expected from their almost strictly piscivorous habits (Fig. 3). Their position along the δ^{13}C range suggests that the fish species they consume rely on a phytoplankton-based (–22‰ to 23‰) food chain rather than on a benthic algal-based food chain (–8‰ to –16‰, Bootsma et al. 1996).

Copadichromis virginalis

Copadichromis virginalis mainly occurs at depths between 30 and 50 m in the north of the SWA (Duponchelle et al. 2003). Everted stomachs were not a problem, and 30 specimens were analysed between November 1998 and May 1999. The average weight of the stomachs contents was 68.7 mg, ranging from 18 to 190 mg for fishes of 70- to 115-mm SL (8–37 g).

Copadichromis virginalis is known as a member of the zooplanktivorous *utaka* group (Iles 1971; Fryer and Iles 1972; Turner 1996). Indeed, more than 95% of the diet was made of zooplankton, mainly copepods (Fig. 1). It was only in this species that a significant amount of cladocerans were found. Larger specimens had slightly more cladocerans in their diets than small specimens did (Appendix A). Other ingested items were fish scales, chironomid larvae, *Chaoborus* adults and larvae, insect adults and larvae, nematodes, macrophytes, other algae, and detritus. *Copadichromis virginalis* had amongst the lowest δ^{15}N in muscle. Stomach content analyses were supported by its isotopic composition, right in the range of the mixed zooplankton species (Fig. 3). The δ^{15}N difference observed between small and large specimens is likely due to a selective predation upon different zooplankton species. Large specimens of *C. virginalis* appear to feed more upon larger predatory zooplankton species than small ones do.

Diplotaxodon limnothrissa

Diplotaxodon limnothrissa was found at depths of 50–125 m, but was mostly abundant between 75 and 100 m (Duponchelle et al. 2003). Despite their deep-water existence, stomachs were not always everted after hauling, and 31 specimens were analysed. The average weight of the stomach contents was 66 mg, ranging from 8 to 272 mg for fishes of 101- to 145-mm SL (20–48 g).

Turner (1994) described *D. limnothrissa* as a zooplankton feeder, with specimens above 12 mm SL feeding mainly on copepods and small specimens of 3 mm feeding on chaoborid larvae and copepods. Allison et al. (1996*a*) reported a mixed diet composed of crustacean zooplankton, *Chaoborus* larvae, *E. sardella* (Usipa) larvae and juveniles, and occasionally phytoplankton. Our observations also suggested a mixed diet: 71% of the diet was made of copepods, *Chaoborus* larvae, adult insects, and Usipa larvae (Fig. 1). This is supported by its δ^{13}C signature (Fig. 3), which is slightly above those of zooplankton species, *Chaoborus* larvae, and mixed adult insects, and below the signature of some insect species such as *Eatonica shoutedini* (Ephemeroptera). Adults insects such as Coleoptera are not likely to account for an important part of *D. limnothrissa* diet because their mean δ^{15}N signature is only about 1‰ lighter (6.58 ± 0.28). The isotopic composition of adults was consistent with a diet partly made of small *E. sardella* (<5 mm), which have a δ^{15}N signature about a trophic level (3‰) lighter (average 4.8‰; Bootsma et al. 1996). The δ^{13}C signature of small *D. limnothrissa* was consistent with a diet based on *Chaoborus* larvae and copepods, as reported by Turner (1996). Large *D. limnothrissa* specimens (100–128 mm SL) had a higher average δ^{15}N signature (7.71 ± 0.68) than the small specimens (70–80 mm: 6.56 ± 0.17), indicating that they relied on food sources of a slightly higher trophic level (Fig. 3). The remaining part of *D. limnothrissa* diet was composed of unidentified material, detritus and other items (cichlid fry, scales, fish eggs, chironomid larvae, cladocerans, bivalves, sand, diatoms, and other algae). Unlike that of *A. mentale* and *C. virginalis*, the diet composition of *D. limnothrissa* varied strongly among months, being dominated by copepods in November 1998, April and May 1999, by *E. sardella* larvae in January 1999, or by *Chaoborus* larvae in March 1999 (Appendix A).

Diplotaxodon macrops

Diplotaxodon macrops is a deep-water species found at depths of 75–125 m (Duponchelle et al. 2003). Stomachs with measurable contents were not as frequent as those found for *D. limnothrissa*, and only 20 specimens were analysed between November 1998 and May 1999. The average weight of the stomach contents was 61.2 mg, ranging from 5.4 to 157.4 mg for fishes of 85- to 118-mm SL (17–42 g).

Turner (1996) reported *D. macrops* was zooplanktivorous. Our results tend to support this statement, as 55% of the overall diet comprised copepods and *Chaoborus* larvae (Fig. 1). Its mean δ^{13}C isotopic signature supported these results (Fig. 3). The remaining part of the diet was composed of chironomid larvae, sand, detritus, unidentified material, and other items (scales, adult insects, cladocerans, macrophytes, diatoms, and other algae). It is important to note that in months when more than only one or two specimens were examined, zooplankton accounted for 84%–99% of the diet (December 1998, April and May 1999) (Appendix A). Chironomid larvae constituted a significant part of the diet only once in November 1998, with a single fish examined. *Chaoborus* larvae were dominant items in February and May 1999 (Appendix A). The diet composition of *D. macrops* was generally similar to that of *D. limnothrissa*, with copepods and *Chaoborus* larvae accounting for most of their diets. However, their feeding strategies appeared to be slightly different, as benthic invertebrates and significant amounts of sand were regularly found in *D. macrops* stomachs, suggesting a benthic foraging activity not observed in *D. limnothrissa*. *D. macrops* δ^{15}N and δ^{13}C signatures also distinguish it from *D. limnothrissa*. Adults relied on enriched N sources and slightly depleted C sources, whereas small individuals relied on enriched N and C sources compared with *D. limnothrissa* (Fig. 3). The few small specimens (<90-mm SL) for which stomachs were found with remaining items, contained almost exclusively copepods and *Chaoborus* larvae (Appendix A). However, as the mean δ^{13}C signature of small *D. macrops* was about 2‰ greater than the mean zooplankton signature, they must also rely on more enriched carbon sources. The significant amounts of sand and benthic invertebrates encountered in stomach contents suggest a benthic foraging activity. The consumed benthic invertebrates probably rely to a significant degree on periphyton, which has an enriched $\delta^{13}C$ signal (–8‰ to –16‰; Bootsma et al. 1996). Also, the fact that small *D. macrops* belong to a higher trophic level (mean $\delta^{15}N$ 8.20‰) than the exclusively zooplanktivorous small *C. virginalis* (5.83‰) indicates they mostly rely on food sources other than zooplankton. In a previous study, *Chaoborus* larvae were found to have a $\delta^{15}N$ of between 5.5 and 7.5 (H. Bootsma, unpublished data), indicating that this organism may account for an important part of the diet of *D. macrops*.

Lethrinops argenteus and *Taeniolethrinops praeorbitalis*

Lethrinops argenteus (= *L. longipinnis* orange head) mainly occurs at depths between 10 and 30 m (Duponchelle et al. 2003). The stomachs of 34 specimens were examined during the period November 1998 – May 1999. The average weight of the stomachs contents was 54.2 mg, with a range of 6–197 mg for fishes of 92- to 142-mm SL (37–87 g). Diet composition of *L. argenteus* was essentially made up of chironomid larvae (Fig. 1), but also included sand, detritus, unidentified material, and other items (scales, fish eggs, insects adults, larvae and pupae, crustacean zooplankton, nematodes, gastropods, bivalves, macrophytes, diatoms, and other algae). Given the nature of the main ingested food item and the presence of large amounts of sand in each sample, this species seems to be a benthic invertebrate feeder, as suggested by its morphology.

Taeniolethrinops praeorbitalis is a shallow water species encountered at depths of 10–30 m (Duponchelle et al. 2003). The stomachs of 13 specimens were examined between November 1998 and May 1999. The average weight of the stomach contents was 49.3 mg, with a range of 5–142 mg for fishes of 97- to 193-mm SL (24–166 g). This species is known to feed primarily on chironomid larvae (Fryer 1959; Eccles and Trewavas 1989; Turner 1996). However, specimens examined by Fryer (1959) were sometimes full of nematodes. Jackson (cited by Turner 1996) reported that *T. praeorbitalis* fed mostly on *Chaoborus* larvae. Konings (1995) reported its main food is insect larvae. Detritus, diatoms, and sand were also reported to occur in its diet (Turner 1996). The 13 specimens we examined fed largely on chironomid larvae, which averaged 46% of the diet (Fig. 1). Overall, copepods accounted for 13% of stomach content, though they were present only in small specimens (Appendix A). The remaining components of the diet were large amounts of sand, detritus, unidentified materials, and other items (scales, insect adults and pupae, nematodes, macrophytes, cladocerans, diatoms, and other algae). No temporal variability in diet composition was noticed, the only variation being the relative proportions of chironomids and sand between months (Appendix A). The small specimens (90- to 130-mm SL) analysed tended to have a smaller proportion of chironomid larvae in their stomachs and larger proportions of copepods and plant material than did large individuals (165–195 mm) (Appendix A).

Lethrinops argenteus and *T. praeorbitalis* had very similar feeding strategies and did not differ in diet composition or in adults' isotopic composition (Table 1). Only the young of *T. praeorbitalis* had enriched $\delta^{13}C$ signatures (Fig. 3; Table 1). Stomach content analysis for both species showed diet composition mainly consisted of chironomid larvae, sand, detritus, and other items. However, *L. argenteus* and *T. praeorbitalis* $\delta^{13}C$ signatures were more enriched than expected if they were relying only on chironomid larvae at depths of 10 and 30 m. As these species are bottom feeders ingesting large amounts of sand, they probably also have other food sources with enriched carbon signals, such as periphyton (Bootsma et al. 1996) or other plant material, which were indeed regularly found in stomachs (macrophytes and unidentifiable algae). Stomach analysis revealed that apart from chironomid larvae, zooplankton and plant material were important components of the diet for both species. However, as the zooplankton has a more depleted $\delta^{13}C$ signal than that of chironomid larvae found in shallow water, it cannot account for the enriched $\delta^{13}C$ signature of small *T. praeorbitalis* and *L. argenteus* individuals compared with large ones (Fig. 3). Oligochaetes, which are difficult to identify in stomachs when digested, have been found to account for more than 50% of the *T. praeorbitalis* diet (W. Darwall, IUCN/SSC UK Office, 219c Huntingdon Road, Cambridge CB3 ODL, UK; will.darwall@ssc-uk.org, personal communication) and might have constituted an important part of the unidentified material in our analysis. Unfortunately, we did not sample a sufficient number of oligochaetes at 10 m for stable isotope analysis, where all the *T. praeorbitalis* analysed for isotopic composition were caught. Nevertheless, given the large difference in $\delta^{13}C$ signatures between oligochaetes at 100 and 30 m (Fig. 3), oligochaetes are likely to have an enriched $\delta^{13}C$ signature in the shallow waters. The benthic foraging habits of *T. praeorbitalis* and *L. argenteus* suggest that they may rely on periphyton with enriched $\delta^{13}C$ signatures found in sediment (Bootsma et al. 1996). The higher $\delta^{13}C$ and lower $\delta^{15}N$ suggest that small *T. praeorbitalis* and *L. argenteus* may rely even more than adults do on benthic algae, and may occupy a shallower habitat.

Lethrinops gossei

Lethrinops gossei is a deep-water species mainly caught at depths of 75–125 m (Duponchelle et al. 2003). Despite its deep-water existence, non-everted stomachs were found, though they were seldom full. The stomachs of 21 specimens were examined between November 1998 and May 1999. The average weight of the stomach contents was 72.7 mg, ranging from 5 to 210 mg for fishes of 101- to 155-mm SL (33–118 g).

Turner (1996) reported that this species fed on benthic arthropods, and Allison et al. (1996*b*) found *Chaoborus* larvae and pupae to make up to 94% of its diet, with some chironomid larvae. In contrast, our results indicated a mixed diet of benthic invertebrates and zooplankton (Fig. 1). Over the sampling period, dominant food items were *Chaoborus* larvae, chironomid larvae, diatoms, and copepods, together making up to 76% of the *L.gossei* diet. Its $\delta^{13}C$ signature, in the range of that of *Chaoborus* larvae and zooplankton, might indicate that this species relies primarily on these food sources (Fig. 3). However, as we do not have stable carbon isotope data for chironomid larvae in deep waters, nor of diatoms specifically, their potential importance in the *L. gossei* diet cannot be excluded. The remaining part of the diet was made of unidentified material, detritus, and other items (scales, insects adults, larvae and pupae, nematodes, macrophytes, and other algae). Diet composition was highly variable from one month to another, being dominated by diatoms in December 1998 and January 1999, by chironomid larvae in April 1999, and by *Chaoborus* larvae in March and May 1999 (Appendix A). As only a very small amount of sand was found in the stomachs, the large amounts of diatoms ingested suggest some planktonic feeding. *Lethrinops gossei* had among the highest average δ^{15}N signatures (8.12) of fishes sampled as part of this study (Fig. 3). Small specimens had enriched δ^{13}C and slightly depleted δ^{15}N values compared with those of large specimens. The smallest specimen found with remaining items in its stomachs was 101-mm SL, and diatoms made up 44% of its diet. Small *L. gossei* may rely even more upon diatoms than the adults, which could account for the difference in isotopic composition.

Mylochromis anaphyrmus

Mylochromis anaphyrmus frequents the shallow waters between 10 and 50 m (Duponchelle et al. 2003). The stomachs of 36 specimens were examined between November 1998 and May 1999. The average weight of the stomachs contents was 45.6 mg, ranging from 8 to 290 mg for fishes of 84- to 151-mm SL (16–125 g).

This species is known as a gastropod feeder (McKaye et al. 1986; Konings 1995; Turner 1996), although copepods, chironomids, algal remains, and arthropod material are sometimes found (Turner 1996). Most of the specimens we examined had large quantities of snail remains in their guts. However, what is presented here is only the stomach content analysis. Gastropods averaged 15% (4%–44%) of the stomach contents (Fig. 1). Chironomid larvae accounted for 41%, adult insects for 10%, and crustacean zooplankton for 5%. However, the isotopic composition of *M. anaphyrmus* was consistent with a diet based mostly on gastropods, for which the average signatures at 30 m (the most common depth of the species in the sampled area) were –22.02 and 3.13 for δ^{13}C and δ^{15}N, respectively (Fig. 3). Often a food source is 0.5‰–1‰ enriched in ^{13}C relative to its consumer (Peterson and Fry 1987). The 1.85‰ found here might be explained by a preference for particular gastropod species with slightly lighter signatures or by feeding partly at shallower depths, where gastropods can be expected to have enriched signals (Bootsma et al. 1996). The remaining part of stomach content was made of sand, unidentified material, and other items (scales, chironomid pupae, *Chaoborus* larvae, insect pupae and larvae, nematodes, bivalves, macrophytes, diatoms, and other algae). Individuals below 100 mm SL tended to have higher proportions of chironomid larvae in their stomachs: more than 99% for the two smallest specimens (80 and 84 mm) (Appendix A).

With the exception of a few species that actually feed upon fish (e.g., *A. mentale*, *D. limnothrissa*), the presence of fish scales in almost every stomach analysed, regardless of species, is probably an artifact caused by the crowding of fishes during the trawl hauling. Indeed, at every haul, medium and large fish, including nonpiscivorous species, had small fish stuck in their mouths.

Resource partitioning

Despite the high variability of stomach fullness encountered during this study, particularly for the deep-water species, a good correspondence between the results of stomach content and stable isotope analyses was observed for most of the nine fish species. Nevertheless, the use of both stomach content and stable isotope analyses (δ^{13}C and δ^{15}N) proved very useful in elucidating dietary differences between species. Every species differed significantly from the others by at least one of the three types of analyses (stomach content, δ^{13}C and δ^{15}N), demonstrating the complementarity of these approaches (Table 1).

Species with very different feeding habits (reflected in their stomach content), such as *C. virginalis*, small *D. limnothrissa*, large *L. gossei*, and large *A. mentale* (Fig. 3), would have been impossible to distinguish without a combined analysis of δ^{13}C and δ^{15}N signatures. They only covered a δ^{13}C range of 0.4‰, but were discriminated by a 2.97‰ δ^{15}N range. Species with a narrower feeding regime, such as *A. mentale* or *C. virginalis*, had an isotopic composition closely matching the stomach content observations. For *M. anaphyrmus*, despite the observed dominance of other food items in the stomachs, the isotopic composition confirmed the previously reported snail diet of the species (McKaye et al. 1986; Eccles and Trewavas 1989; Konings 1995). The stomach contents we observed reflect feeding habits for several hours prior to capture, which appear to have been different from the longer term feeding habits, as reflected in isotopic composition. Stomach content analysis indicated temporal trends of diet composition for both *L. argenteus* and *T. praeorbitalis*, mainly dominated by chironomid larvae. However, stable isotope analysis suggested that algal food items were likely playing an important role in the diet of these species, particularly for the small specimens. Differences in feeding habits and in isotopic composition are expected between species as morphologically different as *A. mentale* and *C. virginalis* or *T. praeorbitalis*. However, significant isotopic differences were found (Table 1) between closely related species with very similar stomach contents, such as *D. limnothrissa* and *D. macrops*, and between typical invertebrate feeders with similar stomach content compositions and identical depth preferences, such as *L. argenteus* and *T. praeorbitalis*. Species with a complex feeding regime, such as *A. macrocleithrum*, *D. limnothrissa*, *D. macrops*, and *L. gossei*, showed important temporal variations in diet composition (Appendix A). These four species heavily fed upon *Chaoborus* larvae when available. For each of these species, *Chaoborus* larvae were dominant items in their stomachs in exactly the same months, March and May, and only in these months (Appendix A). This suggests that the observed feeding regimes were related to temporal fluctuations in food resources, although we do not have data to back up this hypothesis. These observations would not have been possible without monitoring stomach contents, and they highlight the complementary nature of stomach content and stable isotope approaches in the study of feeding habits and trophic patterns of complex fish communities.

These observations also emphasised the importance of *Chaoborus* for the deepwater demersal fishes. *Alticorpus macrocleithrum*, *D. limnothrissa*, *D. macrops*, and *L. gossei* averaged 30–43% of the total biomass in the deep waters (75–125 m) over a 1-year monthly demersal trawl survey in the SWA of the lake (Duponchelle et al. 2003). Added to other species relying heavily on *Chaoborus*, such as the catfish *Synodontis njassae* (Allison et al. 1996*a*, 1996*b*), which averages about 10% of the total fish biomass in the deep waters (Duponchelle et al. 2003), about 50% of the fish biomass depends, at least partly, upon *Chaoborus*. This supports the recent work of Allison et al. (1996*a*, 1996*b*), and suggests that fish production would not be increased by the introduction of other planktivorous fish species, as has been suggested in the past (Turner 1982; Walczak 1982). Our results also partially support the hypothesis of Allison et al. (1996*b*) that "because *C. edulis* feeds on crustacean zooplankton, demersal fish production may therefore be principally sustained through the pelagic food chain rather than from benthic detrital sources." They only partially support this hypothesis because they do confirm the importance of *C. edulis* as a food source for benthic fishes, but they also show that there is a heavy reliance upon benthic prey organisms for most species. Isotopic composition clearly illustrates the diet separation among these demersal fish: one on the hand there is the pelagic phytoplankton food chain, centred near a δ^{13}C of –23‰ with at least three trophic levels (zooplankton and *Chaoborus* larvae, zooplanktiverous fishes, such as *E. sardella* and *C. virginalis*, and fishes of a higher trophic level such as *A. mentale*, *A. macrocleithrum*, *D. limnothrissa*, *D. macrops*, and *L. gossei*, some of which feed upon other fishes). On the other hand, there is an ascending line towards heavier carbon and lighter nitrogen sources represented by *L. argenteus* and *T. praeorbitalis*, which most likely represents, in large part, a periphyton-based food web. In fact, given the much heavier δ^{13}C signature of periphyton (Bootsma et al. 1996), the shift to heavier carbon and lighter nitrogen likely represents mixed feeding on both the periphyton-based source and the phytoplankton-based source. This is interesting, in that it suggests that benthic algal production is contributing to energy flow of the offshore fishes at depths of 10–30 m.

These examples demonstrate the existence of distinct feeding strategies between species with apparently similar diets and feeding behaviors, and support the assertion that important resource partitioning exists among Lake Malawi haplochromine cichlids (Bootsma et al. 1996; Genner et al. 1999*a*; Turner 1996). As suggested by Bootsma et al. (1996), this partitioning can be achieved by either of the following: (1) feeding on different food types, such as *A. macrocleithrum*, *A. mentale*, *Diplotaxodon macrops*, and *L. gossei* (each of these species inhabit the deep waters below 75 m, but feed on different sources), or (2) feeding on similar food types but from different locations (i.e., spatial partitioning), such as *D. limnothrissa* and *D. macrops*. Although they had similar stomach contents (Table 1), their feeding strategies were different: the presence of benthic invertebrates and sand in *D. macrops* suggested a benthic foraging activity not observed in *D. limnothrissa*, which was supported by their different δ^{15}N signatures.

If the apparent partitioning of resources is critical for the maintenance of these species-rich fish communities, then changes in water quality and habitat structure may have serious implications for diversity in Lake Malawi and other African rift valley lakes. Studies in Lake Tanganyika (Alin et al. 1999; Donohue and Irvine 2004) provide strong evidence that increased sediment loads result in reduced diversity of benthic invertebrates. Recent data (Bootsma et al. 2003; Hecky et al. 2003) suggest that riverine inputs of nutrients and suspended sediment to Lake Malawi are increasing, and nutrient and sediment loads from some rivers draining heavily impacted watersheds are exceptionally high. The data presented here suggest that food resource partitioning is a common practice within the species-rich demersal fish community of Lake Malawi; therefore, any decline in diversity of benthic invertebrates resulting from these increased sediment loads will likely increase the potential for competitive exclusion within the fish community.

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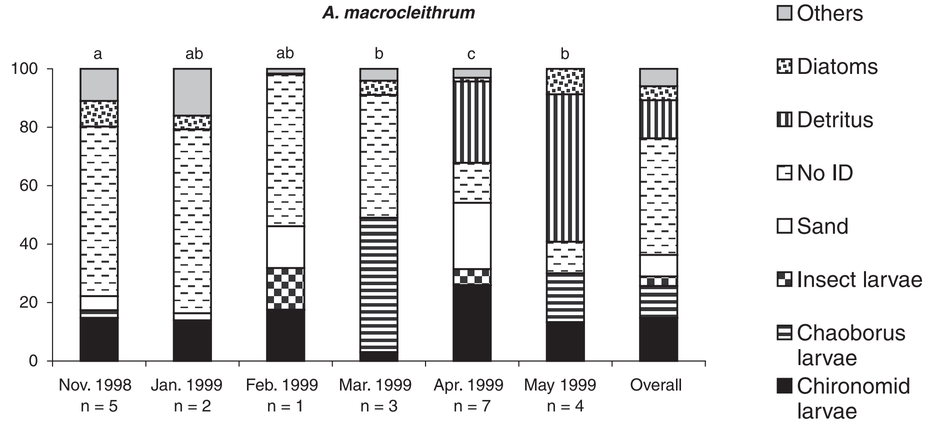
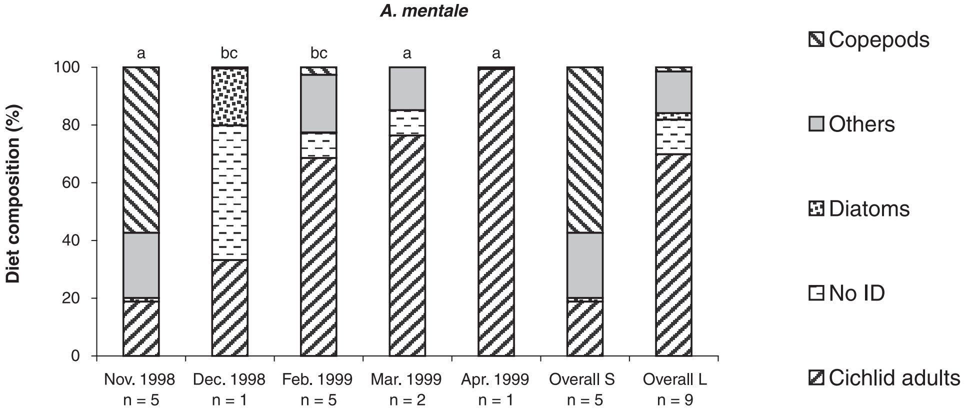
(Appendix A follows.)

Appendix A

Fig. A1. Overall and monthly diet composition (% stomach content) of nine demersal cichlid fishes in the SWA of Lake Malawi. “Others” refers to materials such as scales, fish eggs, insects adults, larvae, and pupae, crustacean zooplankton, nematodes, gastropods, bivalves, macrophytes, diatoms, and other algae making up less than 2% of the diet. Unidentifiable materials were recorded as “No ID”. Different letters indicate significant differences between months ($\alpha = 0.05$). The overall diet composition was divided between small (S) and large (L) specimens when small individuals were analyzed. A distinction was made between small and large individuals when a significant correlation was observed between size and either $\delta^{15}N$ or $\delta^{13}C$ in Fig. 2. For *Alticorpus mentale*, small ranged from 110 to 117 mm and differed significantly from large specimens (170–245 mm, $p < 0.001$). For *Copadichromis virginalis*, small ranged from 70 to 85 mm and did not differ from large specimens (90–115 mm, $p = 0.525$). For *Diplotaxodon macrops*, small ranged from 85 to 99 mm and did not differ from large specimens (105–118 mm, $p = 0.679$). For *Mylochromis anaphyrmus*, small ranged from 80 to 99 mm and did not differ from large specimens (101–151 mm, $p = 0.152$). For *Taeniolethrinops praeorbitalis*, small ranged from 97 to 127 mm and did not differ from large specimens (168–183 mm, $p = 0.864$). (Figure A1 is concluded on the following pages.)





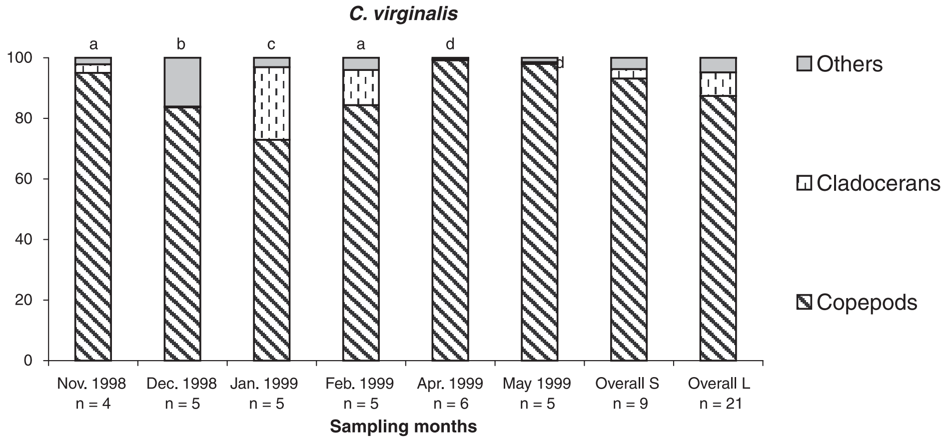


Fig. A1 (*continued*).

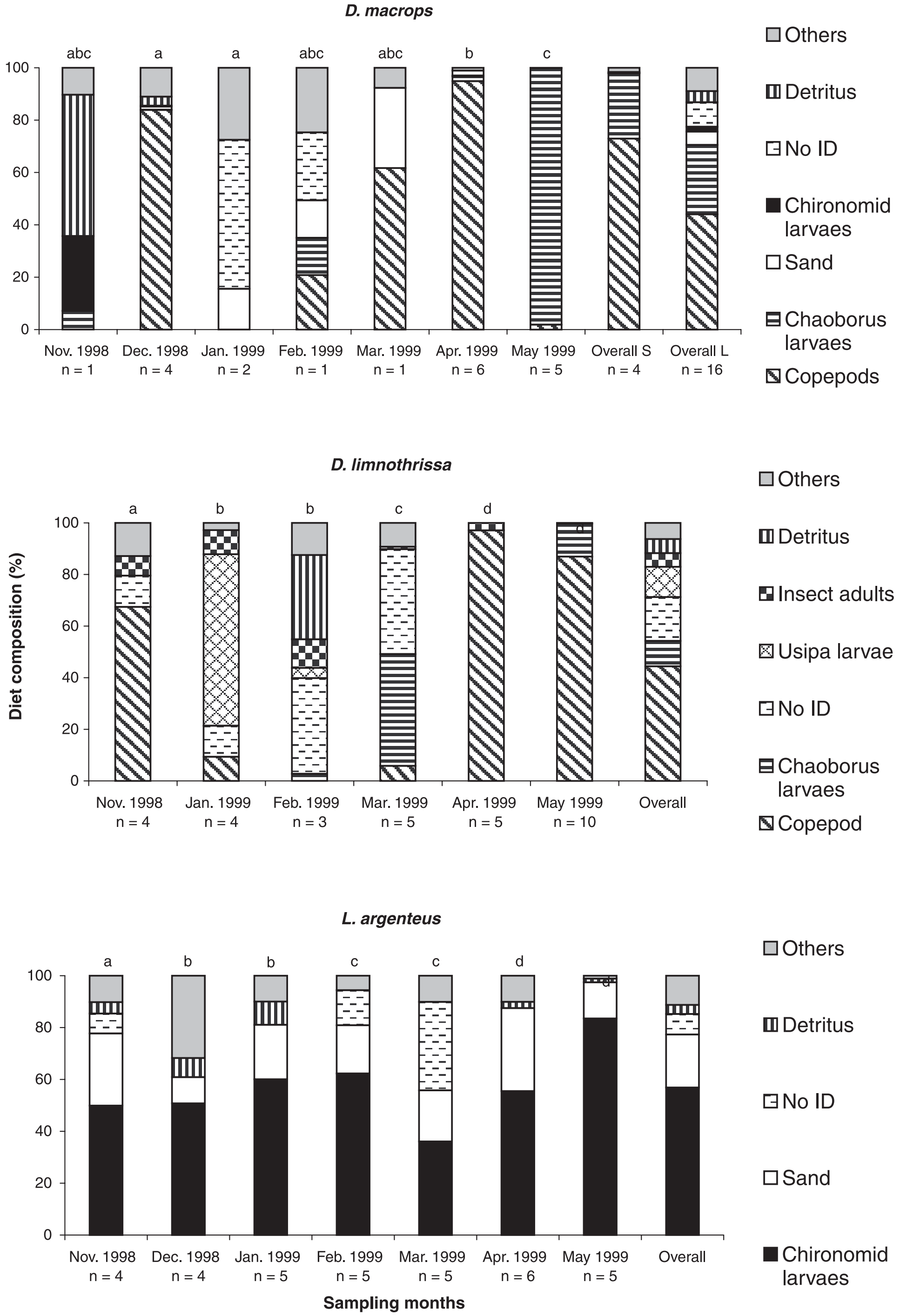


Fig. A1 (*concluded*).