Chapter 4: Temporal diet patterns of some Lake Malawi demersal fish species as revealed by stomach contents and stable isotope analysis

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Introduction

Cichlids have evolved an astonishing diversity of feeding adaptations and behaviours that enable them to utilise virtually any kind of food, from phytoplankton, epilithic and epiphytic algae, plants, detritus, zooplankton, molluscs, insects, benthic invertebrates, fish eggs, larvae, eyes, and scales, to whole fish (reviews in Fryer & Iles 1972, Ribbink 1990, Yamaoka 1991). The role of the feeding apparatus and trophic specialisations in the adaptive radiation of African cichlids has often been discussed (Fryer & Iles 1972, Liem 1980, 1991, McKaye & Marsh 1983, Ribbink et al. 1983, Reinthal 1990, Ribbink 1990, Yamaoka 1991). The understanding of how such rich and diverse fish communities with apparently similar food requirements can coexist still challenges ecologists. In Lake Malawi, since Fryer's (1959) suggestion that the mbuna community was violating the Gaussian principle of competitive exclusion, several studies have provided evidences that food partitioning may reduce interspecific competition and allow coexistence among rock-dwelling cichlids fishes (McKaye & Marsh 1983, Marsh & Ribbink 1985, Reinthal 1990, Bootsma et al. 1996, Genner et al. 1999a, 1999b, 1999c). Similar conclusions have resulted from research in Lake Tanganyika (Sturmbauer et al. 1992) and Victoria (Bouton et al. 1997). However, while diet, feeding behaviour and trophic specialisations have been, and still are, intensely studied in Malawian rock-dwelling species, very little is known of the divers offshore (sensu Turner 1996) cichlid communities. Apart from the zooplanktivorous utaka group (*Copadichromis spp.*) (Fryer & Iles 1972), the chambo (*Oreochromis spp.*, Turner et al. 1991b) and the pelagic species, whose feeding ecology was recently thoroughly studied (Allison et al. 1996, Ngatunga & Allison 1996), the only information available on the diet of offshore fishes comes from Eccles & Trewavas (1989) and Turner (1996). These studies resulted in useful now insights into fish feeding habits, but they were limited by the relatively small numbers of observations and the limited time span over which fish stomach contents were monitored. The currently running European Union Project: "The trophic ecology of the demersal fish community of lake Malawi/Niassa", partly aimed at filling this gap, will improve our knowledge. However, the seasonal variability of fish diet is not a priority of the EU Project. The temporal aspect of demersal fish diets was investigated in the context of a general program designed to assess the seasonal progression of distribution, abundance and diversity of the fish species exploited by demersal trawling and to determine their main life history characteristics. Such a study had been considered when the new "Ecology program" had started in June 1998, but had been cancelled because the research actions already undergone were too time and people-consuming to allow the addition of another program. However, when a new staff member detached from the World University Service of Canada (WUSC) joined the ecology team of the project in October 1998, the study was reconsidered and initiated in November 1998. However, since the program ended in June 1999, an entire annual cycle could not be studied. We decided to determine the diet and its potential seasonal variability for the nine target species retained for the life history study (*Lethrinops gossei*, *Lethrinops argenteus* = *L. longipinnis 'orange head'*, *Diplotaxodon limnothrissa*, *Diplotaxodon macrops*, *Copadichromis virginalis*, *Mylochromis anaphyrmus*, *Alticorpus mentale*, *Alticorpus macrocleithrum* and *Taeniolethrinops praeorbitalis*) with both monthly stomach content and stable isotope analysis. Whereas stomach content analysis provides insight into the ingested food items over a short time period, stable isotope signatures represent a spatio-temporal integration of the assimilated food over long time periods varying from months to years depending on fish growth rates (Peterson & Fry 1987, Hesslein et al. 1991, 1993, Bootsma et al. 1996, Gannes et al. 1997, Gorokhova & Hansson 1999, Fry et al. 1999). Stable isotope analysis is particularly useful for deep-water species that often have inverted stomachs when retrieved from trawls.

Material and methods

Stomach content analysis

Seasonal variability of diet was estimated over 8 months for the nine target species. Fish were collected from the monthly trawl survey in the north of the South West Arm (SWA). Every month from November 1998 to May 1999, 20 specimens of each species were sampled from the main catch as soon as the total catch weight was estimated. 15% formalin was injected in the abdominal cavity of each fish to ensure the preservation of food items and the fish were fixed in 10% formalin for later examination. A frequently encountered problem when trawling below 50m depth is that the stomachs are often burst out of the fish mouths during hauling. For *Alticorpus mentale*, whose stomachs were almost systematically empty, every specimen from the whole catch was checked for intact stomachs. Even apparently intact stomachs often contained only very little amounts of remaining food items.

When enough intact stomachs were available, 5 specimens of each species were analysed each month for diet composition. For the sake of data compatibility, the method used was the modified version of the "point method" (Hynes 1950) selected by the ongoing EU Project: "The trophic ecology of the demersal fish community of lake Malawi/Niassa" (Darwall, 1999). The weight of the stomach plus content and the stomach minus content were determined to the nearest 0.001g. Total weight of stomach contents was calculated as the difference between the two weights. The stomach content was then examined under binocular microscope (10X to 40X magnification). All identifiable items were grouped into separate piles and allocated one of the following value: 16, 8, 4, 2, 1, or P (if present but in negligible amounts). The most abundant items were allocated a 16 and the others items were allocated a 16, 8, 4, 2, 1 or P depending upon their abundance relative to the most abundant item. All the small items unidentifiable under the binocular were pooled under a pile of "Small Unidentified" and allocated a value according to their relative proportion of the total stomach content. The pile of small unidentified items was then mixed with a small quantity of water (approximately 4× volume of the pile) and agitated thoroughly to break up any compacted lump. The sample was then left to settle out and the excess water removed. The remaining solution was homogeneously mixed and a small quantity (approx. 0.1 ml) was poured onto a slide under a slip cover. The slide was marked into quarters to define 4 sub-samples. The whole slide was then analysed under 40X to 400X magnification to identify the full range of food items. Each sub-sample was analysed under 40X magnification and each item was allocated a number of points as described above. When the four sub-samples were quite variable, the process was repeated with a second slide to get a total of eight estimates. The composition of the small unidentified pile was then converted in percentage composition of each of its constituents and expressed as a percentage of the total stomach content. The percentage composition was calculated for each item as its own points value divided by the combined total of points for all items combined, multiplied by 100. In order to avoid giving too much weight to stomachs with only very little content, for every month each diet item value was weighted by the total weight of the stomachs analysed for that given month (W. Darwall, pers. com.).

Items which made up less than 2% of the diet each were lumped together and referred to as "others". Non identifiable materials were recorded as "No ID".

Stable isotope analysis

Fish samples for stable isotope analysis were collected by trawling during the January 1999 cruise. About six specimens of each of the nine target species, three small and three large whenever possible, were collected. Only dorsal muscle tissue was analysed. The potential food sources were collected during the April 1999 cruise. Benthic invertebrates and gastropods were sorted out from grab samples at 10, 30, 50, 75, 100 and 125 m depth. Sediment samples were taken from the upper layer 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 at the Environmental Isotope Laboratory at the University of Waterloo, Canada. Samples were run for Nitrogen and Carbon analysis on an Isochrome Continuous Flow Stable Isotope Mass Spectrometer (Micromass) coupled to a Carlo Erba Elemental Analyzer (CHNS-O EA1108). 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, is often used as a monitoring standard – ('EIL' denotes Internal Standards with values calculated using International Standards). The error for clean ball-milled standard material is +/- 0.2‰ for Carbon and +/- 0.3‰ for Nitrogen. This error can be expected to increase depending on the homogeneity, type and amount of sample used in analysis. A truer representation of sample reproducibility can be gained through sample repeats. Standards are placed throughout each run at a range of weights to allow for an additional linearity correction, when necessary, due to machine fluctuations or samples of varying signal peak areas. Nitrogen and Carbon concentrations are calculated based on Carlo Erba Elemental Standards B2005, B2035 and B2036 with an error of +/- 1%.

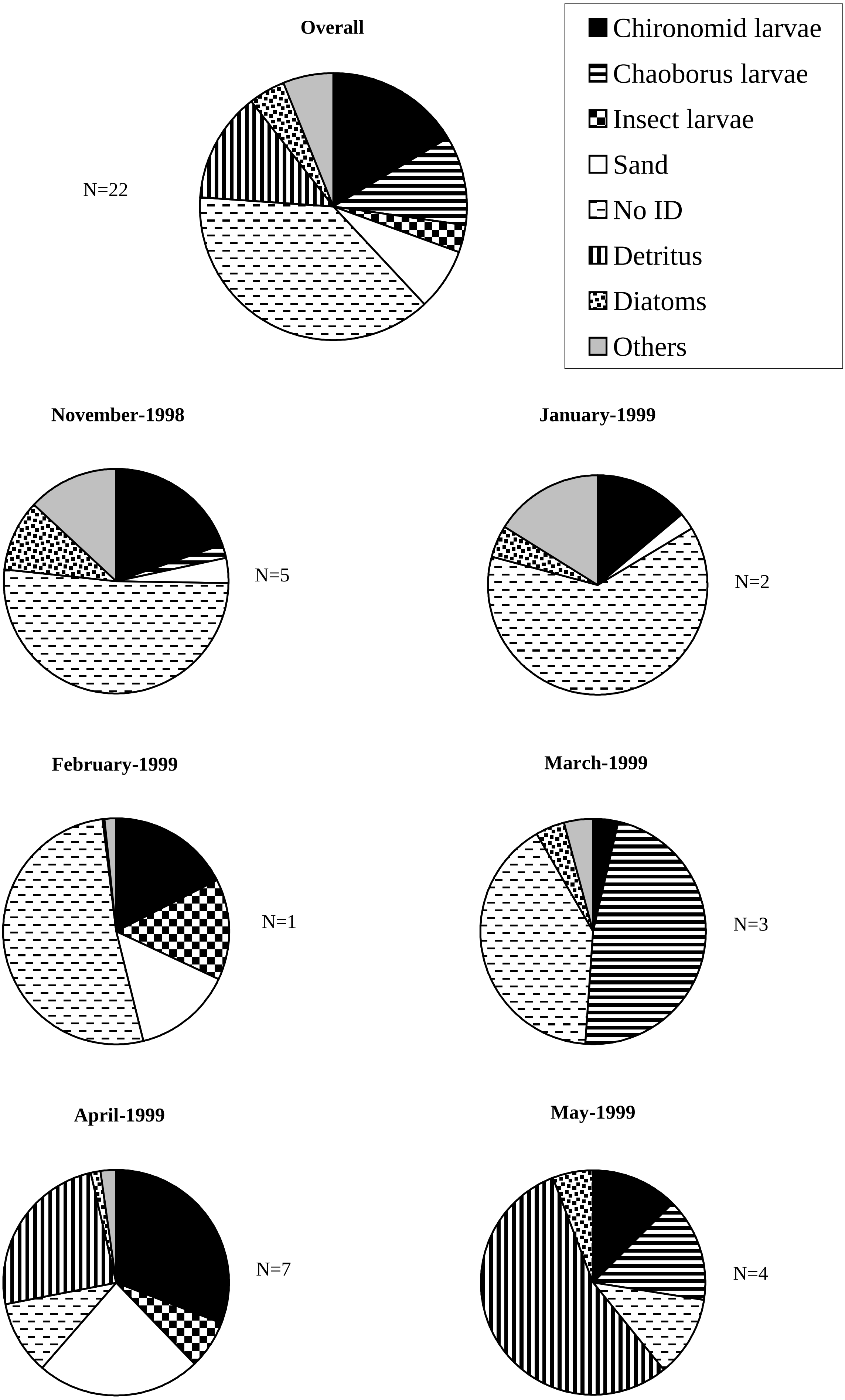


Figure D1. Overall and monthly diet composition (% wet weight) of *Alticorpus macrocleithrum* . See text for details on "Others" items.

Results and Discussion

Stomach content analysis

Alticorpus macrocleithrum

A. macrocleithrum is a deep water species found between 75 and 125 m. As for most of the deep water species, stomachs were very often inverted during trawl hauling. Only 22 specimens with remaining items in their stomachs were caught between November 1998 and May 1999. Weight of stomach contents averaged 31.2 mg and ranged from 6.4 to 96.8 mg for fishes of 103 to 137 mm SL (31-67 g). Diet composition (as percentage of the wet weight) at each sampled month and all months pooled are presented in Figure D1.

As inferred from its anatomy by Stauffer & McKaye (1985), *A. macrocleithrum* appears to be a benthic invertebrate feeder. About 51% of the diet was not identifiable though, recorded either as detritus or "no id". The other 49% were constituted 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, present at every sampled date and lake fly (*Chaoborus*) larvae, though they were found only in March and May. Owing to its short gut and deep water existence, Stauffer & McKaye suggested *A. macrocleithrum* was not feeding on algae or phytoplankton. However, at every month except in February (0.3%), diatoms constituted between 1.4 and 10.5% of the diet. Diatoms might be ingested incidentally with sediment and sand while digging to catch the invertebrates. However, diatoms accounted for 10.5 of the diet in November, when only a small quantity of sand had been ingested (compared to February and April) and for 4.1% in March where almost no sand was ingested. Next the proportion of diatoms ingested appeared too high to be incidental.

Although the high proportion of detritus and unidentified materials at every month tended to screen the potential seasonal patterns, some food items occurred in the diet only at some months (ex. *Chaoborus* and insect larvae) suggesting *A. macrocleithrum* feeds opportunistically upon these items when available, either because they were the most abundant items at the moment or because they are preferred items.

Alticorpus mentale

A. mentale is also a deep water species mostly abundant between 75 and 125 m. As stomachs were almost always empty, every specimen from the whole catch was checked for intact stomach. Despite this effort, only 14 specimens had remaining items in their stomachs during the period from November 1998 to May 1999. Weight of stomachs contents averaged 1374.8 mg and ranged from 10.2 to 6549.2 mg for fishes of 110 to 245 mm SL (25-279 g). Diet composition (as percentage of the wet weight) at each sampled month and all months pooled are presented in Figure D2.

As expected from its morphology, *A. mentale* is a piscivore. At any sampled date except December when 47% of the stomach content was unidentifiable, more than 75% of its diet consisted of adult cichlid fishes, often *Aulonocara minutus*. Other items were cichlid fry, scales, eggs, chironomid larvae, *Chaoborus* larvae, insect pupae, crustacean zooplankton, nematodes, sand, macrophytes and other algae. A significant amount of diatoms was recorded only once from a single large specimen (245 mm SL) in December, in which they made up to 19.7% of the stomach contents. No seasonal pattern was observed during the sampling period. An interesting observation, not apparent on the figures, was that of five relatively small

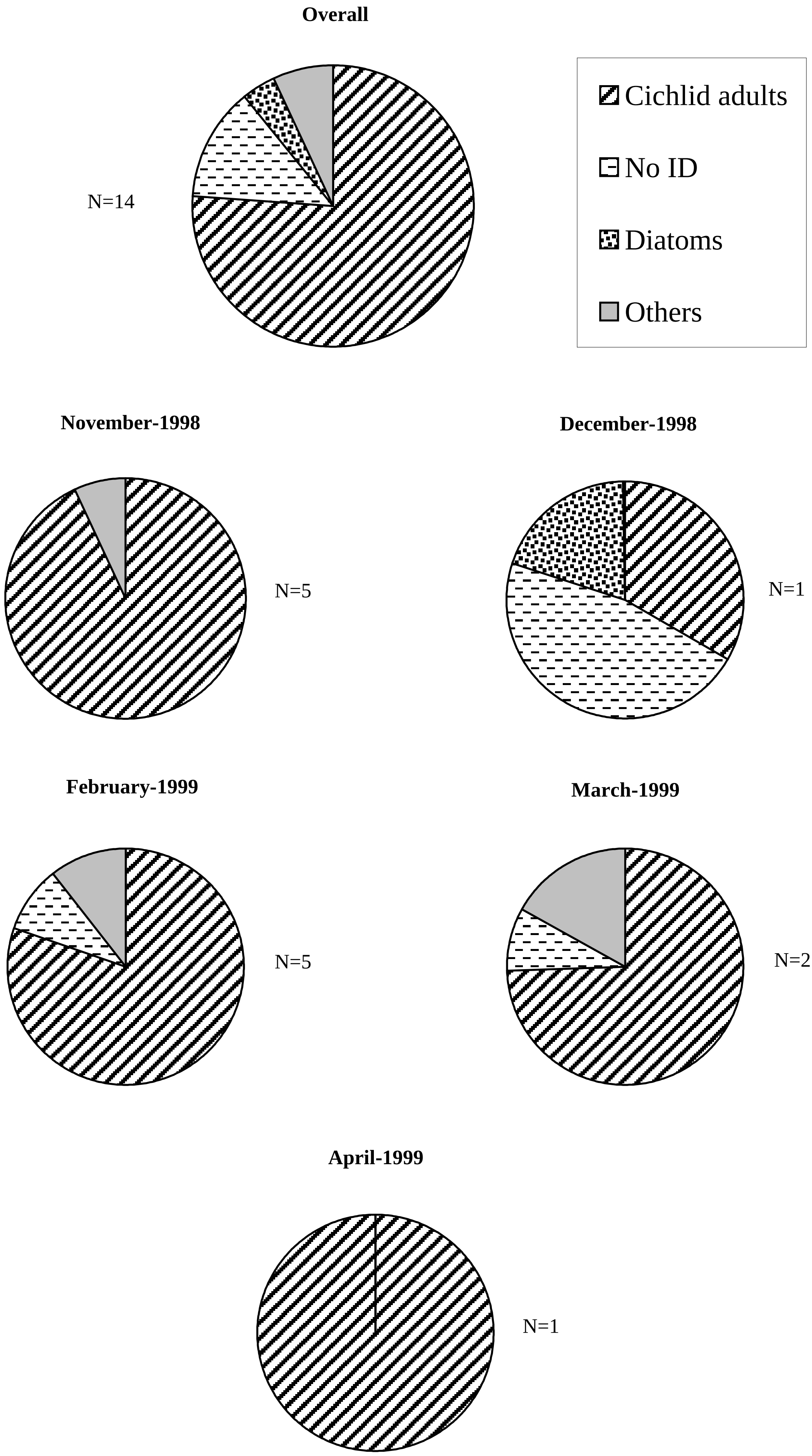


Figure D2. Overall and monthly diet composition (% wet weight) of *Alticorpus mentale* . See text for details on "Others" items.

individuals measuring between 110 and 117 mm, four fed principally (61 to 84% of the diet) on zooplankton (mostly copepods), and the fifth one fed on fish (94%). This pattern was not represented in the figures because the stomach content of these four small specimens were too light to account for a significant part of the weighted monthly mean diet.

Copadichromis virginalis

C. virginalis mainly occurs at depths between 30 and 50 m in the north of the SWA. Inverted stomachs were not a problem and 30 specimens were analysed between November 1998 and May 1999. Weight of stomachs contents averaged 68.7 mg and ranged from 18 to 190 mg for fishes of 70 to 115 mm SL (8-37 g). Diet composition (as percentage of the wet weight) at each sampled month and all months pooled are presented in Figure D3.

C. virginalis is known as a member of the zooplanktivorous *utaka* group (Iles 1971, Fryer & Iles 1972, Turner 1996). Indeed, more than 95% of the diet was made of zooplankton, mainly copepods. It was only in this species that significant amount of cladocerans were found. No seasonal pattern was observed, crustacean zooplankton constituting more than 95% of the diet at any sampled date except December 1998, when the "others" components of the diet accounted for 17%. Other items were fish scales, chironomid larvae, *Chaoborus* adults and larvae, insects adults and larvae, nematodes, macrophytes, other algae and detritus. No particular trend relative to size was observed.

Diplotaxodon limnothrissa

D. limnothrissa was found at depths from 50 to 125 m, but was mostly abundant between 75 and 100 m. Despite their deep water existence, stomachs were not always inverted after hauling and 31 specimens were analysed. Weight of stomachs contents averaged 66 mg and ranged from 8 to 272mg for fishes of 101 to 145 mm SL (20-48 g). Diet composition (as percentage of the wet weight) at each sampled month and all months pooled are presented in Figure D4.

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) reported a mixed diet composed of crustacean zooplankton, *Chaoborus* larvae, *Engraulicypris sardella* (*usipa*) larvae and occasionally phytoplankton. Our observations support the statement of a mixed diet: 71% of the diet was made of copepods, *Chaoborus* larvae, adult insects and *usipa* larvae. The remaining part of the diet was composed of unidentified material, detritus and "others" items (cichlid fry, scales, fish eggs, chironomid larvae, cladocerans, bivalves, sand, diatoms and other algae). Unlike for *A. mentale* and *C. virginalis*, diet composition strongly varied among months, being either dominated by copepods in November 1998, April and May 1999, by *usipa* larvae in January 1999 or *Chaoborus* larvae in March 1999. As for *A. macrocleithrum*, Chaoborus larvae were almost exclusively present in the diet in March and May 1999 (also some in February). *D. limnothrissa* appears to feed opportunistically on a few preferred food items depending upon their availability. No particular trend relative to size was observed in the narrow size range studied.

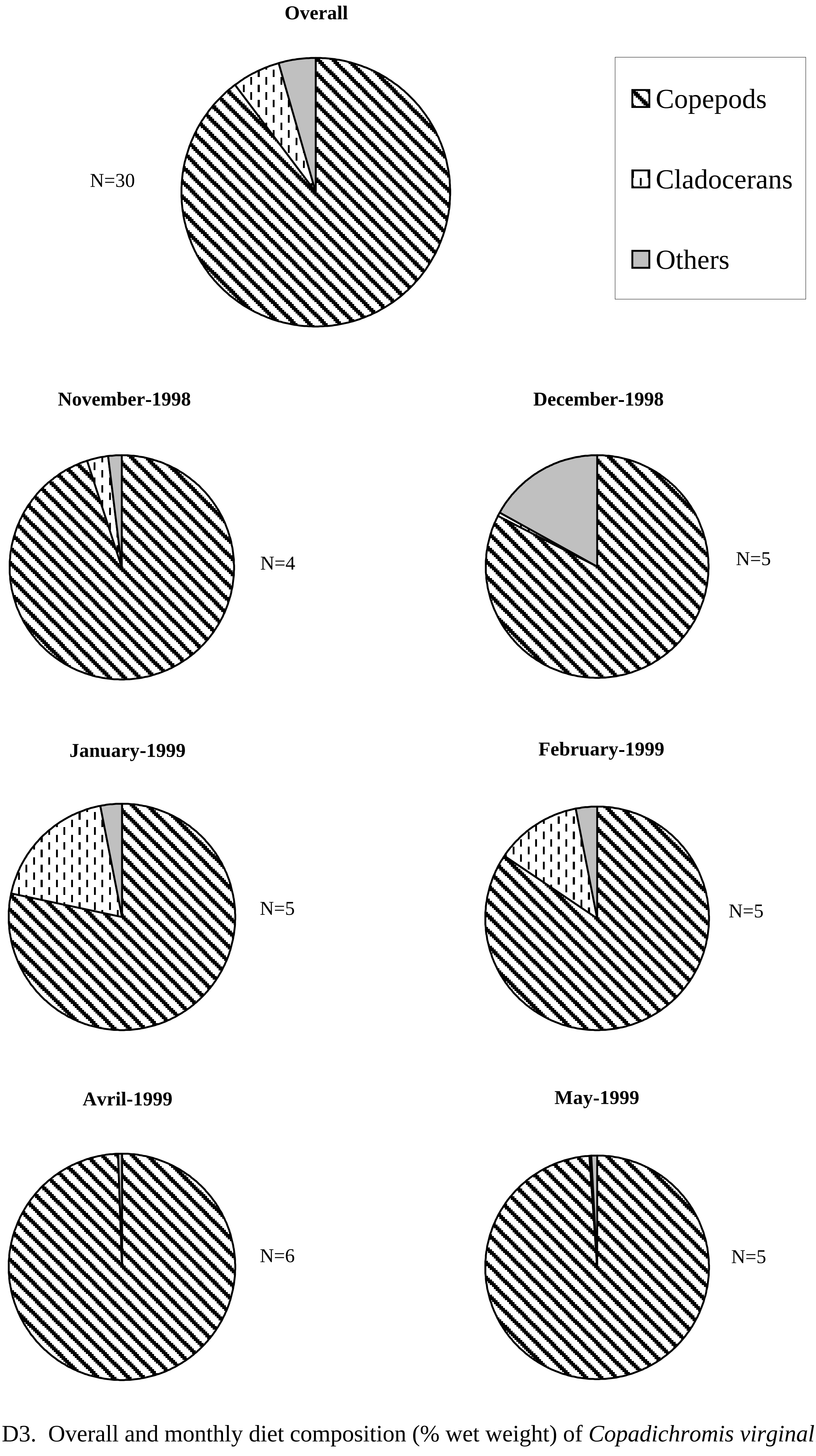


Figure D3. Overall and monthly diet composition (% wet weight) of *Copadichromis virginalis* . See text for details on "Others" items.

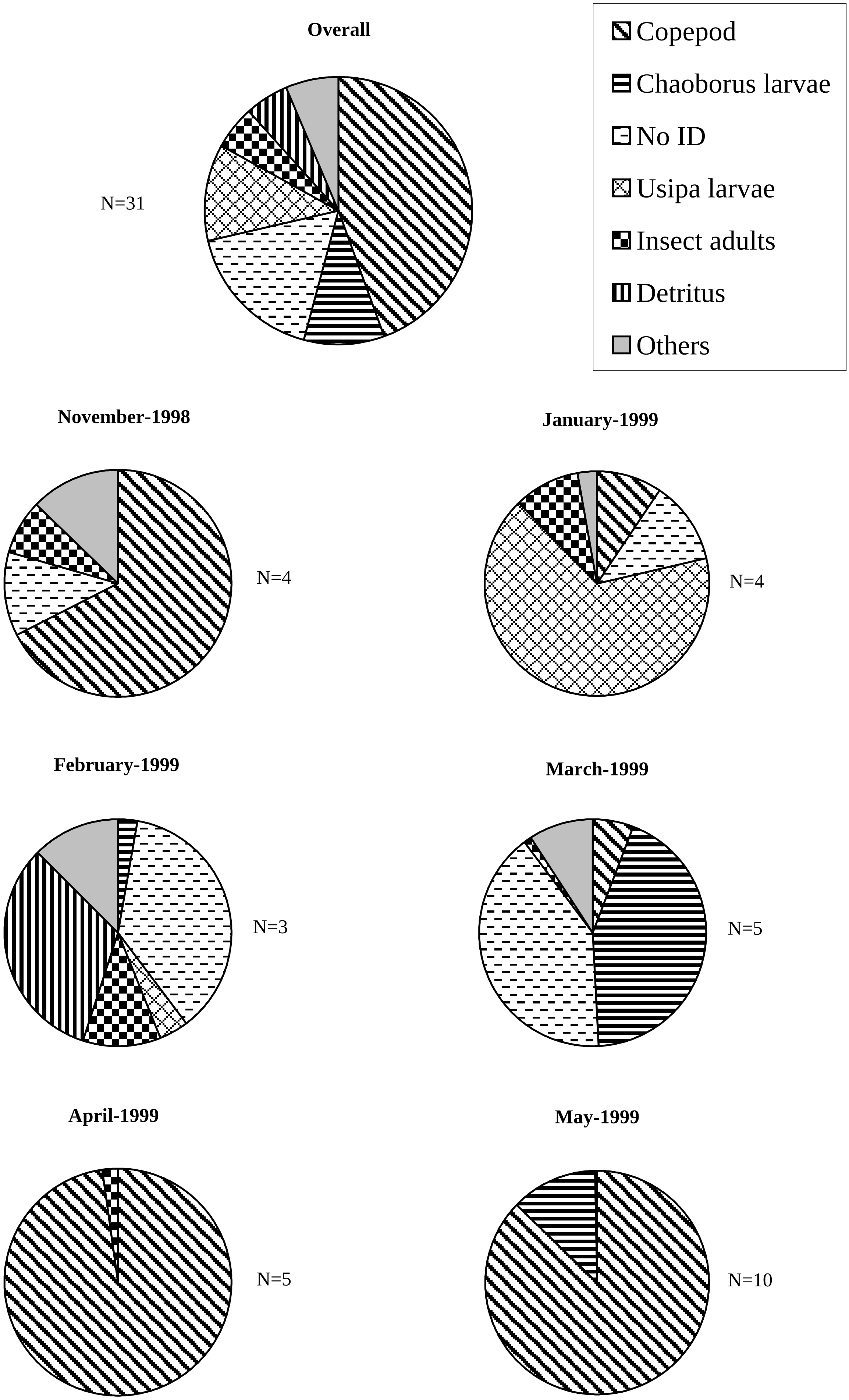


Figure D4. Overall and monthly diet composition (% wet weight) of *Diplotaxodon limnothrissa* . See text for details on "Others" items.

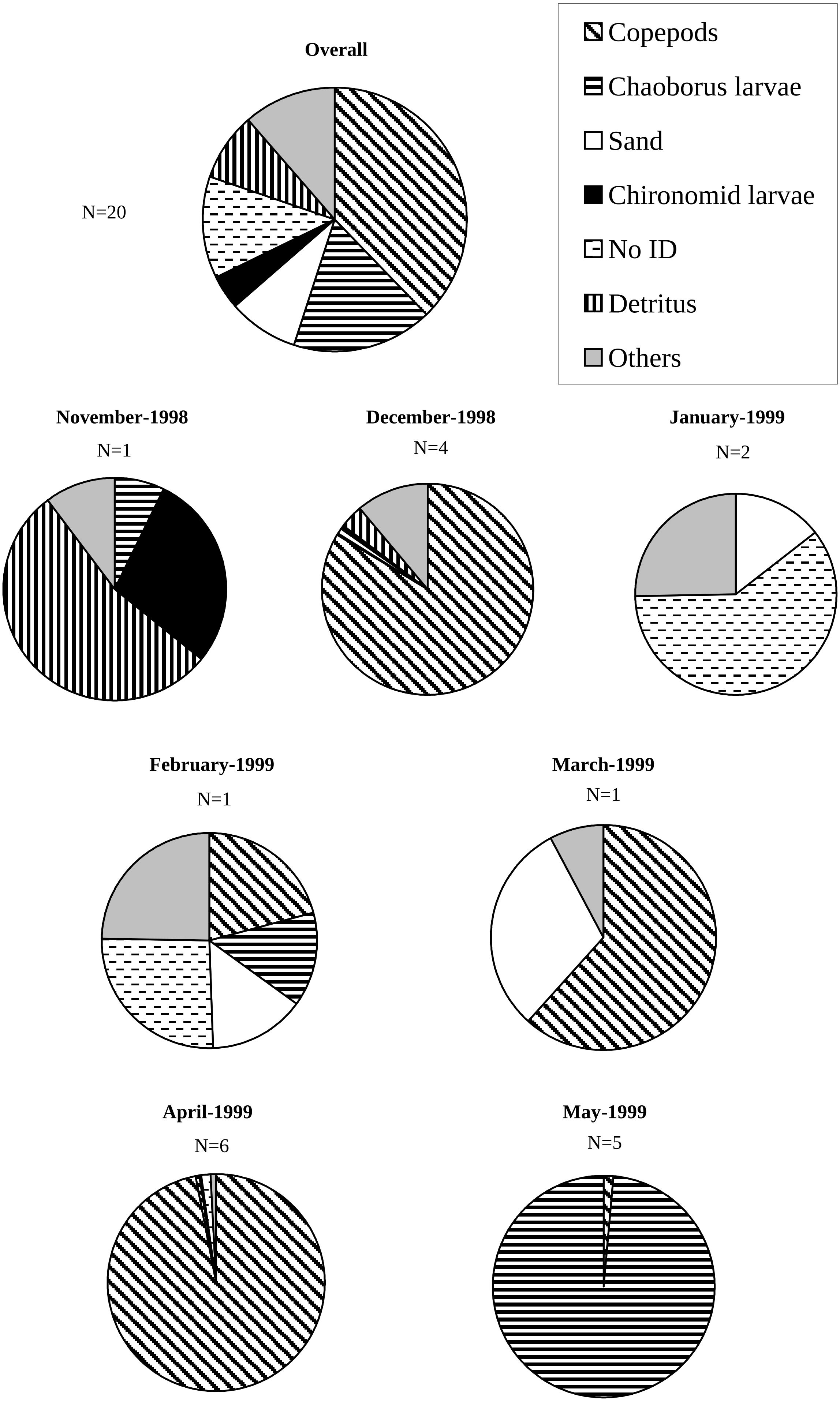


Figure D5. Overall and monthly diet composition (% wet weight) of *Diplotaxodon macrops* . See text for details on "Others" items.

Diplotaxodon macrops

D. macrops is a deep water species found from 75 to 125 m. Stomachs with remaining items were not as frequent as for D. limnothrissa and only 20 specimens were analysed between November 1998 and May 1999. Weight of stomachs contents averaged 61.2 mg and ranged from 5.4 to 157.4 mg for fishes of 85 to 118 mm SL (17-42 g). Diet composition (as percentage of the wet weight) at each sampled month and all months pooled are presented in Figure D5.

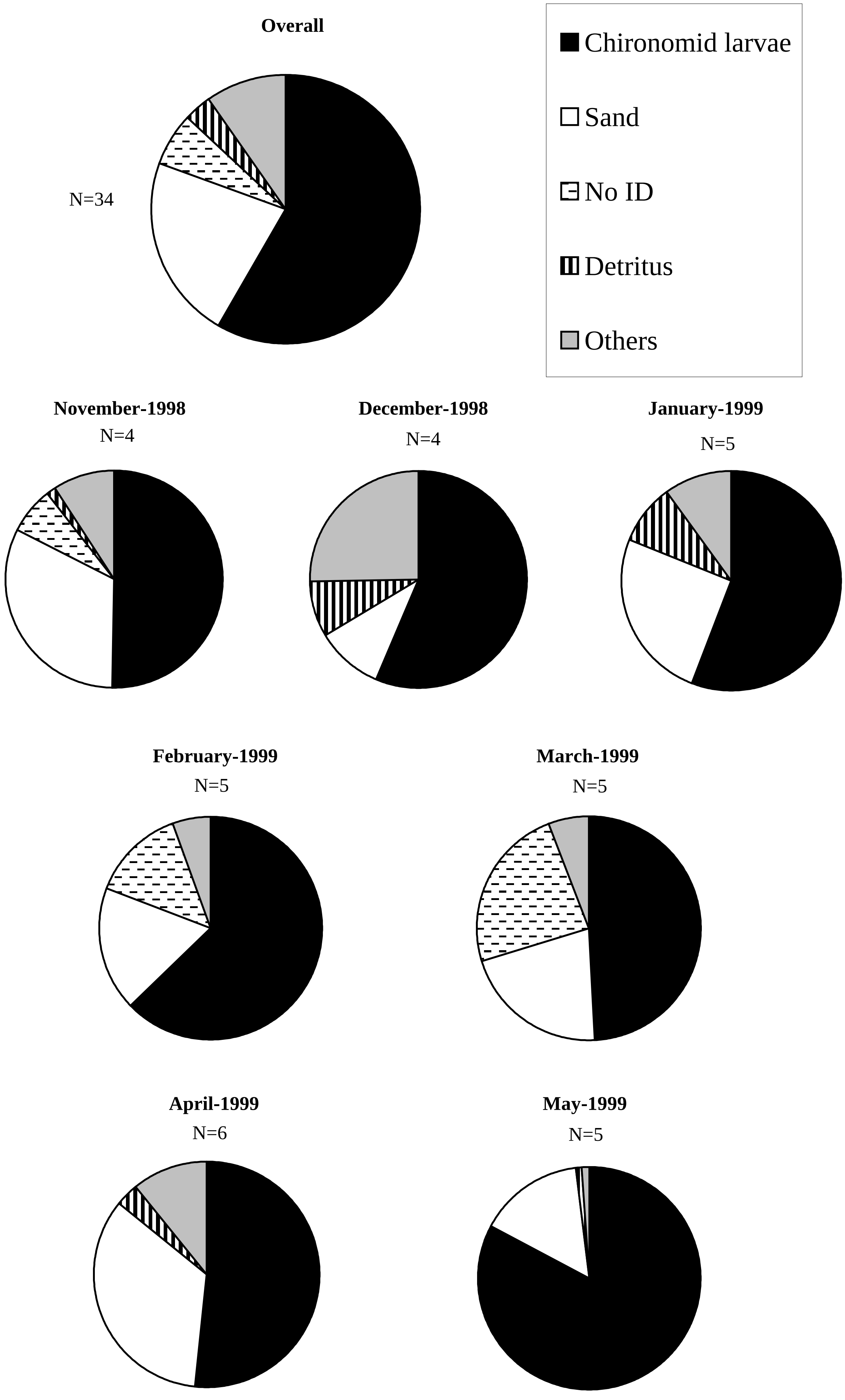
Turner (1996) stated D. macrops was zooplanktivorous. Our results tend to support this statement as 55% of the diet was made of copepods and *Chaoborus* larvae. The remaining part of the diet was constituted of chironomid larvae, sand, detritus non identified material and other items (scales, adult insects, cladocerans, macrophytes, diatoms and other algae). It is important to notice that at months when more than only one or two specimens were examined, zooplankton accounted for 84 to 99% of the diet (December 1998, April and May 1999). 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. Like for *D. limnothrissa*, diet composition strongly varied among months for D. macrops, which seemed to switch opportunistically on some preferred items according to their relative availability. No particular trend relative to size was observed over the size range examined.

Diet composition of *D. macrops* was globally similar to that of *D. limnothrissa*, copepods and Chaoborus larvae accounting for most of their diet. However, their feeding strategy appeared slightly different as benthic invertebrates and important amount of sand were regularly found in *D. macrops* diet, suggesting a digging activity not observed in *D. limnothrissa*.

Lethrinops argenteus

L. argenteus (=*'longipinnis orange head'*) mainly occurs at depth between 10 and 30 m. The stomachs of 34 specimens were examined during the period from November 1998 to May 1999. Weight of stomachs contents averaged 54.2 mg and ranged from 6 to 197 mg for fishes of 92 to 142 mm SL (37-87 g). Diet composition (as percentage of the wet weight) at each sampled month and all months pooled are presented in Figure D6.

Diet composition of *L. argenteus* was almost identical from one month to another, being essentially constituted of chironomid larvae (49 to 82%), sand, detritus, non identified material and other items (scales, fish eggs, insects adults, larvae and pupae, crustacean zooplankton, nematods, gastropods, bivalvs, macrophytes, diatoms and other algae). Given the nature of the main food item and the presence of large amounts of sand at each month, this species seems to be a benthic invertebrate feeder specialised on chironomid larvae.



Overall

November-1998

December-1998

January-1999

February-1999

March-1999

April-1999

May-1999

Figure D6. Overall and monthly diet composition (% wet weight) of *Lethrinops argenteus* . See text for details on "Others" items.

Lethrinops gossei

L. gossei is a deep water species mainly caught from 75 to 125 m depth. Despite is deep water existence, stomachs not inverted were found though they were seldom full. The stomachs of 21 specimens were examined between November 1998 and May 1999. Weight of stomachs contents averaged 72.7 mg and ranged from 5 to 210 mg for fishes of 101 to 155 mm SL (33-118 g). Diet composition (as percentage of the wet weight) at each sampled month and all months pooled are presented in Figure D7.

Turner (1996) stated this species fed on benthic arthropods. Our results rather indicated a mixed diet constituted of benthic invertebrates and zooplankton. Over the sampling period, dominant food items were *Chaoborus* larvae, chironomid larvae, diatoms and copepods, making up to 76% all together. 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. Diatoms might appear to be ingested incidentally, but as only a very small amount of sand was found in the stomachs and given the large amounts of diatoms found, the hypothesis of accidental ingestion is unlikely. No particular trend relative to size was observed. *L. gossei* appeared to switch opportunistically on a few preferred food items according to their availability.

Mylochromis anaphyrmus

M. anaphyrmus frequents the shallow waters between 10 and 50 m depth. The stomachs of 36 specimens were examined between November 1998 and May 1999. Weight of stomachs contents averaged 45.6 mg and ranged from 8 to 290 mg for fishes of 84 to 151 mm SL (16-125 g). Diet composition (as percentage of the wet weight) at each sampled month and all months pooled are presented in Figure D8.

This species is known as a gastropod feeder (McKaye et al. 1986, Eccles & Trewavas 1989, Konings 1995, Turner 1996, Msukwa & Ribbink 1997), although copepods, chironomids, algal remains and arthropod material are sometimes found (Turner 1996). Most of the specimens we examined had lots of snail remains in their guts. However, what is presented here is only the stomach content analysis. Gastropods made up to an averaged 16% (4-44%) of the stomach content only. Chironomid larvae accounted for 41%, adult insects for 10% and crustacean zooplankton for 5%. The remaining part of stomach content was made of sand, non identified material and other items (scales, chironomid pupae, *Chaoborus* larvae, insect pupae and larvae, nematodes, bivalves, macrophytes, diatoms and other algae). Dominant components of stomach contents were the same from one month to another, but the relative proportion of these items slightly varied among months. No particular trend relative to size was observed except that 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).

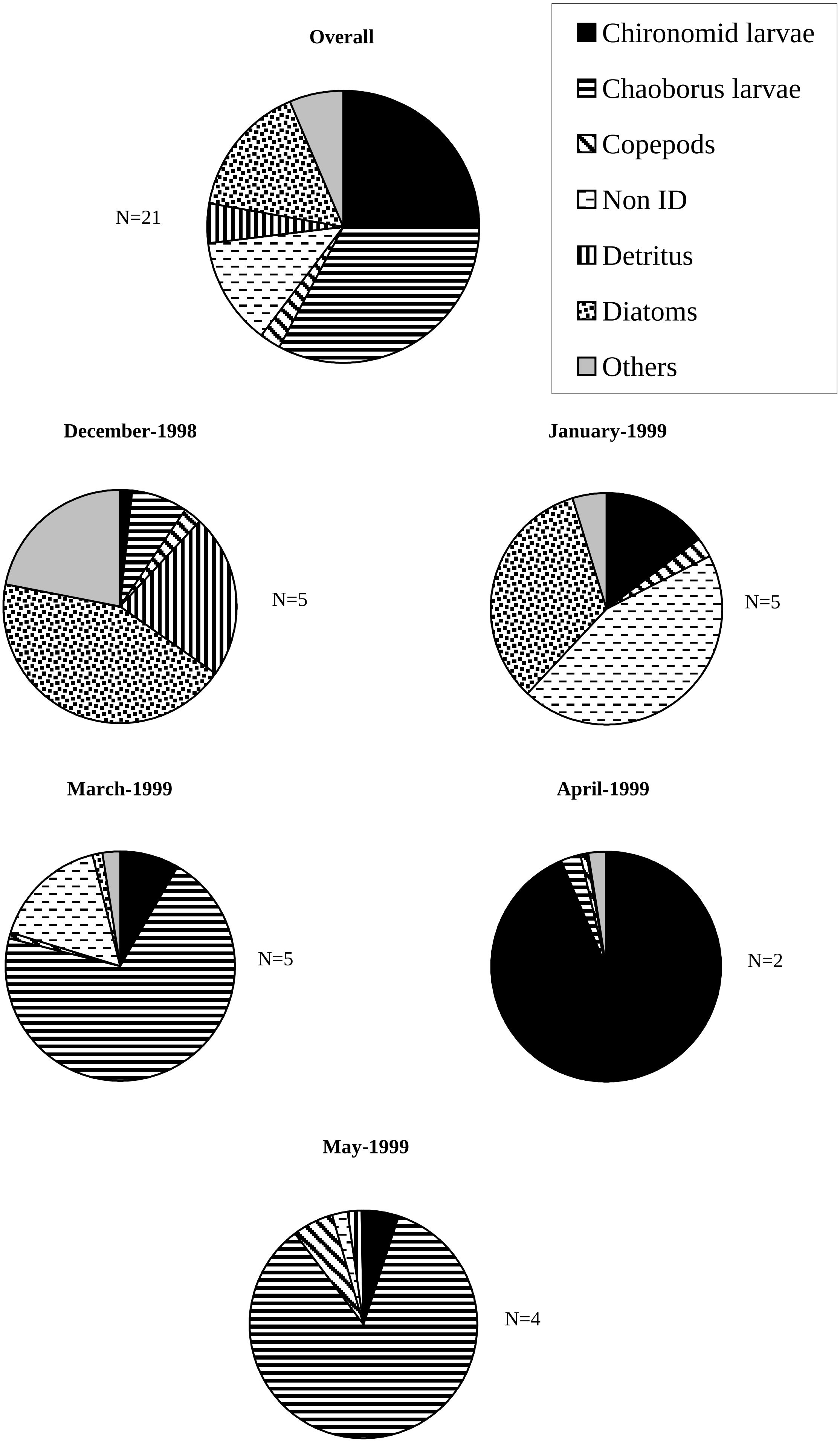


Figure D7. Overall and monthly diet composition (% wet weight) of *Lethrinops gossei* . See text for details on "Others" items.

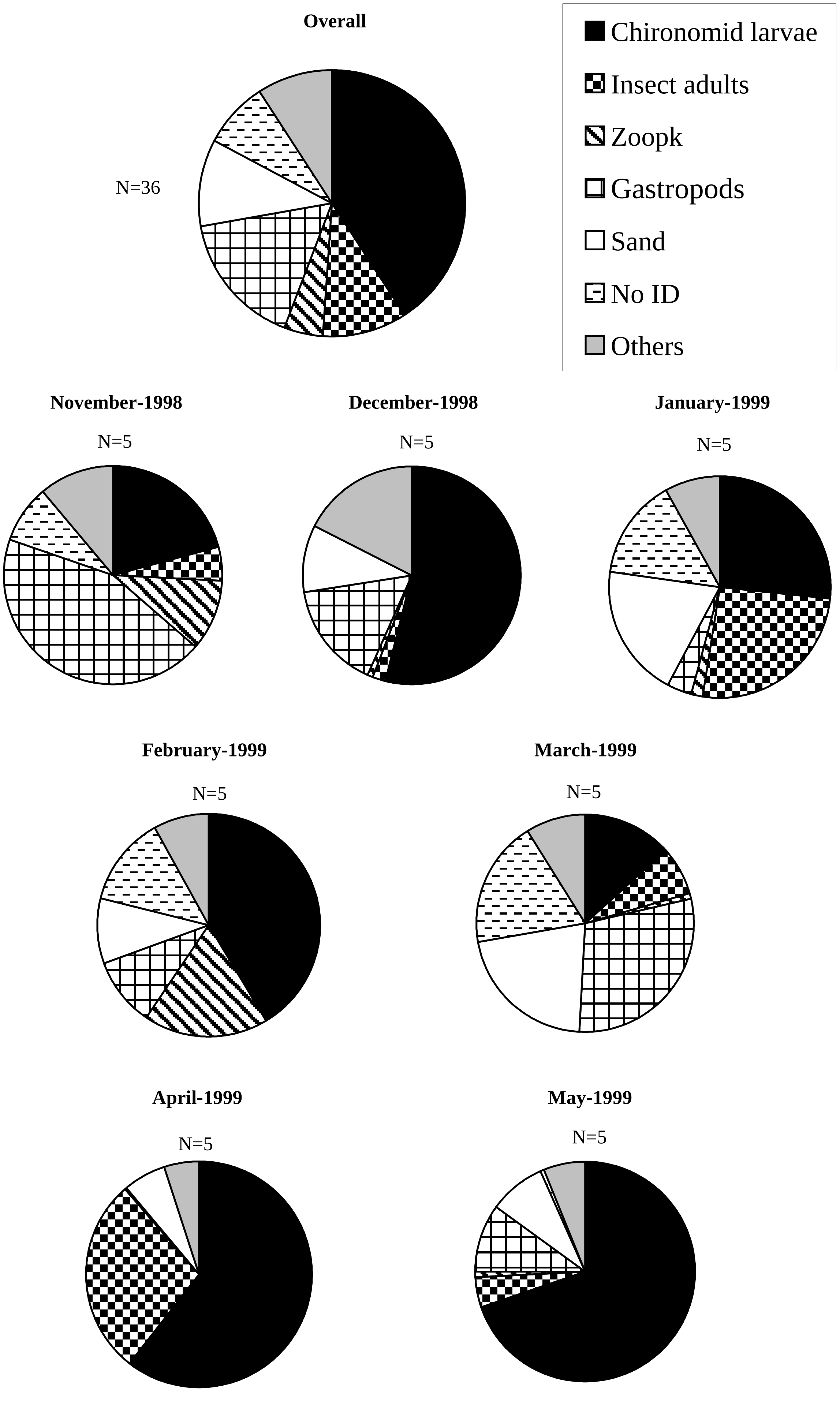
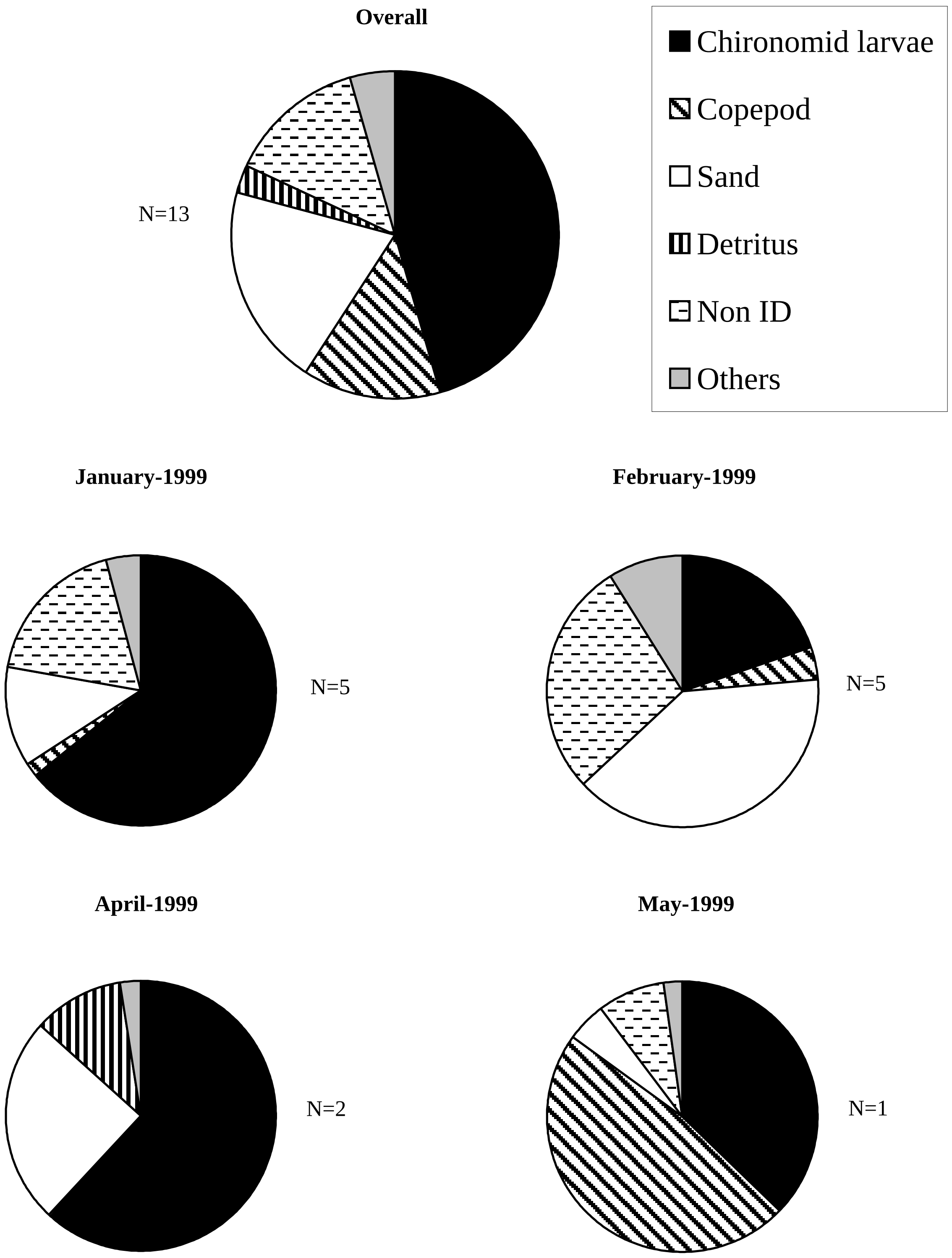


Figure D8. Overall and monthly diet composition (% wet weight) of *Mylochromis anaphyrmus* . See text for details on "Others" items.


Overall

January-1999

February-1999

April-1999

May-1999

Figure D9. Overall and monthly diet composition (% wet weight) of *Taeniolethrinops praeorbitalis* See text for details on "Others" items.

Taeniolethrinops praeorbitalis

T. praeorbitalis is a shallow water species encountered from 10 to 30 m depth. The stomachs of 13 specimens were examined between November 1998 and May 1999. Weight of stomachs contents averaged 49.3 mg and ranged from 5 to 142 mg for fishes of 97 to 193 mm SL (24-166 g). Diet composition (as percentage of the wet weight) at each sampled month and all months pooled are presented in Figure D9.

This species is known to feed primarily on chironomid larvae (Fryer 1959, Eccles & Trewavas 1989, Turner 1996). However, specimens examined by Fryer (1959) were sometimes full of nematodes. Jackson (cited by Turner 1996) reported T. praeorbitalis fed mostly on *Chaoborus* larvae. Konings (1995) stated 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. Copepods accounted for 13%, though they had been abundant in one specimen only in May 1999. The remaining components of the diet were large amounts of sand, detritus, non identified materials and other items (scales, insect adults and pupae, nematodes, macrophytes, cladocerans, diatoms and other algae). Apart from the one specimen with lots of copepods in May, no temporal variability in diet composition was noticed, the only variation being the relative proportions of chironomids and sand between months. The small specimens (90-130 mm SL) analysed tended to have a smaller proportion of chironomid larvae in their stomachs and larger proportions of copepods and plant material than large individuals (165-195 mm).

With the exception of a few species, which actually feed upon fish (*A. mentale, D. limnothrissa…*), the presence of fish scales in almost every stomach analysed, regardless of species, probably represents an artefact caused by the piling up of fishes during the trawl hauling. Indeed, at every haul, medium and large fish, including non piscivorous species, had small fish stuck in their mouths.

Stable isotopes analysis

As already emphasised by Bootsma et al. (1996), the use of both $\delta^{13}C$ and $\delta^{15}N$ signatures is very useful in separating fish with identical $\delta^{13}C$ signals but different feeding habits. Without the $\delta^{15}N$ signatures, it would have been impossible to distinguish between species such as *C. virginalis*, small *D. limnothrissa*, *L. gossei* and large *A. mentale* for example, which all have very different feeding regimes: zooplankton feeders, benthic invertebrate feeder and piscivore.

Except for *M. anaphyrmus*, there was significant intra-specific variability of both $\delta^{13}C$ and $\delta^{15}N$ for all species (Figure D10). This was particularly striking for *A. mentale*, which covered a $\delta^{13}C$ range of 4°/$_{oo}$ and about 2.5°/$_{oo}$ in $\delta^{15}N$. For most of the species, this variability was mainly explained by size differences among individuals, as illustrated by the circles and written sizes on Figure D10. In general, smaller specimens had a lower $\delta^{15}N$ signature than larger ones, indicating they were on a lower trophic level. Intra-specific variations of $\delta^{13}C$ also showed small specimens fed on different items than large ones. As a consequence, small and large specimens of the species *A. mentale*, *C. virginalis*, *D. limnothrissa* and *T. praeorbitalis*, were subsequently separated in the analysis.

The average isotopic composition of the nine target species and their potential food sources are presented on Figure D11. Owing to low sample size for most of the food sources, samples were analysed for $\delta^{13}C$ only and few $\delta^{15}N$ signatures are available. Adult mayfly

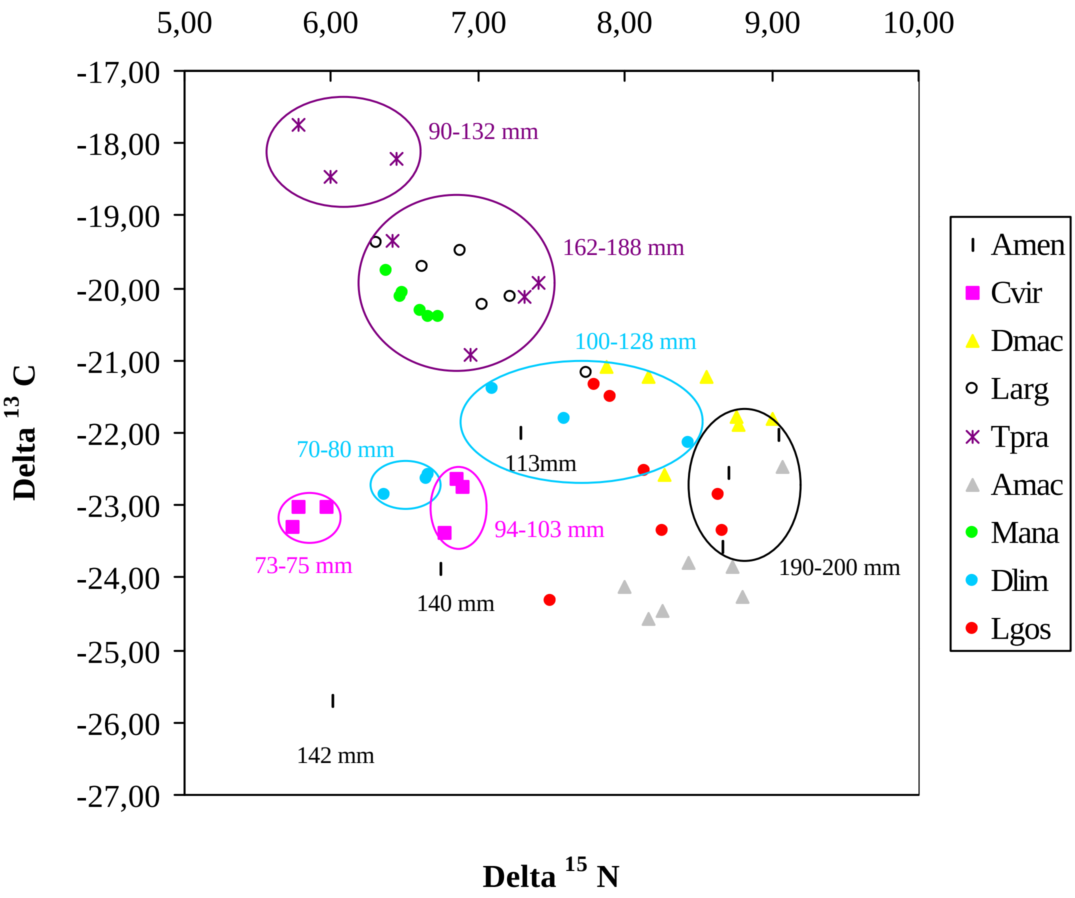


Figure D10. Individual isotopic composition of some demersal cichlid fish species in South West Arm of Lake Malawi. Amac = *Alticorpus macrocleithrum*, Amen = *Alticorpus mentale*, Cvir = *Copadichromis virginalis*, Dlim = *Diplotaxodon limnothrissa*, Dmac = *Diplotaxodon macrops*, Larg = *Lethrinops argenteus*, Lgos = *Lethrinops gossei*, Mana = *Mylochromis anaphyrmus*, Tpra = *Taeniolethrinops praeorbitalis*. Numbers represent the standard length or standard length ranges of specimens.

isotopic composition is not displayed on this figure because they can not be a significant food sources for these fish owing to their high mean $\delta^{15}N$ signatures: 7.82. The nine fish species displayed a $\delta^{15}N$ range of just over 3°/₀₀, which corresponds approximately to one trophic level (3 to 5°/₀₀ Peterson & Fry 1987, Hesslein et al. 1991, Bootsma et al. 1996). For most of the nine fish species, stable isotope results were consistent with stomach content analysis.

A. macrocleithrum had the second highest $\delta^{15}N$ signature (8.49), just below that of the piscivorous *A. mentale*. It was found to have a mixed diet composed mainly of benthic invertebrates, chaoborid larvae and unidentified material. Zooplankton and oligochaetes were also regularly found in its stomachs. The isotopic composition of this fish was consistent with these observations as it was intermediate between the lightest $\delta^{13}C$ signatures (zooplankton *Diaphanosoma excisum, Tropodiaptomus cunningtoni* and Oligochaetes at 100 m) and the heavier *Chaoborus* larvae, average zooplankton and sediment between 75 and 125 m (Figure D11).

The large specimens (190-200 mm SL) of *A. mentale* had the highest $\delta^{15}N$ signature, as expected from its almost strictly piscivorous habits (Figure D11). The smaller specimens (113-142 mm) had a lighter $\delta^{15}N$ and lighter $\delta^{13}C$ composition. Stomach contents of all the small specimens analysed contained over 60% zooplankton, except for one individual who had fed on fish (95%). Carbon isotopic composition of small *A. mentale* matched these observations, being intermediate between the different zooplankton species.

C. virginalis had amongst the lowest $\delta^{15}N$ in muscle. Stomach content analysis revealed this species feeds almost exclusively on zooplankton, which was supported by its isotopic composition, right in the range of the different zooplankton species (Figure D11). The $\delta^{15}N$ difference observed between small and large specimen is likely due to a selective predation upon different zooplankton species. Large specimens of *C. virginalis* probably feed more upon larger predatory zooplankton species than small ones.

Large *D. limnothrissa* specimens (100-128 mm SL) had a higher average $\delta^{15}N$ signature (7.71) than the small specimens (70-80 mm) (6.56), indicating they relied on food sources of a slightly higher trophic level (Figure D11). Temporal trends of stomach content analysis revealed a mixed diet composed of zooplankton, Chaoborus larvae, usipa and adult insects. This is supported by its $\delta^{13}C$ signature, which is slightly above those of zooplankton species, Chaoborid larvae, mixed adult insects and below the signature of some insect species such as Eatonica shoutedini (Ephemeroptera). It must be stressed that the Coleoptera can not account for an important part of *D. limnothrissa* diet because their mean $\delta^{15}N$ signature is only about 1°/₀₀ lighter.

D. macrops mean $\delta^{15}N$ signature (8.49) places this species on top of the represented trophic level with *A. mentale* and *A. macrocleithrum* (Figure D11). As for *D. limnothrissa*, stomach content analysis revealed a mixed diet in which crustacean zooplankton and Chaoborus larvae accounted for more than 50%. Its mean $\delta^{13}C$ isotopic signature supported these results. It was about 2°/₀₀ above the main zooplankton and chaoborid larvae signatures, indicating that this species relies also on heavier ^{13}C sources. Adults insects such as Coleoptera, which indeed have heavier ^{13}C signals, were often found in stomachs.

L. argenteus and *T. praeorbitalis* had almost exactly the same isotopic composition (Figure D11) and the heaviest $\delta^{13}C$ signature after the small specimens of *T. praeorbitalis*. Monthly stomach analysis for both species showed very similar diet composition mainly made of chironomid larvae, sand, detritus and other items. However, *L. argenteus* and *T. praeorbitalis* $\delta^{13}C$ signatures were heavier than expected if they were relying only upon chironomid larvae at 10, 30 and 50m (which is the depth distribution of these species in the sampled area, except for *T. praeorbitalis* only found at 10 and 30 m). As these species are

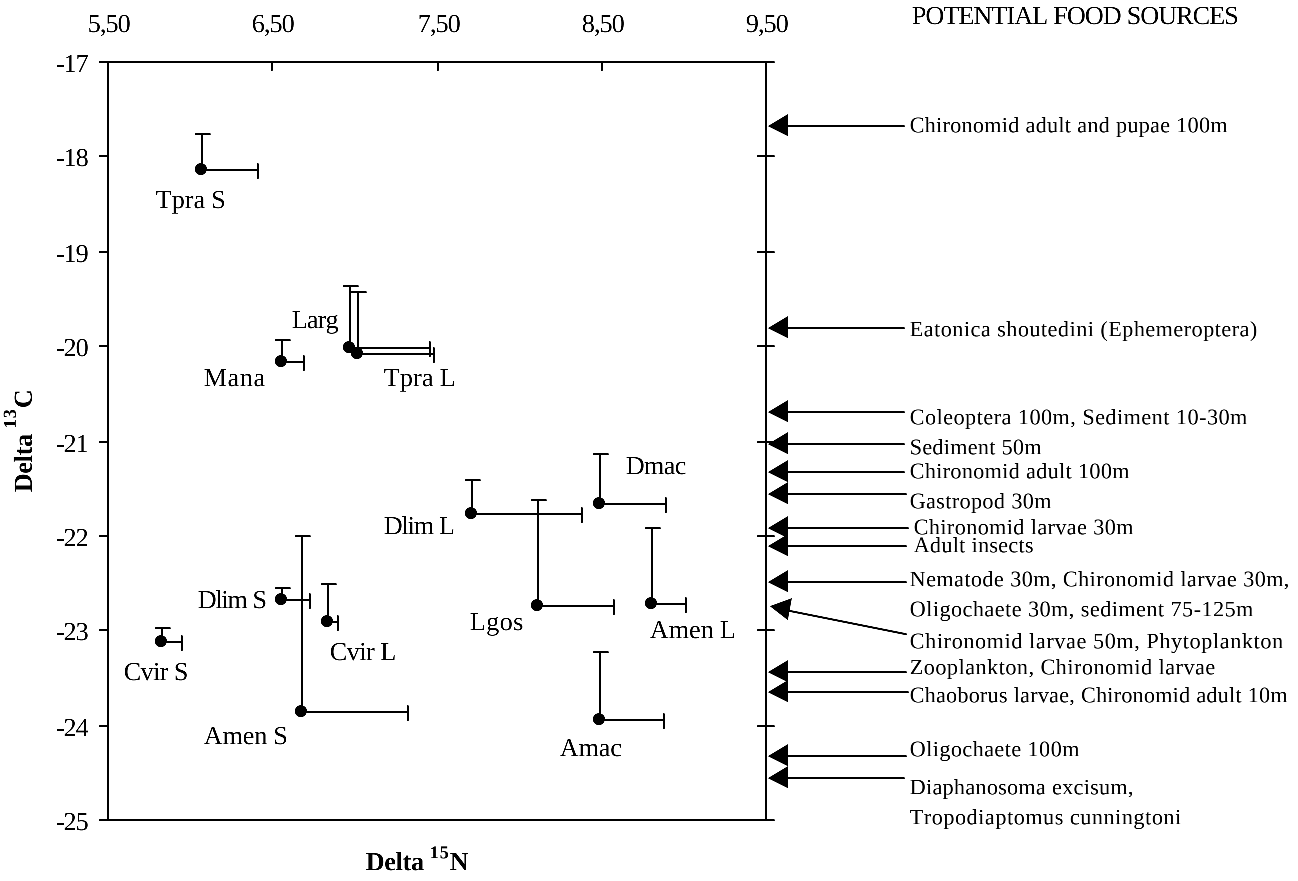


Figure D11. Mean isotopic composition (± standard deviation) of some demersal cichlid fish species and their potential food sources in South West Arm of Lake Malawi. Amac = *Alticorpus macrocleithrum*, Amen = *Alticorpus mentale*, Cvir = *Copadichromis virginalis*, Dlim = *Diplotaxodon limnothrissa*, Dmac = *Diplotaxodon macrops*, Larg = *Lethrinops argenteus*, Lgos = *Lethrinops 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 δ^{13}C values of Hemiptera, Ephemeroptera and Corixidae. Zooplankton refers to the averaged δ^{13}C values of various crustacean copepod species (*Diaptomus vraepelini*, *D. dimixtus*, *Mesocyclops neglectus*, *M. leukarti*).

bottom feeders ingesting large amounts of sand, they probably also have other food sources with heavier carbon signals like periphyton (Bootsma et al. 1996) or other plant material, which were indeed regularly found in stomachs.
As observed in stomach content analysis, small specimens (90-130 mm SL) of *T. praeorbitalis* tended to have a different diet composition than large individuals (160-195 mm), which was reflected in their isotopic composition. Small individuals had heavier δ^{13}C and lighter δ^{15}N signals. Stomach analysis revealed that apart from chironomid larvae, zooplankton and plant material were important components of their diet. However, as the zooplankton has a lighter ^{13}C signal than chironomid larvae found in shallow water, it can not account for the heavier ^{13}C signature of small *T. praeorbitalis* compared to large ones. Oligochaetes, which are difficult to identify in stomachs when digested, have been found to account for more than 50% of *T. praeorbitalis* diet (W. Darwall, pers. com.) and might have constituted an important part of the unidentified material in our analysis. Unfortunately, we did not get enough oligochaetes at 10 m, where all the *T. praeorbitalis* analysed for isotopic composition were caught, to analyse them for isotopic composition. Nevertheless, given the large difference in δ^{13}C signal between oligochaetes at 100 m and 30 m (Figure D11), oligochaetes are likely to have a heavier ^{13}C signature in the shallow waters, but probably not heavy enough to actually account for a large part of *T. praeorbitalis* isotopic composition. The sand-digging habits of this species suggests that it may rely on vegetal materials (periphyton debris) with heavier ^{13}C signals found in sediment. The higher δ^{13}C and lower δ^{15}N suggest that small *T. praeorbitalis* may rely even more than adults on benthic algae, and may occupy a shallower habitat.

The deep water *L. gossei* had an average δ^{15}N signature among the highest (8.12) (Figure D11). Its diet composition as revealed by stomach contents varied much from one month to another, the main food items being *Chaoborus* larvae, chironomid larvae, diatoms, crustacean zooplankton and other less important items. Its δ^{13}C signature, about 1°/$_{oo}$ above that of *Chaoborus* larvae and zooplankton, might indicate that this species mainly relies on these food sources. However, as we do not have carbon signals of chironomid larvae in deep waters nor of diatoms, their potential importance in *L. gossei* diet can not be excluded.

M. anaphyrmus is commonly referred to as a gastropod-eater and most of the specimens examined had lots of snail remains in their guts. However, gastropods represented only a small fraction (16%) of the stomach contents in which chironomid larvae accounted for 41%, adult insect 10% and zooplankton 5%. Despite the weak occurrence of gastropods in stomach contents, *M. anaphyrmus* ^{13}C average signature (–20.17) was consistent with a diet mostly based on gastropods, for which the average signature at 30 m (most common depth of the species in the sampled area) was –22.02 (Figure D11). Usually a food source is on average 1°/$_{oo}$ heavier in ^{13}C than its consumer. The 2% 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 heavier signals (Bootsma et al. 1996).

Conclusions

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 analysis was observed for most of the nine fish species. Stable isotope results proved very useful in clarifying the observed patterns. Species with the narrower feeding regime such as *A. mentale* or *C. virginalis* had an isotopic composition exactly matching the stomach content observations. For *M. anaphyrmus*, despite the dominance of other food items in the stomachs at every sampled months, the isotopic composition confirmed the previously reported snail diet of the species (McKaye et al. 1986, Eccles & Trewavas 1989, Konings 1995, Turner 1996, Msukwa & Ribbink 1997). Stomach content analysis indicated regular temporal trends of diet composition for both *L. argenteus* and *T. praeorbitalis*, mainly dominated by chironomid larvae. However, stable isotope analysis revealed that the apparently secondary vegetal food items were playing an important role in the diet of these species, particularly for the small specimens of *T. praeorbitalis*. Isotopic composition clearly illustrated the diet separation among these demersal fish: on one hand there is the pelagic phytoplankton food chain, centered on –23°/$_{oo}$ with at least two trophic levels and intermediate feeding levels and on the other hand there is an ascending line towards heavier carbon source, which is most likely a periphyton-based food web represented by *T. praeorbitalis*. The ascending line to heavier carbon and lighter nitrogen likely represents mixed feeding on the periphyton-based source and the phytoplankton-based source, though there was no piscivore specialising on *T. praeorbitalis* in our collection. This is interesting in that it does indicate that benthic algal production is contributing to energy flow of the demersal fishes even well away from shore.

Species with a complex feeding regime such as *A. macrocleithrum*, *D. limnothrissa*, *D. macrops* and *L. gossei* showed important temporal variations in diet composition. These variations, which at first look appeared to be of opportunistic nature, are likely to be influenced by seasonal trends in food availability. Indeed, these four species fed upon *Chaoborus* larvae when available. For each of these species, *Chaoborus* larvae were dominant items in their stomachs at exactly the same months, March and May, and only at these months. This strongly suggests that the observed opportunistic feeding regimes were related to the seasonal and/or temporal fluctuations of their preferred food sources availability.

These results emphasise the complementary nature of stomach content and stable isotope approaches in the study of feeding habits and trophic patterns of complex fish communities. There appears to be a heavy reliance by most demersal fish on benthic organisms as a food source and little complete dietary overlap, supporting the belief that these fish must partition their resources in order to coexist (Bootsma et al. 1996, Turner 1996). If the habitat was to become more homogeneous (as a result of increased sedimentation, reduced water clarity, etc.), it can be expected that benthic organisms will be affected and that the potential for competitive exclusion will increase.