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Notes and Comments

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FOOD PARTITIONING AMONG LAKE MALAWI NEARSHORE FISHES AS REVEALED BY STABLE ISOTOPE ANALYSES

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Within the Great Lakes of Africa there exist the world's most diverse communities of freshwater fishes (Fryer and Iles 1972, Greenwood 1974, Ribbink et al. 1983). In particular, the nearshore waters of Lakes Malawi and Tanganyika contain flocks of species, mostly members of the family Cichlidae, which may attain densities of up to 22 species and >500 individuals in a 50-m² area (Ribbink et al. 1983). While many of these cichlid species are very similar in general body morphology, there is high interspecific diversity in neurocranial morphology and dentition (Fryer and Iles 1972, Reinthal 1990a). This morphological diversity suggests that interspecific differences in feeding strategies may play an important role in reducing interspecific competition and maintaining high species diversity (Fryer and Iles 1972, Reinthal 1990a). Yet the results of studies investigating feeding habits of cichlids have been equivocal. Initial studies of the stomach contents of rock-dwelling fishes (Fryer 1959, Ribbink et al. 1983) showed little or no evidence of food partitioning. This, along with laboratory studies (Liem 1984), suggested that herbivorous cichlids, while being facultative specialists, are generally nondiscriminatory feeders. In reviewing the available literature on cichlid feeding habits, Greenwood (1981:71) concluded that "there is apparently complete interspecific overlap in environmental requirement." If this is true, then partitioning may occur only during periods of low food supply (McKaye and Marsh 1983).

More recent research (Van Oijen 1982, Reinthal

1990b) has found significant variation of stomach contents among cichlid species. However, because stomach contents represent food consumed over a small time period and within a small area, these results do not conclusively demonstrate whether food partitioning is the exception or the rule. Other disadvantages of stomach content analyses include difficulty of identification and uncertainty over whether all observed stomach contents are assimilated to the same degree, or if some components, such as cyanobacteria, are indigestible (Fryer 1959, Ribbink et al. 1983, Reinthal 1990b).

In this note we present evidence for food resource partitioning among fishes of Lake Malawi, Africa, by comparing the stable isotope composition ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of a number of nearshore fish species and their potential food sources. Because a fish's isotopic composition represents a spatio-temporal integration of the composition of assimilated food, this approach circumvents many of the problems in stomach analyses noted above.

Methods

Adult rock-dwelling fishes were caught in block nets at depths between 1 and 4 m at Otter Point, near the southern end of Lake Malawi. All other species were obtained by trawling in the southeast arm of the lake, except for the small cyprinid *Engraulicyprus sardella* (an obligate planktivore included for comparison), which was obtained from local fishermen. Except for *E. sardella*, which were collected in August 1992, all fish samples were collected during January and February 1991. For most fish samples only muscle tissue was analyzed, but due to their small size entire individuals of *E. sardella* were analyzed. A diver collected epilithic algae, sandy sediment, macrophytes, pelecypods, and gastropods by hand. Zooplankton were collected by 50-m vertical tows with a 50- μm mesh zooplankton net. Suspended particulate matter was collected by passing 2–3 L of water through a 50- μm mesh filter, to remove most zooplankton, followed by filtration onto a quartz glass fiber filter. Epilithic algae, macrophytes, sediment samples, and zooplankton were acidified before analysis to remove inorganic carbon.

Isotopic analyses were carried out on a VG Micro-mass 602E dual inlet mass spectrometer and a VG Optima automated mass spectrometer (VG Isotech, Middlewich, Cheshire, England) following the methods described by Hesslein et al. (1989). The instrument standard deviation is 0.05‰ and 0.15‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements, respectively. $\delta^{13}\text{C}$ values were determined relative to the PDB standard (the belemnite carbonate standard from the Peedee Formation, South Carolina, USA) as $\delta^{13}\text{C}(\text{‰}) = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$,

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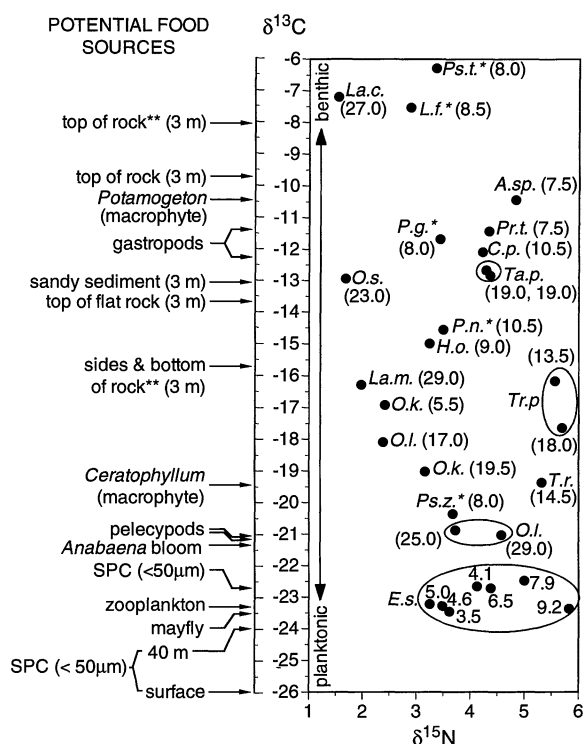


FIG. 1. Isotopic composition of Lake Malawi nearshore fishes and potential food sources. All fish species are cichlids, except for two *Labeo* species and *Engraulicyprus sardella* (Cyprinidae). Numbers shown in parentheses represent standard lengths in centimetres. Species marked with * belong to a group of closely related lithophilous cichlids, commonly referred to as "mbuna." Potential food samples marked with ** were collected from the same rock. *Ps.t.* = *Pseudotropheus tropheops*; *La.c.* = *Labeo cylindricus*; *L.f.* = *Labeotropheus fuelleborni*; *A.sp.* = *Aulonocara* sp.; *Pr.t.* = *Protomelas taeniolatus*; *P.g.* = *Petrotilapia genalutea*; *C.p.* = *Ctenopharynx pictus*; *Ta.p.* = *Taeniolethrinops praeorbitalis*; *O.s.* = *Oreochromis squamipinnis*; *P.n.* = *Petrotilapia nigra*; *H.o.* = *Hemtilapia oxyrhynchus*; *Tr.p.* = *Trematocranus placodon*; *La.m.* = *Labeo mesops*; *O.k.* = *Oreochromis karongae*; *O.l.* = *Oreochromis lidole*; *T.r.* = *Tilapia rendalli*; *Ps.z.* = *Pseudotropheus zebra*; *E.s.* = *Engraulicyprus sardella*; SPC = suspended particulate carbon.

where R is the $^{13}\text{C}:^{12}\text{C}$ ratio. $\delta^{15}\text{N}$ values were determined relative to the $^{15}\text{N}:^{14}\text{N}$ ratio of air.

Results

Among the potential food sources analyzed, a strong distinction in $\delta^{13}\text{C}$ was observed between nearshore benthic samples and planktonic samples. Relative to planktonic samples, benthic samples were much more enriched in ^{13}C and displayed a wider range of $\delta^{13}\text{C}$ values (Fig. 1). Similar results have been reported for other aquatic ecosystems (Fry et al. 1983, Hamilton and Lewis 1992), although we are unaware of any published benthic $\delta^{13}\text{C}$ value as high as -8.1‰ . While

small differences in $\delta^{13}\text{C}$ may result from differences in algal species composition (Zohary et al. 1994), the wide range observed in Lake Malawi is likely due to differences in the severity of CO_2 limitation (Rau et al. 1992, Hecky and Hesslein 1995) caused by large differences between pelagic and benthic photosynthetic rates (Bootsma 1993).

The $\delta^{13}\text{C}$ values measured for nearshore fishes covered a range nearly as broad as that measured for potential food sources. As expected, the semi-pelagic planktivore, *Engraulicyprus sardella*, had a $\delta^{13}\text{C}$ similar to that measured for zooplankton and suspended particulate carbon. Other species filled the range between planktivore and obligate benthic feeder.

While species separation was greatest along the $\delta^{13}\text{C}$ axis, $\delta^{15}\text{N}$ also proved useful in elucidating dietary differences. Several species that were poorly separated on the $\delta^{13}\text{C}$ axis were well separated on the $\delta^{15}\text{N}$ axis. For example, the difference in $\delta^{13}\text{C}$ between *Oreochromis squamipinnis* and *Taeniolethrinops praeorbitalis* is $<0.3\text{‰}$, but the $\delta^{15}\text{N}$ difference is 2.6‰ .

Discussion

Interpretation of isotopic composition. In comparing the isotopic compositions of different fish species and food sources, there are four factors to consider in data interpretation. (1) If two individual fishes have complete dietary overlap, they will have nearly identical isotopic compositions (DeNiro and Epstein 1978, Hesslein et al. 1991). (2) Because there is very little isotopic fractionation of carbon during trophic transfer (DeNiro and Epstein 1978, Fry and Sherr 1989), and because the increase in $\delta^{15}\text{N}$ with trophic transfer is relatively constant (between 3.0 and 5.0‰, Minigawa and Wada 1984, Hesslein et al. 1991) a difference in the isotopic composition of two individuals reflects a difference in feeding strategies of those individuals. (3) If two individual fishes have similar isotopic compositions, they do not necessarily have similar feeding strategies. It is quite possible that two or more food sources have identical isotopic compositions (e.g., the macrophyte *Potamogeton* falls within the $\delta^{13}\text{C}$ range covered by shallow epilithic periphyton) or that a fish's isotopic composition represents the integration of a variety of food sources with a wide range of isotopic compositions. (4) As the endpoints of the isotopic range are approached, the probability of a narrow dietary breadth increases, and relationships between food and consumers can be defined more precisely.

We observed a broad range of isotopic values among nearshore species, suggesting that these species do not feed indiscriminately (based on factor 1). Distinctions between some species, such as the lithophilous *Pseudotropheus tropheops* and the more pelagic *Oreochromis lidole*, might be expected. However, the results

show that even within a monophyletic (or at least very closely related) group of "herbivores" (Fryer and Iles 1972, Ribbink et al. 1983, Moran et al. 1994; indicated with * in Fig. 1), there are large differences in feeding strategies. *Pseudotropheus tropheops* is an obligate periphyton feeder, while its congener, *Pseudotropheus zebra*, has a strong preference for plankton. For adult-fish muscle tissue, the rate at which isotopic composition responds to a change in diet is on the order of weeks to years (Hesslein et al. 1993, Peterson et al. 1993). Therefore, the observed differences in isotopic composition reflect dietary differences that persist over similar time scales or longer. Nearshore benthic photosynthesis in Lake Malawi does not appear to exhibit any seasonality that can be related to lake hydrodynamics or climatic conditions (Bootsma 1993), so it is unlikely that food partitioning prior to the sampling period was caused by lower-than-average food availability.

Among the species sampled there are several that have similar isotopic compositions. In each case there is observational evidence that these similarities result from the utilization of different food sources that have similar isotopic compositions. Within the group consisting of *Protomelas taeniolatus*, *Ctenopharynx pictus*, and *Taeniolethrinops praeorbitalis* (Fig. 1), *P. taeniolatus* nips epilithic algae and benthic invertebrates, with an apparent preference for chironomid larvae (Ribbink et al. 1983), *C. pictus* "vacuums" rock surfaces and consumes primarily benthic copepods (Ribbink et al. 1983), and *T. praeorbitalis* sifts invertebrates from mouthfuls of sand (Fryer and Iles 1972). The closely grouped *Petrotilapia nigra* and *Hemitalapia oxyrhynchus* both feed on algae, but *P. nigra* scrapes periphyton from rock surfaces (Ribbink et al. 1983) and may feed on plankton (Reinthal 1990b) while *H. oxyrhynchus* nibbles periphyton off of the macrophyte *Vallisneria* sp. (Fryer and Iles 1972). The isotopically light $\delta^{13}\text{C}$ of *Pseudotropheus zebra* and *Oreochromis lidole* (Fig. 1) indicates that both of these species rely on a phytoplankton-based food chain, but *P. zebra* is primarily a rock-dweller (Fryer and Iles 1972, Ribbink et al. 1983) while *O. lidole* lives further offshore and feeds on plankton or sandy sediment (Fryer and Iles 1972, Turner et al. 1991).

The nitrogen isotope ratio has been shown to be a useful indicator of trophic level for pelagic fishes (Fry 1988, Hesslein et al. 1991), and the general increase in $\delta^{15}\text{N}$ with size of *Engraulicyprus sardella* probably reflects a shift in trophic level with age. The use of $\delta^{15}\text{N}$ to infer trophic position for nearshore fishes is complicated by the possibility of differences in the $\delta^{15}\text{N}$ of the various autotrophs that form the base of nearshore food chains. At present we do not know the magnitude of these differences. However, for species be-

longing to food chains with the same autotroph base, the $\delta^{15}\text{N}$ will still reveal differences in trophic position. For example, *Oreochromis squamipinnis* and *Taeniolethrinops praeorbitalis* both feed on sandy sediment (Fryer and Iles 1972, Turner et al. 1991) and therefore must ultimately rely on the same autotrophic carbon source, but the difference in $\delta^{15}\text{N}$ of 2.6‰ between the two species suggests that *O. squamipinnis* is primarily an algae eater while *T. praeorbitalis* relies more heavily on benthic invertebrates, in agreement with the observations of this genus made by Fryer and Iles (1972). Observations of feeding habits and stomach contents (Fryer 1959, Fryer and Iles 1972, Ribbink et al. 1983) indicate that other species with high $\delta^{15}\text{N}$ values (*Aulonocara* sp., *Protomelas taeniolatus*, *Ctenopharynx pictus*, *Trematocranus placodon*) may also selectively feed on benthic invertebrates, suggesting $\delta^{15}\text{N}$ measurements will prove to be useful in accurately defining feeding strategies and trophic positions among Lake Malawi nearshore fishes.

Resource partitioning mechanisms. There are two mechanisms that may cause the distinct isotopic differences among fish species. First, species may be stenophagous, in which case the isotopic composition of a species largely reflects that of a single food source. Alternatively, species may have broad, overlapping diets, but preferences for specific food items and/or feeding locations vary between species. Among the nearshore fishes of Lake Malawi there is convincing evidence for both mechanisms. In order to be near the extremes of the $\delta^{13}\text{C}$ gradient, *P. tropheops* and *P. zebra* must be stenophagous, the former relying almost exclusively on shallow periphyton, and the latter feeding largely on planktonic organisms. This is precisely the conclusion reached by Reinthal (1990b), who found *P. tropheops* stomach contents to consist largely of *Calothrix* (a benthic filamentous cyanobacteria) while *P. zebra* contained abundant planktonic diatoms. Out of the seven species examined by Reinthal, these two were found to have the smallest dietary breadths.

Although some species with intermediate $\delta^{13}\text{C}$ values may also be stenophagous, the difficulty in distinguishing species based on stomach contents (McKaye and Marsh 1983, Ribbink et al. 1983, Turner et al. 1991) indicates that, for many species, there is broad dietary overlap. In this case, differences in species-specific isotopic values must be due either to spatial partitioning (i.e., a single food type may vary in isotopic composition, depending on where it is found) or to small differences in preference for specific items within the food suite. In fact, selection for specific food resources may often be achieved by spatial partitioning, since the ability of most species to selectively pick out specific food items from a given micro-habitat is probably very limited (Ribbink et al. 1983). For some of the species

analyzed, there already exists evidence of spatial partitioning. Among the *Oreochromis* species, adult *O. lidole* are considered the most pelagic (Fryer and Iles 1972, Turner et al. 1991), and the $\delta^{13}\text{C}$ data support this belief.

Interspecific differences in isotopic composition, combined with similarity in stomach contents, imply that species using similar food types occupy different habitats. Conversely, in order to have different isotopic compositions, species occupying the same habitat must utilize different food types. Such a lack of interspecific correlation between the use of two resources (food and space), which Schoener (1974) calls "complementarity," is a strong indication that feeding differences are not the result of stochastic variability, but are the product of competition and specialization. The data presented here provide preliminary evidence that such complementarity exists among nearshore fishes in Lake Malawi.

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SUCCESS OF A ROOT HEMIPARASITIC PLANT IS INFLUENCED BY SOIL QUALITY AND BY DEFOLIATION OF ITS HOST

Veikko Salonen¹ and Susanna Puustinen¹

Several species in the Scrophulariaceae family are root hemiparasites, meaning that the plants are capable of robbing nutrients, water, and even organic compounds from their hosts through haustorial root connections (e.g., Press et al. 1988, Seel and Press 1993, 1994). Attachment to a host is necessary for most root hemiparasites for normal growth and reproduction (e.g., Seel and Press 1993, 1994). In general, the host plants clearly suffer from being parasitized; the parasite can reduce, for example, growth and reproduction of the host (Gibson and Watkinson 1991, Matthies 1995). However, different types of host plants have been shown to differ in resistance to hemiparasites (Snogerup 1982). Plant size and morphology, growth rate, photosynthesis, time of flowering, number of flowers, and carbon, nitrogen, and water relations of the parasite can differ markedly between hosts (Snogerup 1982, Gibson and Watkinson 1991, Seel and Press 1993, 1994). Besides being influenced by the host's species-specific properties, the success of the parasitic plant can be assumed to depend on the condition of its host.

The host plants are often not exposed to parasitism alone but simultaneously to other factors, such as disease, competition, or herbivory, reducing their ability to host other plants. Capability of the hosts to com-

pensate for heavy tissue losses due to grazing or mowing may be of great importance for success of the parasitic plants connected to them. The consequences of defoliation to plants are dependent on a number of factors, such as the amount of tissue removed (Oosterheld 1992, Obeso and Grubb 1994), availability of resources (Chapin and McNaughton 1989, Georgiadis et al. 1989), and timing of the damage (Oosterheld and McNaughton 1991, Obeso and Grubb 1994).

In this study, we examined the consequences of a partial defoliation of the host plant to the host itself and, in particular, to the parasitic plant attached to it. To our knowledge, so far no other studies have examined the effects of either grazing or artificial defoliation of the host plant on success of the parasitizing plant. We studied this relationship with *Agrostis capillaris*, a perennial grass, and *Rhinanthus serotinus*, an annual facultative root hemiparasite, both plant species common in different types of grassland vegetation. In these habitats, *R. serotinus* can frequently be found to parasitize *A. capillaris*. The specific aims of this study were to determine if (1) partial defoliation of the host plant affects the growth and reproduction (flower production) of the parasitizing plant, (2) the host's ability to host the parasite after defoliation is influenced by quality of the substrate, (3) variation in timing of partial defoliation of the host affects success of the parasite.

Materials and Methods

Seeds of both *R. serotinus* and *A. capillaris* were collected in early September from several plants growing in a roadside grassland site at Konnevesi, central Finland (62°37' N, 26°21' E). The seeds of *R. serotinus* were incubated between moist filter papers at 4°C for ≈3 mo, after which time they started to germinate. The newly germinated seeds were then planted in pots filled with moist mould. A large number of seeds of *A. capillaris* were simultaneously sown in moist mould where they germinated in a few days.

A total of 60 even-aged *A. capillaris* seedlings, each

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