INVASION OF LAKE VICTORIA BY THE LARGE BODIED HERBIVOROUS CLADOCERAN *DAPHNIA MAGNA*

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ABSTRACT

Zooplankton collections from offshore Lake Victoria during the early to mid 1990s contained a *Ctenodaphnia* species that is morphologically similar to *Daphnia monacha* (*D. lumholtzi* var. *monacha*) which is present in Lakes Edward and Albert. Direct comparison of the Lake Victoria specimens with representative *D. monacha* from the Rift Valley lakes reveals that the taxa are not the same, however. Instead, the Lake Victoria animals conform more closely to the morphology of *Daphnia magna*. The large body size of *D. magna* makes it unlikely that it was overlooked by previous investigators of the lake. Instead, it appears that food web alterations of Lake Victoria created occasional conditions of relaxed planktivory by fish to such a degree that an herbivore of unusually large size could establish viable populations. The observation runs counter to prevailing paradigms about the small size structure of tropical zooplankton communities compared with those in temperate zones. The observation is consistent with claims that biological interactions rather than physical and chemical factors are the typical determinants of zooplankton size structure in the tropics.

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1. INTRODUCTION

Predation is a strong organizing force in zooplankton communities. Size structure and species composition are consequences of complex interplay between visual orienting predators such as fish and mechanical or tactile predators such as *Chaoborus* and carnivorous copepods. Evidence for the role of predation comes from both temperate and tropical locations. Intentional or accidental introductions of planktivorous fish into African lakes and reservoirs have provided striking demonstrations of the power of visual planktivory (e.g., Gliwicz, 1985; Dumont, 1986; Marshall, 1991), either through direct predation or through a variety of indirect effects (Gliwicz, 1994).

One of the key studies in the development of understanding about visual predation and zooplankton community structure concerned tropical Cladocera in the Rift Lake sources of the White Nile (Green, 1967, 1971). Green demonstrated that a large bodied *Ctenodaphnia* known as *Daphnia lumholtzi* var. *monacha* (or *D. monacha* in earlier work) was confined to offshore waters of Lakes Albert and Edward, owing to relaxed magnitudes of predation by fish in those regions. The older terminology "D. *monacha*" is adopted in this paper for the purpose of clearly delineating two distinct morphological forms. Nearshore, *D. monacha* virtually vanished from the plankton and was replaced by *Daphnia lumholtzi*. *D. lumholtzi* has a smaller core body size and a smaller eye, making it less visually conspicuous. It also possesses exuberant tail and helmet spines which amplify its effective size to "gape-limited" predators (Zaret, 1980) and thereby help to frustrate their attempted attacks. Tollrian (1994) demonstrated that postembryonic elongation of the spines of *D. lumholtzi* is stimulated by kairomones released by fish. Experimental studies have demonstrated that the spines inhibit feeding by juvenile Centrachidae (Swaffer and O'Brien, 1996; Kolar and Wahl, 1998), in part by increasing the required handling time for spined prey.

Daphnia lumholtzi has a broad regional distribution in East Africa, south and Southeast Asia, and Australia (Benzie, 1988). Recently it has been introduced into North America and has colonized habitats northward along the Mississippi Valley into the Great Lakes. In Africa it occurs not only in the rift lakes of the White Nile, but in Lake Victoria as well. It co-occurs in Lake Victoria with one member of the subgenus *Daphnia*, *Daphnia longispina*, as well as with a variety of other Cladocera. Crustacean zooplankton of Lake Victoria have been the object of repeated study during the 20th century (Worthington, 1931; Worthington and Ricardo, 1936; Rzoska, 1957, 1975; Mavuti and Litterick, 1991). The lake is distinguished from other African Great Lakes in part by its greater species richness of diaptomid copepods (Lehman, 1996).

Diaptomidae are more abundant offshore than nearshore in Lake Victoria (Branstrator *et al.*, 1996), which is consistent with a gradient of decreasing planktivory by fish away from shore. Diaptomids and cyclopoid copepods are better at evading capture by teleost fish than are most Cladocera. Relative vulnerability of these two Copepoda suborders cannot be easily generalized, because responses can be both system and species specific (e.g., Drenner *et al.*, 1978; Mookerji *et al.*, 1998;

Nassal *et al.*, 1998; Viitasalo *et al.*, 1998), and are influenced by prey size and fecundity as well as taxonomy. Experience with planktivore introductions in Africa, however, has been that diaptomids are differentially reduced in environments of high predation intensity (e.g. Dumont, 1986; Marshall, 1991). The plankton community of Lake Victoria is consistent with the hypothesis that planktivory by fish is greater nearshore than offshore.

The food web of Lake Victoria has been in a state of flux throughout the 1980s and 1990s owing to changes in climate, land use, and fisheries (Lehman, 1998a, 1998b). Fish community changes included reductions in both herbivorous and zooplanktivorous species (Lowe-McConnell, 1997; Witte *et al.*, 1992). Not surprisingly, the zooplankton community has experienced changes, as well (Mwebaza-Ndawula, 1994).

Zooplankton collections obtained in 1992 from offshore Lake Victoria contained a large new daphnid that had not previously been a reported part of the community. The species was a *Ctenodaphnia*, possessing large cephalic fornices and conforming generally with published descriptions of the *Daphnia monacha* in Lake Albert. Branstrator *et al.* (1996) reported the presence of the novel species in collections made during April and May, 1992.

Subsequently, D. Verschuren (personal communication) pointed to the presence of ephippial eggs characteristic of *Daphnia magna* in surface sediments of Lake Victoria. The discovery called into question the identity assigned to the large *Ctenodaphnia* first seen in 1992. In order to resolve the issue, we inspected an archival collection of Lake Victoria zooplankton samples spanning the years 1991 to 1995, and compared the *Ctenodaphnia* contained within them with specimens of *D. monacha* collected from Lakes Edward and Albert in March and April of 1995.

2. METHODS

2.1 Sample Sites and Collection Methods

All of the zooplankton collections in this study were obtained with 0.5-m diameter nets constructed of 100-mm aperture Nitex that were hauled by hand from designated depths to the surface at ca. 0.5 m sec $^{-1}$ while the research vessel lay at anchor. Nets were manufactured by Research Nets, Inc. of Bothell, Washington, U.S.A., and had an aspect ratio of 1:5 diameter:length. Typically four replicate vertical hauls were combined in the field and preserved with 4% sucrose-formalin. Most samples were split quantitatively in Jinja, Uganda at the Fisheries Research Institute (FIRI), with one-half of the collection deposited at the University of Michigan in Ann Arbor and the remainder deposited at FIRI.

2.2 Microscopy and Documentation

Archival samples in Ann Arbor were stained with Eosin Y and diluted to total volumes ranging from 300 ml to 1200 ml. Successive quantitative 5 ml subsamples were withdrawn for enumeration. All *Daphnia* present in the aliquots were identified to species. Multiple subsamples were drawn until the number of *Daphnia* encountered exceeded 100 individuals. Larger volumes of the collections were searched for presence of large bodied *Ctenodaphnia*, in order to establish their temporal pattern of occurrence.

Similarity between *D. magna* and *D. monacha* called for detailed comparison of several key characteristics. These features were photographed and are reproduced here to document both similarities and differences among the taxa. Eighteen samples were inspected, several of which had been previously part of the report by Branstrator *et al.* (1996). Large *Ctenodaphnia* were distinguished by presence of cephalic fornices; no males or ephippia were encountered in the collections we inspected. Specimens were examined as whole mounts and in dissected detail.

Representative specimens were withdrawn from the collections and placed in glycerin for detailed examination and dissection. Morphological features were distinguished with the aid of an Olympus BHA compound microscope, using interference contrast optics at magnifications up to 1000X. Digital images of key distinguishing features were recorded for documentary purposes.

Size frequencies of *Daphnia* in some samples were measured by ocular micrometer measuring from the midpoint of the eye to the base of the tail spine. Clutch presence was recorded for ovigerous females in order to estimate the size at first reproduction. Clutch sizes could not be estimated reliably because the samples contained numerous loose eggs.

3. RESULTS

Morphological differences permit discrimination of three *Daphnia* species from Lake Victoria, none of which are identical with *D. monacha* from Lakes Albert and Edward. The Lake Victoria samples included two members of the subgenus *Ctenodaphnia*, identified as *D. lumholtzi* (typical spined form) and *D. magna*. The most common daphnid in Lake Victoria is a member of the subgenus *Daphnia*: *D. longispina*.

3.1 Carapace Valve Margins

Figure 1 shows ventral carapace margins of four taxa, three of which are members of the subgenus *Ctenodaphnia*. *D. lumholtzi* are distinguished by stout and widely spaced spines along the ventral margin of the valves. Setae are more densely arrayed along the ventral valve margin for *D. magna* from Lake Victoria compared with *D. monacha* from Lake Albert. In fact, *D. magna* have double the number of setae per

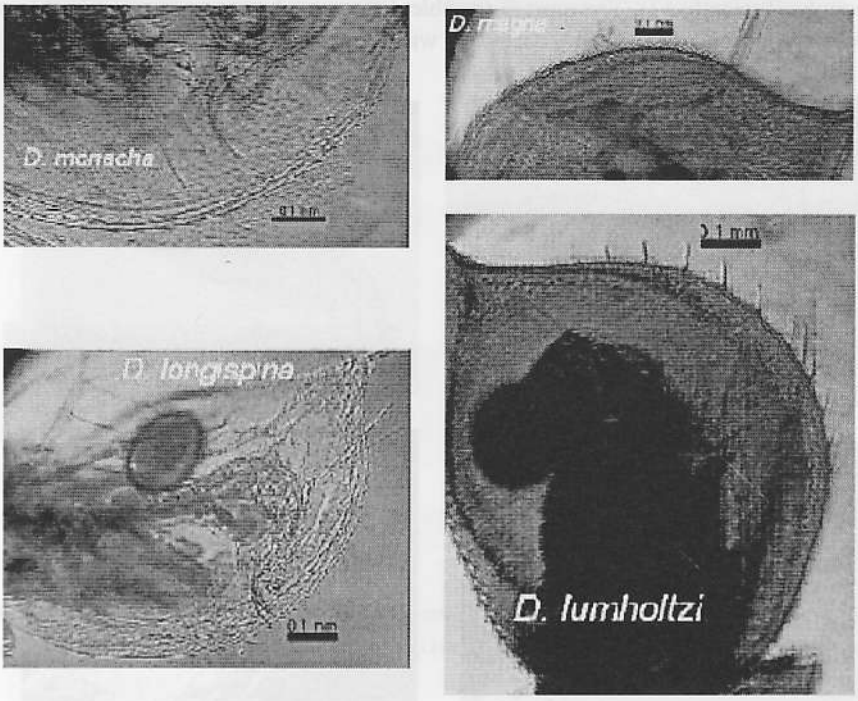

Figure 1. Carapace valve margins of *Daphnia monacha* (Lake Albert), and *D. longispina*, *D. magna*, and *D. lumholtzi* (Lake Victoria). All scale bars are 0.1 mm.

unit length compared with *D. monacha*. The valve margin of *D. monacha* is most similar to that of *D. longispina* in that the setae appear more conspicuous toward the posterior ventral margin of the valves.

3.2 Postabdomen

Figure 2 compares postabdomens among *Daphnia*. *D. longispina* is distinguished by its linear margin, diminishing length of anal spines from distal to proximal, and though not illustrated, distinctive brownish pigmentation of the terminal claw. All three *Ctenodaphnia* exhibit non-linear margins that are sinusoidal to varying degrees, least so with *D. lumholtzi*. The anal spines of *D. lumholtzi* are robust, short, and they taper in length proximally. They are also fewer in number, often as few as 10, compared with the other species. The postabdomens of *D. monacha* and *D. magna* are superficially similar, but the sinusoidal shape is more strongly expressed in *D. magna*, and *D. magna* bear a greater number of anal spines (typically 16) than do *D.*

monacha (typically 13). The most noticeable difference, however, is a gap in the anal spines at the anus of *D. magna*, but not so with *D. monacha*.

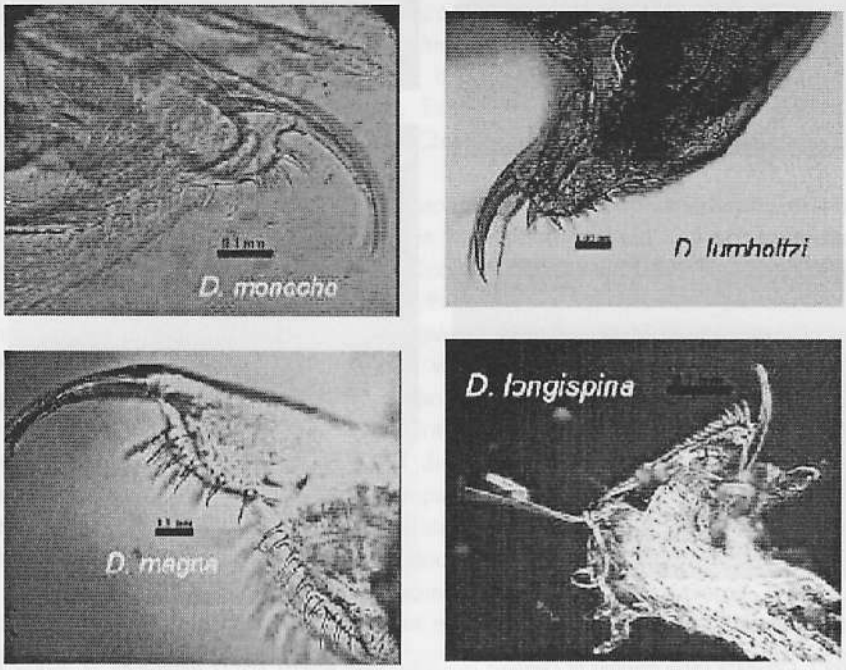

Figure 2. Postabdomens of *Daphnia* from Lakes Albert and Victoria, as identified in Figure 1.

3.3 Postabdomenal Claw

Figure 3 demonstrates the postabdomenal claws of the *Ctenodaphnia*. *D. lumholtzi* has a basal comb with dense elongated teeth, distinguished from uniformly short serrations that constitute the two distal combs of the claw. Both *D. monacha* and *D. magna* exhibit three distinct combs along the claw, with the middle teeth longest, and distal teeth shortest. The claws are not distinguishable by shape alone.

3.4 Fornices

The three *Ctenodaphnia* (*D. lumholtzi*, *D. monacha*, and *D. magna*) bear distinctive fornices; *Daphnia longispina* lacks fornices. *D. monacha* fornices have more acute apices than those of *D. magna*, though not nearly so acute or elongate as in the case of *D. lumholtzi* (Figure 4). The differences in shape between *D. monacha* and D. *magna* are subtle but consistent.

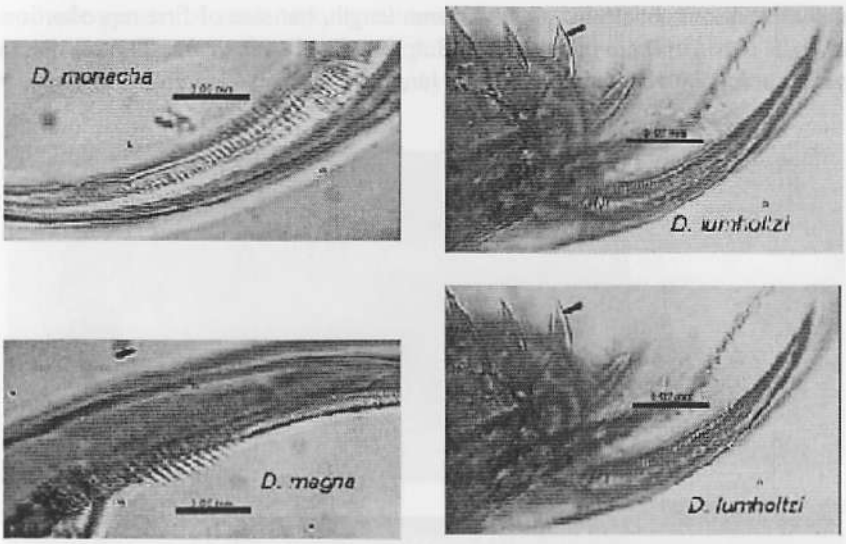

Figure 3. Postabdomenal claws from *Daphnia* specimens identified in Figures 1 and 2. *D. lumholtzi* (right) is illustrated at two different focal planes. All scale bars are 0.02 mm.

3.5 Eye and Rostrum

Differences also occur in the eye, rostrum, and general shape of the heads (Figure 5). *D. monacha* and *D. magna* differ by number and arrangement of lenses around the eye. *D. monacha* has more lenses than *D. magna* and they typically surround the entire eye. *D. lumholtzi* also has more lenses than *D. magna* but they do not surround the entire eye. *D. longispina* has the same arrangement as *D. magna* with a row of lenses along only the crown of the eye. Eye size also varies among specimens, but as Green (1971) noted, there is a positive correlation with body size. The rostrums of *D. monacha* and *D. magna* are similar, and the ventral margins of the heads are slightly arcuate compared with *D. lumholtzi*. The head of *D. monacha* is typically more broadly rounded than that of *D. magna*. Ocelli are conspicuous for all taxa.

3.6 Size Distributions

In addition to distinguishing morphological characteristics, there are overt differences in the size distributions of the various *Daphnia* species. *D. magna* in Lake Victoria attain lengths exceeding 2 mm that are considerably larger than any specimens of *D. monacha* found in Lake Albert (Figure 6). *D. longispina* and *D.*

monacha produce neonates of about 0.5 mm length, but size of first reproduction is about 0.75 mm for *D. longispina*, and 1.1 mm for *D. monacha*. The smallest *D. magna* recorded with eggs was 1.0 mm in length.

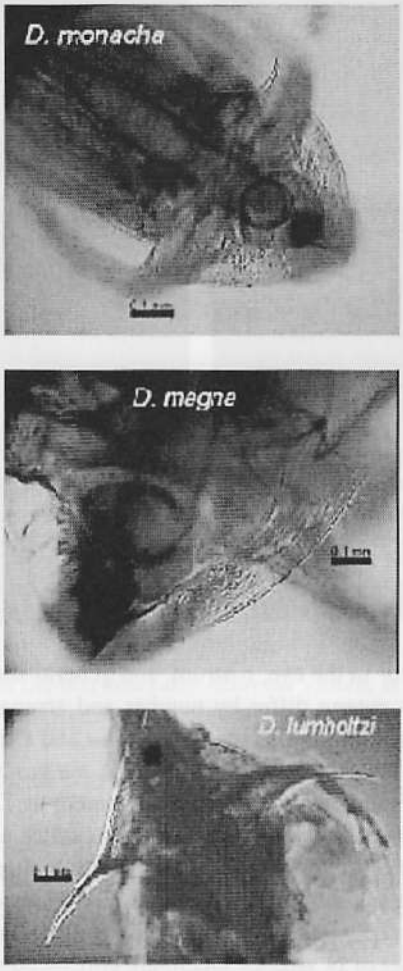

Figure 4. Fornices of *Daphnia* species from Lakes Albert and Victoria.

3.7 Seasonal Occurrence

D. longispina is a perennial member of the offshore zooplankton in Lake Victoria (Figure 7), but D. *magna* occurs episodically and inconsistently. The first known recorded occurrence of *D. magna* in the lake, April 1992, also seems to have been one of the most abundant. The peak abundances recorded for *D. magna* occurred in April 1992 during the rainy season but also in January 1994 during the dry season.

No simple pattern of seasonality is evident. This sporadic occurrence of *D. magna* may be a consequence of its high susceptibility to fish predation, and it may reflect opportunistic successes governed mainly by local planktivore abundance.

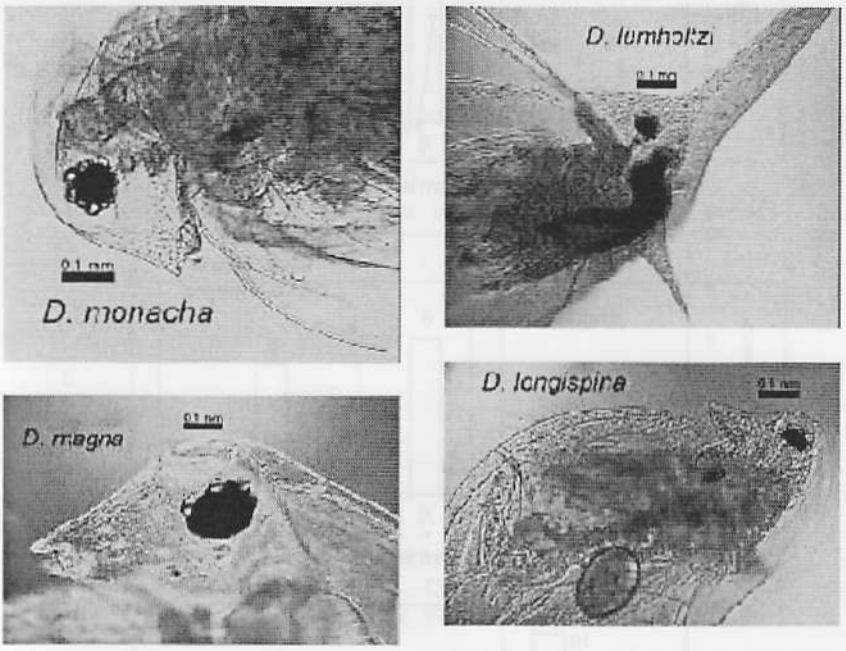

Figure 5. Eye and rostrum of *Daphnia* from Lakes Albert and Victoria. All scale bars are 0.1 mm.

4. DISCUSSION AND CONCLUSION

Based on review of existing plankton collections, there is no doubt that the large *Ctenodaphnia* first reported in Lake Victoria by Branstrator *et al.* (1996) was in fact *Daphnia magna*. There are sufficient similarities between *D. magna* and *D. monacha* that the taxa could easily be confused in the absence of reference specimens from the Rift Valley lakes. In the course of this study, we inspected *Daphnia* present in the equivalent of more than 100 m^3 of water from the offshore region of Lake Victoria.

Among the *Ctenodaphnia* present, not one could be reliably identified as *D. monacha*. Taxonomic nuances notwithstanding, the ecological significance of finding such a large-bodied cladoceran in the offshore waters of Lake Victoria must signal profound changes in the planktivory levels there. The explosive growth of introduced Nile perch during the 1990s is known to have decimated native stocks of haplochromines, including zooplanktivorous species. The ecological vacuum created

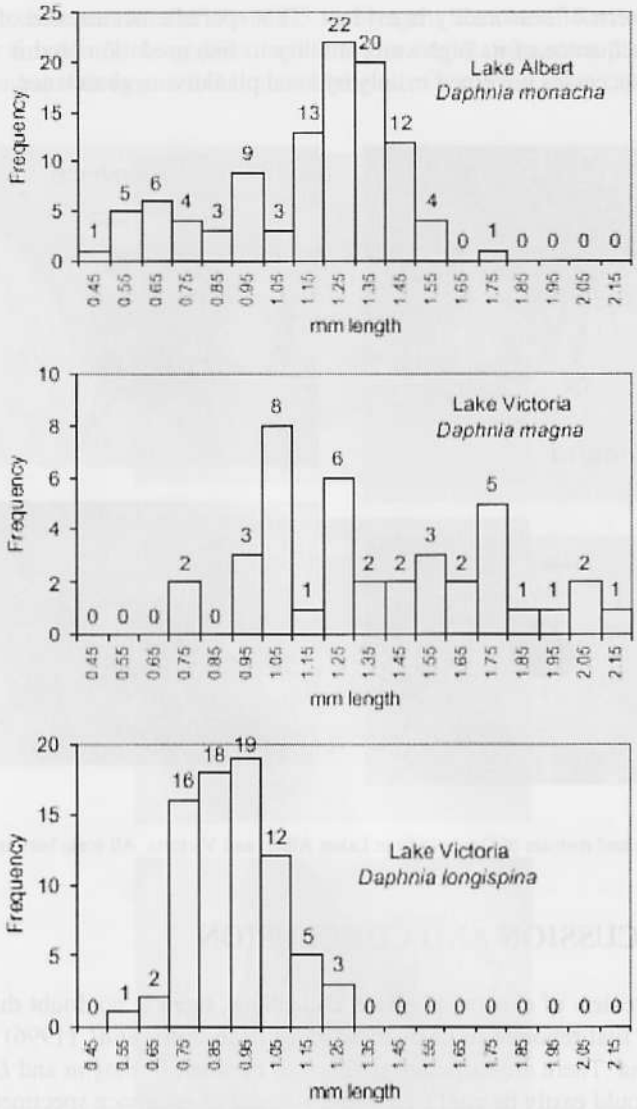

Figure 6. Size frequency for *D. monacha* from 29 March 1995 Lake Albert (upper); *D. magna* (middle), and *D. longispina* (lower) from 16 April 1992 Lake Victoria.

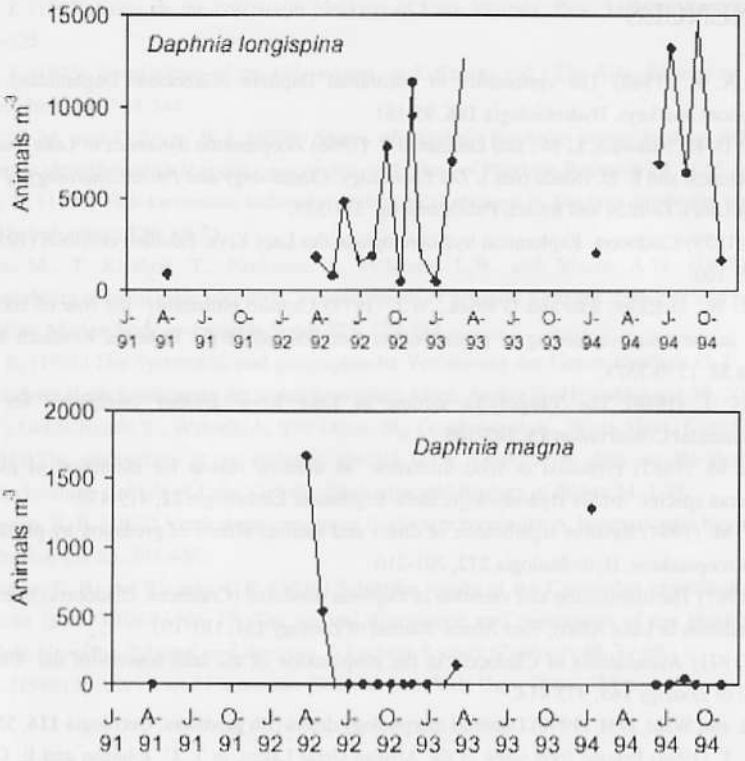

Figure 7. Occurrence of *D. longispina* (lower) and *D. magna* (upper) in Lake Victoria.

by collapse of a resident fish community seems to have created the opportunity for successful colonization of the lake by an atypical and unexpected herbivore.

One additional consequence of this study has been the documentation of striking and consistent morphological differences between *D. lumholtzi* and the taxon labeled *D. lumholtzi* var. *monacha* by Wagler in 1936. It seems untenable to us that these are polymorphisms of the species, and we therefore reverted to the older name *D. monacha* in this report. At this point, we can confirm the presence of *D. lumholtzi* in Lakes Victoria, Edward, and Albert. *D. monacha*, however, seems still to be absent from Lake Victoria.

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