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Zooplankton Diversity in Philippine Lakes*

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Abstract

Sustainable fisheries development partly depends on the availability of adequate zooplankton as principal food items of early life history stages of economically important fish species as well as of the adults of some species such as clupeids (e.g., *Sardinella tawilis* of Lake Taal in Batangas). The broad characteristics of the composition of freshwater zooplankton (Rotifera, Cladocera and Copepoda) of natural and man-made lakes in the Philippines are compared with those of the Oriental Region, in particular, and other tropical regions, in general. Two species of calanoid copepods are endemic, a somewhat remarkable occurrence considering that calanoids are represented by only five known species in the Philippines and absent in many large tropical lakes. *Daphnia*, which almost invariably influences food-web interactions and structures of plankton communities in temperate lakes, still has to be recorded.

Introduction

The study of the diversity of zooplankton in tropical lakes, such as the lakes in the Philippines, elicits more questions after one seems to have found some answers. Are the tropical freshwater zooplankton really less diverse than those in temperate lakes? Why is *Daphnia*, arguably the living icon of studies of zooplankton in lakes, rare or absent in tropical waters? How important are the zooplankton to the fish? Does the fish community decide which species of zooplankton may be present in a tropical lake, as well as when and where these zooplankters may persist?

This paper expounds on the views of Dr. C.H. Fernando of the University of Waterloo and others who have worked on tropical freshwater zooplankton and the related topics on fish-plankton interactions and fish production. It discusses the diversity of the three major groups of zooplankton: Rotifera, Cladocera and Copepoda in the Oriental Region (Southeast Asia) as a whole and in the Philippines in particular, focusing on the major natural lakes and a man-made lake.

*This presentation honors **Asuncion Amila An Lim**, alumna of Mindanao State University and Siliman University. She would have been a worthy collaborator in the study of the Zooplankton of Lake Lanao had she lived longer.

Overview of Literature

Dussart *et al.* (1984) provided a review of the systematics, distribution and ecology of freshwater zooplankton in the four major regions with tropical conditions (Africa, Australia, Asia, South America, and Asia); an extensive bibliography is given. The taxonomy and distribution of freshwater zooplankton in the Philippines were reported in Mamaril and Fernando (1978) and Mamaril (1986). Lai *et al.* (1979) dealt with the taxonomy and affinities of Philippine Calanoida (Copepoda). A review of studies on Philippine zooplankton is presented in Mamaril (1997).

In the Philippines, zooplankton work appear to be subsumed under the more inclusive sphere of "fisheries" (e.g., Baluyut 1983; Montemayor 1984-1985; Pantastico *et al.* 1985). Lake monitoring protocols that include zooplankton are essentially fisheries-based (Zafaralla *et al.* 1989; Zafaralla *et al.* 1992; Santiago AE, pers. comm.).

Ecological aspects of freshwater zooplankton were considered in Lake Mainit and Lake Lanao, both in Mindanao, by Lewis (1973a, 1975, 1979). The influence on populations of Cladocera and Rotifera of physico-chemical parameters associated with water level changes in La Mesa Dam in Quezon City were investigated by Lacuna (1992) and Vocalan (1992). Autecological studies on the calanoid copepod *Filipinodiaptomus insulanus* in La Mesa Dam were conducted by Palomar (1997), Abesamis (1997) and Pioquinto (1997). In a freshwater biotope that dominates Southeast Asian landscapes, Romano (1996) compared changes in species composition of Cladocera in Bulacan during one rice crop cycle in ricefields where commercial fertilizers were applied.

Are tropical freshwater zooplankton less diverse?

Whereas tropical freshwater ichthyofauna are highly diverse, freshwater zooplankton are far less diverse than marine zooplankton (Fernando 1994). Fernando (1980a, 1980b) pointed out that (i) the species composition differs between tropical and temperate regions, (ii) there are fewer tropical freshwater zooplankton, Cladocera in particular, than their temperate counterparts, and (iii) the Cladocera and Copepoda are smaller in size and low in biomass.

The freshwater zooplankton of South East Asia (Oriental Region), including that of the Philippines, are typically tropical. Fernando (1980b) characterized the species composition as monotonously uniform with the same few species of limnetic Cladocera and Copepoda, especially Cyclopoida, occurring throughout the region.

Trends among Rotifera in Philippine Lakes

Southeast Asian Rotifera are represented mainly by the genus *Brachionus* and *Keratella tropica*, both limnetic species (Table 1). *Brachionus calyciflorus*, *B. caudatu*, and *K. tropica* are deemed the three commonest rotifers (Fernando 1980b). In the Philippines, *B. calyciflorus* along with *B. patulus*, *B. quadridentatus* and the closely related *Platyias quadricornis* are very common (Mamaril 1986). These species are found in various freshwater biotopes in the Philippines, including astatic habitats. Several species of *Lecane* (under subgenera *Lecane*, *Hemimonostyla*, and *Monostyla)* are present, although these are mainly littoral forms.

Table 1. Provisional list of species of Rotifera and their distribution in the Philippines*

	Laguna	Lanao	Taal	Mainit	LaMesa	Others
Brachionus angularis	‡		†	†		
Brachionus calyciflorus	†		†	†		
Brachionus caudatus	†					
Brachionus diversicornis			†			
Brachionus falcatus	†		†	†	†	
Brachionus forficula	†		†	†		
Brachionus havaenensis			†			
Brachionus leydigii						†
Brachionus patulus	†			†	†	
Brachionus plicatilis			†			
Brachionus quadridentatus	†		†	†		
Brachionus rubens						†
Brachionus urceolaris	†		†			
Keratella cochlearis		†			†	
Keratella procurva	†	†	†			
Keratella tropica	†		†	†		
Keratella valga valga			†	†	†	
Platyias quadricornis	†	†		†	†	
Dipleuchlanis propatula	†				†	
Euchlanis dilatata	†	†		†	†	
Tripleuchlanis plicata			†			
Lophocharis salpina						†
Mytilina bisulcata	†				†	
Mytilina ventralis						†
Trichotria tetractis					†	
Macrochaetus collinsi				†		
Manfredium eudactylotum						†
Anuraeopsis fissa				†		
Lecane (Lecane) ceylonensis						†
Lecane (Lecane) crepida					†	
Lecane (Lecane) curvicornis	†					
Lecane (Lecane) curvicornis var. miamiensis					†	
Lecane (Lecane) curvicornis var. nitida						†
Lecane(Lecane) elegans						†
Lecane (Lecane) hastata				†		
Lecane (Lecane) hornemanni					†	
Lecane (Lecane) leontina	†	†			†	
Lecane (Lecane) ludwigii					†	
Lecane (Lecane) luna	†	†	†	†	†	†
Lecane (Lecane) papuana	†			†	†	
Lecane (Lecane) ploenensis						†
Lecane (Lecane) subtilis						†
Lecane (Lecane) ungulata			†	†	†	
Lecane (Hemimonostyla) sympoda					†	
Lecane (Hemimonostyla) undulata					†	
Lecane (Monostyla) bulla	†	†		†	†	†
Lecane (Monostyla) closterocerca					†	
Lecane (Monostyla) decipiens					†	

*Major lakes and a man-made lake (La Mesa Dam); others refer to ponds, ditches, rivers, etc.
N.B. Some species of Rotifera in Laguna de Bay were reported in Vallejo *et al.* (1984).

Table 1.Provisional list of species of Rotifera (continued)

	Laguna	Lanao	Taal	Mainit	LaMesa	Others
Lecane (Monostyla) lunaris					†	
Lecane (Monostyla) perpusilla						†
Lecane (Monostyla) pyriformis					†	
Lecane (Monostyla) quadridentata					†	
Lecane (Monostyla) stenroosi	†			†	†	
Lecane (Monostyla) thienemanni		†				
Lecane (Monostyla) unguitata					†	
Colurella colurus						†
Lepadella acuminata						†
Lepadella ovalis						†
Lepadella patella			†		†	
Lepadella rhomboides						†
Cephalodella forficula						
Dicranophorus robustus		†			†	
Proalides sp. (?)		†				
Polyarthra vulgaris	†	†		†	†	
Asplanchnopus multiceps		†			†	
Trichocerca brachyurum (?)		†				
Trichocerca capucina	†				†	
Trichocerca dixon-nuttali			†			
Trichocerca rattus		†				
Sinantherina spinosa					†	†
Conochiloides dossuarius		†		†	†	
Hexarthra intermedia		†			†	
Hexarthra fennica			†			
Tetramastix opoliensis	†	†			†	
Filinia longiseta	†					
Testudinella patina	†	†	†		†	†

Trends among the Cladocera in Philippine Lakes

The scarcity of Cladocera in the tropics is said to be due to (i) the relative rareness of *Daphnia*; (ii) the absence of representatives of families that are a feature of temperate lakes - Leptodoridae, Holopedidae and Polyphemidae; (iii) the absence of large Cladocera such as *Eurycercus* and *Saycia*, two of the largest Chydoridae; and (iv) only a few endemic Cladocera (Fernando 1980b). The individuals are said to be small in size and low in biomass as well.

Tropical Cladocera may not be as depauperate as they are thought to be if comparisons between cladoceran fauna in tropics and temperate regions are based on a unit areal basis (Dumont 1994). Temperate species are not much greater in total number than tropical species. At times, there may be more species in certain regions of the tropics than in comparable temperate areas. Single samples in the tropics may contain as many as 20-25 co-occurring species of Cladocera. An upper limit of ca. 50 species of Cladocera per lake seems to be the norm. In the Philippines, the most number of co-occurring species (17) was recorded in a single sample collected in Bustos Dam in Bulacan, Luzon, in 1975 (Mamaril 1986). The dam had a dike only a few meters high, which at the time of sampling, was breached by fast-flowing waters due to heavy rains. Philippine Cladocera consist of ca. 49 species (Mamaril and Fernando 1978, Mamaril 1986) (Table 2).

Table 2. Provisional list of species of Cladocera and their distribution in the Philippines*

	Laguna	Lanao	Taal	Mainit	LaMesa	Others
Diaphanosoma sarsi		‡	‡	‡	‡	
Diaphanosoma excisum	‡					
Diaphanosoma modigliani		‡			‡	
Latonopsis australis		‡	‡			
Pseudosida bidentata	‡	‡			‡	
Bosmina longirostris		‡	‡	‡		
Bosmina fatalis	‡	‡	‡		‡	
Bosminopsis deitersi		‡				
Simocephalus latirostris						‡
Simocephalus vetulus			‡			
Simocephalus acutirostratus						‡
Ceriodaphnia cornuta		‡	‡			
Ceriodaphnia pulchella						‡
Scapholeberis kingi	‡	‡				
Moinodaphnia macleayi			‡			
Moina micrura	‡	‡			‡	
Moina brachiata						‡
Moina macrocopa						‡
Echinisca rosea	‡	‡				
Macrothrix triserialis						‡
Macrothrix spinosa	‡	‡			‡	
Grimaldina brazzai						‡
Guernella raphaelis		‡				‡
Ilyocryptus spinifer	‡	‡	‡			‡
Pleuroxus aduncus					‡	
Pleuroxus similis						‡
Alonella excisa					‡	
Dadaya macrops					‡	‡
Dunhevedia crassa		‡	‡		‡	‡
Dunhevedia serrata		‡			‡	
Chydorus barroisi		‡	‡	‡		
Chydorus ventricosus			‡		‡	
Chydorus parvus					‡	
Chydorus eurynotus		‡			‡	
Leydigia acanthocercoides		‡			‡	‡
Alona cambouei					‡	
Alona circumfimbriata					‡	
Alona davidi	‡	‡			‡	
Alona pulchella						‡
Alona pseudanodonta						‡
Alona guttata		‡				
Kurzia longirostris	‡	‡			‡	
Euryalona orientalis	‡					
Camptocercus uncinatus						‡
Indialona globulosa	‡	‡				
Indialona macronyx						‡
Biapertura karua		‡			‡	
Biapertura pseudoverrucosa	‡	‡	‡		‡	‡
Biapertura affinis					‡	
Oxyurella singalensis	‡					‡

*Major lakes and a man-made lake (La Mesa Dam); others refer to ponds, ditches, rivers, etc

Among the major lakes, Lake Lanao appears to have the largest number of species of Cladocera (ca. 25) (Table 2) which are however mainly littoral forms (Mamaril 1986). Twenty-four (24) species (Table 2) have been reported in La Mesa Dam a man-made lake, from several samples collected intermittently from 1975 to 1992 (Mamaril and Lopez 1995).

In Lake Lanao, Lewis (1979) listed only four limnetic cladoceran species, two of which are species of *Diaphanosoma*. This genus is represented by at least four species in the Philippines (Table 2) and elsewhere in the tropics, whereas only up to two species have been recorded in the temperate zone (e.g., Britain and Ontario, Canada) (Fernando 1980b; Dumont 1994). Dumont (1994) considers Diaphanosoma (and other Sididae) and Moina among the tropical Cladocera as species replacements of *Daphnia*. The genus *Moina*, especially *M. micrura*, which is commonly present in the pelagial of tropical lakes, is spared from intense fish predation because of small size and body transparency. In contrast, *Ceriodaphnia* has fewer species in the tropics (Fernando 1980b). *Ceriodaphnia cornuta*, an ubiquitous tropical species, most likely consists of several taxa. These small *Daphnia*-species (*Moina* spp., *Diaphanosoma* spp., *Ceriodaphnia* spp., and *Bosmina* spp.) appear to be taken by invertebrate predators (Dumont 1994), as is the case in Lake Lanao, rather than by vertebrate predators.

The tropics lack large Chydoridae such as *Eurycercus* and *Saycia*, and the Oriental Region has only quite a few endemic Cladocera (Fernando 1980b). *Eurycercus*, *Saycia* and another large cladoceran *Simocephalus* (Daphniidae) are common in the littoral of temperate regions. *Simocephalus* is said to be very rare in tropical regions. In the Philippines, Simocephalus is represented by three species, of which *S. latirostris* is the only one common (Table 2). However, one of the rarest Cladocera as well as endemic in South East Asia, *Indialona macronyx*, is found in the Philippines (Mamaril and Fernando 1978; Mamaril 1986). A few specimens were also found in a man-made pond in the Quezon City campus of the University of the Philippines (Mamaril, pers. obs.).

Daphnia vanishes in the tropics

Why is *Daphnia*, which is so common and numerically dominant in temperate lakes, so rare in the tropics and absent in the Philippines? Locally, *Daphnia pulex* was reported by Wright (1928) in a sample collected "in the vicinity of Manila" but Fernando (1980b) considered *D. pulex* a very doubtful record. Cheng and Clemente (1953) recorded 14 species of Cladocera but no *Daphnia* during a two-year collection effort in and around Manila. No *Daphnia* was included in Mamaril (1986). An attempt to introduce *Daphnia* in Mindanao was made a few years ago (Escudero, pers. comm.).

Various interlocking hypotheses were proposed by Fernando (1980a; 1980b), Fernando *et al.* (1987) and Dumont (1994) to explain the rareness of *Daphnia* in the tropics. One favored explanation is that *Daphnia* is eliminated by heavy fish predation all-year round. Fernando (1980b) cited as possible exceptions Lake Lanao and Lake Toba in Sumatra, Indonesia, which have low fish diversity and low yield and yet have no *Daphnia*. However, Lake Lanao which used to have 18 or so endemic species of Cyprinidae had a diverse ichthyofauna (Herre 1933 cf. Greenwood 1984; Frey 1969; Kornfield 1982; Kornfield and Carpenter 1984).

Was there a Lake Lanao planktivore?

Given the long history of Lake Lanao, which is in dispute (Frey 1969; Kornfield and Carpenter 1984), *Daphnia* would have had sufficient time to colonize the lake in the same manner that the endemic cyprinids had enough time to evolve, possibly by intra-lacustrine speciation or other means (Kornfield and Carpenter 1984). Does the evolution of the cyprinids imply that ecological conditions carved out unfilled feeding niches for presumptive planktivores, in spite of Lanao being a relatively small lake (as compared to large species-rich tropical lakes such as Tanganyika, Victoria and Malawi)? Did one or more plankton-feeding cyprinids wipe out *Daphnia*? Gut analyses of one of the cyprinids, *Puntius sirang* (locally known as 'sirang' or 'tumaginting'), revealed that it consumed a greater proportion of phytoplankton than zooplankton (Sanguila *et al.* 1975; Escudero *et al.* 1980). Unfortunately, with the near-total anthropogenic extinction of the Lanao cyprinids, their food and feeding ecology would remain largely unknown.

Clues and more questions

Escudero *et al.* (1980) and Escudero (1995) provided clues on the probable feeding habits of *Puntius sirang* in Lake Lanao. They described the fishing technique to catch this "small, gregarious pelagic fish". Strong light from pressurized kerosene lamps is used in attracting 'sirang' toward a net which is operated like a purse seine from two small boats which encircle the school of fish. Further, 'sirang' fishing is said to be restricted to the southern end of the lake, which Frey (1969) described as the deepest part (z_m = 112 m). These observations dramatically have parallels with what are currently known about the schooling plankton-feeding pelagic species, *Sardinella tawilis* (family Clupeidae) locally known as 'tawilis', in Lake Taal in Batangas, Luzon. The size range reported by Escudero *et al.* (1980) for the Lanao cyprinid was 47-124 mm whereas Aypa *et al.* (1991) reported 47-130 mm for the Taal clupeid! Are these endemic species analogous to ecological equivalents?

Cyprinids are similarly found in Lake Manguao, a small shallow lake (640 ha) in Palawan, an island which has strong zoogeograpical affinities with Borneo. Davies and Green (1990) reported a fairly diverse zooplankton community which has a calanoid copepod, *Tropodiaptomus vicinus*, as the prominent limnetic species. The fish fauna include three cyprinids, *Puntius manguaoensis* and *P. bantolanensis* which are both endemic and *Rasbora argyrotaenia* (Day 1914 cf. Davies and Green 1990). The two endemic species are thought to have descended from the same ancestral stock (possibly *Puntius binotatus*) of the Lanao cyprinids. No fish species has exploited the limnetic zone of Lake Manguao inspite of the rich food base available. *Puntius* spp. were caught exclusively in the littoral. *Puntius* and *Rasbora* have long coiled intestines characteristic of omnivores. The limnetic cladoceran *Diaphanosoma* sp. is present but there is no *Daphnia* (Davies and Green 1990). A somewhat similar situation prevails in Lake Maughan, a deep crater lake in South Cotabato in Mindanao. The lake was likely fishless and yet had no *Daphnia*. Tilapia were introduced only in the mid-1980s (Mamaril, pers. obs.).

The case of the missing *Daphnia* - a multi-causal event?

The contention that *Daphnia* are rare in the tropics because of fish predation was questioned by Fernando *et al.* (1987). Fernando and Holcík (1982, 1985) demonstrated that pelagic fish are almost completely absent in tropical lakes and reservoirs, thus fish predation may not fully explain the rareness or absence of *Daphnia*. Although 10 species of *Daphnia* have been recorded in Africa, a large area of equatorial rainforest Africa lacks *Daphnia*. The too constant environmental conditions in the tropics seem unsuitable for *Daphnia* (Dumont 1980).

Other probable causes of the perceived low diversity and small size of tropical zooplankton that have been proposed are uniform high temperatures, lack of continuity of large bodies of waters (both in space and time), non-availability of suitable food particle size and low oxygen levels. Size-selective predation by fish may be a probable cause (Fernando 1980a, 1980b) but may not explain the size differences between species in contiguous zones (Fernando 1980b).

Trends among Copepoda in tropical freshwaters

In the Philippines, as in the rest of Southeast Asia, the Cyclopoida are dominated by the predatory *Mesocyclops leuckarti* and the algivorous *Thermocyclops crassus* (Fernando 1980b, Mamaril 1986) (Table 3). The single ubiquitous tropical species, M. leuckarti, is probably a complex of several species (Fernando, pers. comm.). Calanoida have a few genera and species that are restricted to local regions (Fernando 1980b). Lewis (1979) pointed out that although the great majority of tropical lakes have at least one species of Cyclopoida, the Calanoida are much more irregular in distribution. Further, calanoids are absent in many large lakes where they can be expected. Of the 15 Sunda lakes in the Oriental region visited by Ruttner (1952 cf. Lewis 1979) only Lake Toba in Sumatra, Indonesia contained a species of calanoid.

Table 3. Provisional list of species of Copepoda and their distribution in the Philippines*

	Laguna	Lanao	Taal	Mainit	LaMesa	Others
Ectocyclops phaleratus		‡	‡			‡
Paracyclops fimbriatus						‡
Tropocyclops prasinus		‡			‡	‡
Eucyclops serrulatus		‡	‡		‡	‡
Mesocyclops leuckarti	‡	‡	‡		‡	‡
Thermocyclops crassus	‡	‡	‡	‡?	‡	‡
Microcyclops varicans	‡	‡	‡	‡	‡	
Ergasilus philippinensis					‡	
Elaphoidella sewelli						‡
Elaphoidella grandidieri		‡				
Filipinodiaptomus insulanus	‡					‡
Monglodiaptomus birulai						‡
Tropodiaptomus gigantoviger	‡					
Tropodiaptomus vicinus		‡	‡?			‡?
Tropodiaptomus australis						‡

*Major lakes and a man-made lake (La Mesa Dam); others refer to ponds, ditches, rivers, etc.
Species marked ‡? has to be verified.

Zooplankton in major lakes in the Philippines

The zooplankton of Laguna de Bay is relatively diverse (Mamaril 1986). At least three brachionid species (3 spp. of *Brachionus* and *Platyias quadricornis*) are among the 21 species of Rotifera present (Table 1). *Filipinodiaptomus insulanus*, an endemic calanoid, is present (Mamaril and Fernando 1978; Lai *et al.* 1979; Mamaril 1986). Another calanoid, tentatively identified as *Arctodiaptomus*, may be present (Rivera, pers. comm.). Fish fry such as those of tilapia are expected to consume part of the lake zooplankton but the extent of fish predation remains to be studied.

Lake Lanao has a comparatively simpler limnetic zooplankton community (Frey 1969; Mamaril and Fernando 1978; Lewis 1979) in spite of its high primary productivity (Lewis 1974) which is enhanced by atelomixis, the nonseasonal remixing of the divided epilimnion (Lewis 1973b). Its year-round composition is not much different from its composition at any one time.

Lake Lanao limnetic zooplankton appear to be 'atypical' of freshwater habitats in the Philippines:

- The rotifer *Brachionus forficula* and the cladocerans *Diaphanosoma modigliani*, *Bosminopsis deitersi* and *Bosmina longirostris* were recorded by Woltereck (1941). The cladocerans were observed in subsequent samples but *Brachionus* spp. were absent (Frey 1969; Mamaril and Fernando 1978; Lewis 1979) (Table 1). Common in the limnetic plankton in most tropical lakes, *Brachionus* spp. are more important in the tropics than in temperate lakes (Green 1972). D. *modigliani* and B. *deitersi* are relatively rare in the Philippines (Mamaril 1986).

- *Tropodiaptomus gigantoviger*, an endemic species of Calanoida (Brehm 1933; Frey 1969; Fernando and Mamaril 1978; Lewis 1979) co-occurs with *Tropodiaptomus* vicinus (Mamaril and Fernando 1978; Lai *et al.* 1979) (Table 3). *T. vicinus* is widely distributed in the Oriental Region (Lai and Fernando 1980). The presence of co-occurring calanoids in Lake Lanao is the more fascinating, even perplexing, if not for the absence of a calanoid in Lake Mainit, which is also in Mindanao (Lewis 1973a; Mamaril 1986). Lewis (1979) observed that calanoids are missing in many large lakes even in those that appear to offer suitable conditions. The fourth largest lake, Mainit, is similar to Lanao in general water quality and plankton composition. Like Lake Lanao, it is a naturally productive lake, a condition belied by its high water transparency (Lewis 1973a).

- The cosmotropical cyclopoid copepod *Thermocyclops crassus* (= *Thermocyclops hyalinus*) is present (Lewis 1979) but the widely distributed *Mesocyclops leuckarti* is conspicuously absent in the limnetic zone (Mamaril 1986).

- Zooplankton diversity and abundance in Lake Lanao are greatly influenced by a planktonic invertebrate obligate predator, *Chaoborus* (Diptera: Chaoboridae). It is the only large non-piscine carnivore preying heavily on zooplankton (Lewis 1975). Surprisingly abundant, highly selective, efficient, and voracious, the instars of *Chaoborus* consume cladocerans in numbers far exceeding the latter's relative abundance in the plankton community (Lewis 1980). *Chaoborus* is an amazing predator of zooplankton for being truly planktonic at one time (when it exhibits vertical migration at night) and for being benthic (in the sediments) (Frey 1969; Lewis 1975). *Chaoborus* was not reported in Lake Lanao by Woltereck (Frey 1969) and Fernando *et al.* (1990) consider it to be less common in tropical waters than in temperate waters. A similar situation occurs in Lake Malawi where *Chaoborus edulis* is the dominant predator of zooplankton (Turner *et al.* 1982).

Lake Taal - a typical tropical lake?

The species composition of the zooplankton in Lake Taal is closest to what may be considered as 'typically tropical' (Tables 1-3). As in most tropical lakes, the limnetic zooplankton show low diversity (Mamaril 1986). The only large-bodied Cladocera observed is *Simocephalus vetulus*. The cladocerans *Bosmina* and *Moina* and calanoid copepods, which are common in Laguna de Bay, are remarkably rare even in limnetic samples. The limnetic species *Diaphanosoma sarsi* and *Ceriodaphnia cornuta* are present (Mamaril, unpubl. data). Among the Rotifera, *Brachionus* is represented by nine species (Mamaril 1986; unpubl. data) (Table 1). Of the nine, three were observed by Zafaralla et al. (1992) and four by UPLBFI (1996). *Keratella tropica* is one of three *Keratella* spp. Cyclopoid copepods are well-represented with five species out of a total of seven species for the entire country (Mamaril 1986; unpubl. data). Calanoids were observed for the first time in a sample collected in August 1989. Specimens of a male diaptomid calanoid were subsequently collected in the same period (Mamaril, unpubl. data). Zafaralla *et al.* (1989, 1992) identified the calanoid as *Tropodiaptomus vicinus*; this has to be further verified. Large numbers of unnamed calanoids are reported in UPLBFI (1996). All in all, Lake Taal has all the elements of a tropical zooplankton assemblage as characterized by Fernando (1980b).

The zooplankton of Lake Taal appear to be more diverse than those of the other major lakes in the Philippines in spite of the presence of a true planktivorous fish, the clupeid *Sardinella tawilis*, which is endemic in Taal. The sardinella preys on all three groups of zooplankton as seen in the guts of 100 'tawilis' caught at night by motorized push nets from August through November 1996 (Flores 1997). This confirms the observations of Castillo *et al.* (1974) and Habito and Mendoza (1987 cf. Zafaralla *et al.* 1989). Herre (1927) however observed some 'tawilis' to consume young silversides (locally known as 'guno'). Shifts to and levels of piscivory by 'tawilis' need to be further investigated to establish whether 'tawilis' is a facultative or obligate planktivore. The features of planktivory has a direct influence on zooplankton diversity, size composition, and abundance (Lazzaro 1987).

Zooplankton and fisheries

The importance of zooplankton as food resource of fish is not limited to pelagic planktivorous species such as *Sardinella tawilis* in Lake Taal and the amazing Tanganyika sardines. The survival of the young of herbivorous fishes such as tilapia may depend on the availability of abundant littoral zooplankton and benthos aided by omnivory and high ecological efficiencies. Planktonic fish larvae (ichthyoplankton) prey on zooplankton and occasionally phytoplankton. Several families of fish consume zooplankton wholly or partly in various stages of their life histories (Lazzaro 1987). Zooplankton are thus crucial to achieving high fish yields in the tropics even if their role seems to be mainly through the young stages of fish (Fernando 1994).

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