


Zooplankton, zooplanktivorous fish and their interactions in Southeast Asian waterbodies with special reference to Sri Lanka: a review

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Abstract Many countries in Southeast Asia have no natural lakes but reservoirs, flood-plains and rivers. The reservoirs are mainly inhabited by riverine fish species and introduced pelagic exotics. Benthivores, herbivores and detritivores dominate, whereas zooplanktivores are relatively rare (generally 4.6-9.5% of the fish community). Therefore, zooplanktivorous fish are not dominant in most Sri Lankan reservoirs and play only a minor role in the food web. In the Southeast Asian region, only small, often pelagic, zooplanktivorous fish species occur. They are either of riverine or marine origin. Observations were made that only six predominantly zooplanktivorous species viz a cyprinid from riverine origin *Rasbora daniconius*, a half beak from marine origin *Hemiramphus limbatus*, the glass perchlet *Ambassis urotaenia* and three freshwater clupeids from marine origin (*Clupeichthys aesarnensis*, *Ehirava fluviatilis*, *Sardinella tawilis*) inhabit the reservoirs in Southeast Asian countries such as Sri Lanka and Thailand and a lake in the Philippines. The highest percentages of zooplanktivory in the tropical region are observed in waterbodies which contain zooplanktivores of marine origin. These small pelagics are very productive, i.e., have relative high Annual Production/Biomass (P/B) ratios. P/B ratios of the small Southeast Asian pelagics ranged generally from 3-6, small clupeids showed the highest P/B ratios. Of the riverine species, *R. daniconius* is the most successful; it is a common species in the Sri Lankan reservoirs. This species is, however, not able to catch the small cladocerans and the cyclopoid copepods efficiently and fails completely to catch the fast moving calanoid copepods. Instead of feeding on larger zooplankton, they often feed on adult winged midges which are floating on the water surface. *H. limbatus* is not abundant in Sri Lankan reservoirs and its distribution is limited where only occasionally its densities are high enough to permit a profitable fisheries. Although the freshwater clupeids seem to be superior in their efficiency of collecting food organisms, their distribution is often limited. Despite their ability to build up stable and large populations in a handful of water bodies in the Philippines and Sri Lanka, they have a problem in dispersing into other freshwater lakes and reservoirs. In Thailand, the situation is different because *C. aesarnensis* is well adapted to riverine conditions and, therefore, present in all reservoirs with inflowing riverine habitats, but in most cases these stocks are still unexploited.

Keywords: fish species of marine origin, fish species of riverine origin, freshwater clupeids, zooplankton body-size

INTRODUCTION

In the tropical waterbodies, the body size of zooplankton is generally smaller than those in cold water lakes and large zooplankton such as *Daphnia* spp. are scarce or lacking. Reduced zooplankton body size in warm waters can be generally attributed to small species replacing larger ones. It is therefore important to understand how size composition of zooplankton is structured in tropical water bodies in relation to predation by zooplanktivorous fish. It must be noted that in the tropics, large zooplanktivorous fish are not found, only small pelagics, small zooplanktivorous fish species which inhabit the pelagic zones (open water) of reservoirs and lakes. The present paper reviews zooplankton,

zooplanktivorous fish and their interactions in eight waterbodies in three in Southeast Asian countries, Sri Lanka, Thailand and the Philippines. The review is based mainly on three sources of information: (1) results from the Austrian-English-Sri Lankan ecosystem study of Parakrama Samudra reservoir carried out from 1979-1982; (2) the results from The Netherlands-Sri Lankan fish and zooplankton studies on Tissawewa reservoir carried out from 1989-1992; and (3) the results from the FISHSTRAT project (1998-2002), a project supported by the European Union which was aimed to develop strategies for partitioning the productivity of Asian reservoirs and lakes between capture fisheries and aquaculture (Amarasinghe et al. 2001). Within the framework of the FISHSTRAT



project, three Sri Lankan reservoirs (Minneriya, Udawalawe, Victoria), one Thai reservoir (Ubolratana) and one crater lake in the Philippines (Lake Taal) were studied.

ZOOPLANKTON

General

Water temperature is one of the most important abiotic factors in aquatic systems because of its effect on the growth and survival of aquatic organisms (Hoekman 2010; Beveridge et al. 2010; Schriever 2015). As the tropical regions receive high annual irradiance and show low daily and annual variations in irradiance, tropical lakes and reservoirs have generally higher water temperatures and show a lower seasonal variation in water temperature than in temperate waterbodies (Lewis 1987).

Body size of zooplankton is a highly important attribute because of the influence it has on bioenergetics in aquatic food webs. Body size affects the manner in which the zooplankton interacts with its resources. Large-bodied zooplankton have higher grazing rates, having ability to graze a wider size range of food items, and therefore have greater top-down effects on resources than small-bodied zooplankton (Carpenter and Kitchell 1988). Likewise body size affects the availability and anti-predator responses of zooplankton to both invertebrate and vertebrate predators (Zaret 1980; Gélinas et al. 2007).

In the temperate region, the relatively large *Daphnia* spp. are a key element in the functioning of many freshwater ecosystems. They often control the algal growth via predation and guarantee the survival of the youngest stages of most freshwater fish species. Further they sustains the pelagic fish production relying on zooplanktivores as realised by obligatory zooplanktivores, facultative zooplanktivores and of piscivores (Lazzaro 1987).

In the tropical warm water lakes and reservoirs, the body size of zooplankton is generally smaller than of those in cold water lakes and *Daphnia* spp. are scarce or lacking (e.g. Fernando 1980; Amarasinghe et al. 1997; Gillooly and Dodson 2000; Havens et al. 2014). This is generally true for cladocerans and cyclopoid copepods, but not for calanoid copepods (Havens et al. 2014).

Although reduced zooplankton body size in warm waters can be generally attributed to small species replacing larger ones (Gillooly and Dodson 2000; Havens et al. 2014), the reason for the smaller body size in the tropical region is at present not clear. It may be due to that large-bodied zooplankton has a lower upper thermal tolerance (Moore et al. 1996), or that large-bodied zooplankton is stronger effected by low oxygen availability mediated by high and uniform temperatures (Chapelle and Peck 1999), or that large-bodied zooplankton is more vulnerable to food limitation (Lehman 1988), and/or that it is a response to the positive size selective predation of the zooplanktivorous fish (Zaret 1980), or a combination of all above.

Zooplankton of Southeast Asian Region

Common microcrustacean zooplankton species of Southeast Asian waterbodies are listed in Table 1. The species composition of copepods and cladocerans in Ubolratana and four Sri Lankan reservoirs was very similar, where the cyclopods were dominated by two species only: *Mesocyclops thermocyclopoides* and *Thermocyclops decipiens*. In all five reservoirs, calanoid copepods were dominated by a single species. In Sri Lankan reservoirs this was *Phyllodiaptomus annae* while in Ubolratana it was *Neodiaptomus botulifer*. All the reservoirs shared many cladoceran species such as *Bosminopsis dietersi*, *Ceriodaphnia cornuta*, *Moina micrura*, *Diaphanosoma excisum* and *D. modigliani*. There were two exceptions, *D. sarsi* was not found in Ubolratana reservoir and *Daphnia lumholtzi* was only common in one location at the Ubolratana reservoir. *D. lumholtzi* was also occasionally observed in the four Sri Lankan reservoirs but always in very low densities.

The zooplankton species composition of Lake Taal was different in several respects. The calanoid copepod species was different, and both cyclopoid species were different too. However, one of these species, *Thermocyclops crassus* is taxonomically closely related to *Thermocyclops decipiens*, which is common in the Sri Lankan and Thai reservoirs. Of the cladocerans, *Bosminopsis dietersi* was not present in Lake Taal, but instead another species of the Bosminidae, *Bosmina fatalis*, was present. Of the Sididae, *Di. excisum* and *Di. modigliani* were lacking, but *Di. sarsi* was present.

Zooplankton in Sri Lankan reservoirs

The zooplankton of five Sri Lankan reservoirs, Minneriya, Parakrama Samudra, Tissawewa, Udawalawe and Victoria, were investigated by Duncan (1983), Amarasinghe et al. (1997) and Amarasinghe et al. (2008) (Table 1). Although four of the reservoirs are located in the south-eastern lowlands and Victoria Reservoir in the Central Hill region, four of the five reservoirs have a similar zooplankton species composition (Table 1). The fifth reservoir, Parakrama Samudra, is a notable

exception where it is the only Sri Lankan reservoir known to have a pelagic zooplankton community which lacks crustacean zooplankton and contains only rotifers (Duncan 1983). The zooplankton community of the four other reservoirs was generally composed of six cladoceran spp. *Bosminopsis dietersi*, *Ceriodaphnia cornuta*, *Moina micrura*, *Diaphanosoma excisum*, *Diaphanosoma modigliani*, *Diaphanosoma sarsi*, two cyclopoid spp. *Mesocyclops thermocyclopoides*, *Thermocyclops decipiens* and one calanoid spp. *Phyllodiaptomus annae*.

Table 1 List of common microcrustacean zooplankton species in Southeast Asian waterbodies based on observations in Philippines (PH), Sri Lanka (SL) and Thailand (TH) according to A = Duncan (1983, 1999), B =Amarasinghe et al. (1997), C = Amarasinghe et al. (2008). Sampled waterbodies are: Minneriya (SL, MIN), Parakrama Samudra (SL, PS), Tissawewa (SL, TI), L. Taal (PH, TA), Ubolratana (TH, UB), Udawalawe (SL, UDA) and Victoria (SL, VI). Abbreviation used: nm= not measured.

Species	Taxonomic group	Max. Length (mm)	Country	Waterbody	Authority
<i>Heliodiaptomus viduus</i>	Calanoid cop.	nm	SL	TI	B
<i>Phyllodiaptomus annae</i> ,	Calanoid cop	1.3	SL	4 res.	B, C
<i>Neodiaptomus botulifer</i>	Calanoid cop	nm	TH	UB	C
<i>Tropodiaptomus vicinus</i>	Calanoid cop.	nm	PH	TA	C
<i>Mesocyclops thermocyclopoides</i>	Cyclopoid cop.	1.0	SL, TH	5 res.	B, C
<i>Microcyclops varicans</i>	Cyclopoid cop.	nm	PH	TA	C
<i>Thermocyclops decipiens</i>	Cyclopoid cop	nm	SL, TH	5 res.	B, C
<i>Thermocyclops crassus</i>	Cyclopoid cop	nm	PH	TA	C
<i>Bosminopsis dietersi</i>	Cladocera	0.4	SL, TH	4 res.	C
<i>Bosmina fatalis</i>	Cladocera	0.4	PH	TA	C
<i>Ceriodaphnia cornuta</i>	Cladocera	0.7	SL, TH, PH	6 water-bodies	B, C
<i>Daphnia lumholtzi</i>	Cladocera	1.5	TH	UB	C
<i>Diaphanosoma excisum</i>	Cladocera	1.3	SL, TH	5 res.	B, C
<i>Di. modigliani</i>	Cladocera	1.3	SL, TH	5 res.	B, C
<i>Di. sarsi</i>	Cladocera	1.3	SL, PH	4 water-bodies.	C
<i>Moina micrura</i>	Cladocera	0.7	SL, TH, PH	6 water-bodies	B, C
Rotifers	Rotifera	0.1	SL	PS	A

ZOOPLANKTIVOROUS FISH

General

Herbivory in fish communities is more prevalent in the tropical region whereas carnivory is more common at higher latitudes (Floeter et al. 2005; Behrens and Lafferty 2007; Gonzalez-Bergonzoni et al. 2012). The possible explanatory mechanisms for the dominance of carnivores at lower temperatures

is that because gut passage rate decreases more rapidly than metabolic rate as temperature declines, and that herbivorous fish may not be able to process enough food material to meet their metabolic demands at cooler temperatures (Floeter et al. 2005).

Recently, Boersma et al. (2015) proposed an alternative hypothesis to explain the dominance of herbivores at higher temperatures. They conclude that respiration rates increase more rapidly than growth rates as temperature increases and this

should result in higher demand for metabolic carbon at higher temperatures. Since algae and plant material contain a higher relative carbon content relative to P and N nutrients than animal food, algal food and plant material will become the preferred food at higher temperatures.

Zooplanktivorous fish in Southeast Asian waterbodies

The percentages of zooplanktivory in Sri Lankan fish communities was generally low, generally between 4.6 and 9.5% (Table 2). This is in contrast with temperate fish communities where the percentage of zooplanktivores is usually in the range of 40-90% (Vijverberg et al. 2014). However, in some Southeast Asian waterbodies higher percentages of zooplanktivory were observed. These waterbodies had one characteristic in common, they contained successful clupeid populations. In Parakrama Samudra reservoir (17.7% zooplanktivores) in Sri Lanka, Ubolratana reservoir (25%) in Thailand and Lake Taal (59%) in the Philippines were observed with successful clupeid populations (Table 2).

Table 2 Percentage zooplanktivory (% , biomass) of six fish communities in Southeast Asian water bodies according to A = Sricharoenndham et al. (2008), B = Vijverberg et al. (20014) and C = Villanueva et al. (2008), PH= Philippines, SL= Sri Lanka and TH= Thailand.

Water body	Zooplanktivory (%)	Country	Authority
Minneriya	5.8	SL	B
Parakrama Samudra	17.7	SL	C
Lake Taal	59	PH	A
Tissawewa	9.5	SL	B
Ubolratana	25	TH	C
Victoria	4.6	SL	B

Small pelagics were studied in five reservoirs (Minneriya, Tissawewa, Udawalawe, Victoria, Ubolratana) and one natural lake (Lake Taal) by Pet et al. (1996) and Ariyaratne et al. (2008). The results are summarized in Table 3. *Rasbora daniconius* (Cyprinidae) was present in all four Sri Lankan reservoirs, whereas the half-beak *Hyporhamphus limbatus* (Hemiramphidae) was present in Minneriya, Tissa wewa and Udawalawe reservoir but not in Victoria reservoir. In Ubolratana reservoir

(Thailand), the clupeid *Clupeichthys aesarnensis* was a common fish species in terms of production and numbers. In Lake Taal (Philippines), two small pelagics were present, the endemic clupeid *Sardinella tawilis* and the glass perch *Ambassis urotaenia* (Ambassidae). *S. tawilis* is the dominant zooplanktivore in Lake Taal, whereas *R. daniconius* was common in three of the four Sri Lankan reservoirs (Minneriya, Tissawewa, Udawalawe). The small clupeid *Ehirava fluviatilis* was only successful in two Sri Lankan reservoirs (Mihindikulasooriya and Amarasinghe 2014). The glass perch *A. urotaenia* and the halfbeak, *H. limbatus*, were the least successful in the Asian waterbodies studied in terms of abundance.

In general small pelagics are very productive, i.e. have a relative high annual Production/Biomass (P/B) ratios, higher than larger fish species living under similar conditions (e.g. Dejen et al. 2009). The annual Production/Biomass (P/B) ratio is the accumulated production over 12 months divided by the average biomass over the same period. The P/B ratios of the small pelagics from Southeast Asia were usually in the range of 3-6. The small clupeids showed the highest production rates (Table 3).

Zooplanktivorous fish in Sri Lankan reservoirs

Sri Lanka, like most other countries in Southeast Asia, has no natural lakes but only reservoirs, floodplains and rivers. The reservoirs are mainly inhabited by riverine fish species and the introduced pelagic exotics (*Oreochromis mossambicus* and *O. niloticus*). Benthivores, herbivores and detritivores dominate, whereas zooplanktivores are relatively rare. The early life stages of all fish species feed upon zooplankton (Fernando 1994). However, because of their small size and short duration of this larval life stage, their share in the total zooplankton predation is likely to be insignificant. Three species of small zooplanktivorous pelagic fish were recorded, but only one species, the cyprinid *R. daniconius* exhibited a relatively high abundance with a wide distribution (De Silva and Sirisena 1987; Amarasinghe 1990; Pethiyagoda 1991; Wijeyaratne and Perera 2001) (Table 3). The halfbeak *H. limbatus* of marine origin, occurs generally at low densities and has a limited distribution.

Table 3 List of zooplanktivorous fish observed in waterbodies in Philippines (PH), Sri Lanka (SL) and Thailand (TH) according to A= Newrkla and Duncan (1984), B = Pet et al. (1996), C= Ariyaratne et al. (2008). Fish length measured as total length (TL). Abbreviation used: nm= not measured.

Species	Common name	Family	Max Length (TL, cm)	P/B	Waterbody, Country	Authority
<i>Ambassis urotaenia</i> Bleeker, 1852	Banded-tail glass perchlet	Ambassidae	14.0	nm	L. Taal PH	C
<i>Hyporhamphus limbatus</i> (Valenciennes, 1847)	Half-beak	Hemiramphidae	17.6	2.0	3 SL res- ervoirs	B, C
<i>Rasbora daniconius</i> (Hamilton, 1822)	Slender Rasbora	Cyprinidae	15.0	3.3	4 SL res- ervoirs	B, C
<i>Sardinella tawilis</i> (Herre, 1927)	Freshwater Sardinella	Clupeidae	13.5	5.0	L. Taal PH	C
<i>Clupeichthys aesarnensis</i> (Wongratana, 1983)	Thai river sprat	Clupeidae	7.0	4.0	Ubolratana res., TH	C
<i>Ehirava fluviatilis</i> Deraniyagala, 1929	Malabar sprat	Clupeidae	5.5	6.0	Parakrama Samudra res., SL	A

The small clupeid *E. fluviatilis* from marine origin, has a limited distribution. Parakrama Samudra reservoir, an ancient reservoir in the Mahaweli River basin supports high densities of *E. fluviatilis* and they are spawning within the reservoir (Newrkla and Duncan 1984). Only one other Sri Lankan freshwater body Rajanganaya reservoir in the Kala Oya River basin is known to be inhabited by *E. fluviatilis* (Amarasinghe and Sriya, 2002; Mihindikulasooriya and Amarasinghe 2014). This species has been reported in several river estuaries of Sri Lanka (Pethiyagoda 1991), but a traditional seasonal fishery is established only in Bolgoda Lake in the Panadura estuary (Amarasinghe and Sriya, 2002). This fishery with the annual yield of about 23.2 kg ha⁻¹ is profitable and sustainable, but it is unlikely that spawning takes place within the estuary (Amarasinghe and Sriya 2002). The size range of the individuals in Parakrama Samudra reservoir and Bolgoda Lake was very similar, both having a maximum length (TL) of 5.5 cm, but the two populations differ in several other life history parameters. Size at first maturity of this species is higher in the estuarine population (35 mm TL) than in the reservoir population (20 mm TL) and the body weight condition is much higher in the estuary (Newrkla and Duncan 1984; Amarasinghe and Sriya, 2002).

Fish – zooplankton interactions in Southeast Asia

Ariyaratne et al. (2008) tested the hypothesis that riverine cyprinid fishes (e.g., *R. daniconius*) feed less efficiently on zooplankton than species from marine origin, e.g. *H. limbatus* and the clupeids *C. aesarnensis*, *E. fluviatilis* and *S. tawilis*. This is based on the notion that at sea, microcrustacean zooplankton is common, but in rivers they are extremely scarce. As a result riverine fish in rivers and streams feed mainly on benthic food organisms and on insects, which are falling out of the trees. Therefore, fish from marine origin should be better adapted to feeding on zooplankton than riverine fish species, but riverine fish should be better adapted to feeding on adult insects. In the Sri Lankan reservoir, Parakrama Samudra, the clupeid *E. fluviatilis* was able to build up a sustainable population with a mean biomass of 60 kg fresh wt ha⁻¹ yr⁻¹ by consuming exclusively on small rotifers (average size 0.05 mm) (Duncan 1999).

Small pelagic species seem to be adapted to some degree to the available size distribution of food organisms. If very large food items were available, even at relatively low densities, the fish develop a strong positive selection for these food items. However, not all fish species were equally efficient. The clupeid, *C. aesarnensis*, was the most effective particulate feeder; they were very efficient in feeding on larger food items such as adult midges and even small fish (Table 4). The other clupeid, *S. tawilis*, was very efficient on large calanoid

copepods. This contrasts with *H. limbatus* and *R. daniconius*. Catching calanoid copepods is not an easy task because they are fast swimmers that can swim against water currents. Cyclopod copepods are slower swimmers than calanoids but faster than cladocerans. The fish catch prey by sucking them in one by one and therefore calanoid copepods, followed by cyclopod copepods have the best chances and cladocerans the poorest chances to escape fish predation (Drenner and McComas 1984). This shows that *S. tawilis* is a very efficient zooplankton feeder. In contrast, *H. limbatus* from coastal marine origin and the indigenous riverine *R.*

daniconius, were mainly selecting slow or immobile prey. The medium and larger-sized cladocerans, which are slow swimmers, and the large adult insects which were floating on the surface are largely immobilized. Thus the fish species of riverine origin was indeed less efficient in feeding on fast moving zooplankton, but not all fish species of marine origin were efficient feeders on fast moving preys. Apparently only the clupeids are very efficient, both on relative large and on relative small preys and on fast moving large calanoid copepods (Table 4).

Table 4 Maximum prey size in the diets of zooplanktivorous fish observed in waterbodies in Philippines (PH), Sri Lanka (SL) and Thailand (TH) according A= Duncan (1999) and B= Ariyaratne et al. (2008). Prey types are indicated: ZOO= microcrustacean zooplankton, RO= rotifers, MA= macrofauna, FISH= fish.

Species	Maximum Prey Length (mm)	Prey type	Waterbody, Country	Authority
<i>Ambassis urotaenia</i>	1.2	ZOO	L. Taal, PH	B
<i>Hyporhamphus limbatus</i>	1.0	ZOO	3 SL res.	B
	6.5	MA	3 SL res.	B
	1.0	ZOO	3 SL res	B
<i>Rasbora daniconius</i>	6.0	MA	3 SL res	B
	7.5	MA	3 SL res	B
	1.2	ZOO	L. Taal, PH	B
<i>Sardinella tawilis</i>	1.2	ZOO	L. Taal, PH	B
<i>Clupeichthys aesarnensis</i>	1.3	ZOO	Ubolratana res., TH	B
	7.8	MA	Ubolratana res., TH	B
	10.0	FISH	Ubolratana res., TH	B
<i>Ehirava fluviatilis</i>	0.12	RO	Parakrama Samudra res. SL	A

Fish – zooplankton interactions in Sri Lankan reservoirs

R. daniconius and *H. limbatus* generally selected the larger cladoceran species (e.g. *Diaphanosoma* spp., *Daphnia lumholzi*) and the, a medium-sized *Moina micrura*, whereas small cladoceran species (e.g. *Bosminopsis dietersi*, *Ceriodaphnia cornuta*) and copepods were negatively selected or avoided (Ariyaratne et al. 2008). On a numerical basis, *R. daniconius* and *H. limbatus* are mainly zooplanktivorous, feeding on large proportions of cladocerans. But, if we compare the diet composition on the basis of biomass, than *R. daniconius* mainly feeds on adult flying insects, whereas *H. limbatus* also consumed a fair proportion of adult insects. The adult insects were probably eaten when floating at the water surface or in the upper water layers. On the basis of biomass, the contribution of insects in the total diet was high for

R. daniconius (ca. 65 %) and for *H. limbatus* (ca. 40%).

In Parakrama Samudra reservoir the clupeid *E. fluviatilis* was feeding on small rotifers whereas in Bolgoda Lake in the Panadura estuary this species was feeding mainly on larger copepods (range: 0.6-1.3 mm). This apparently resulted in a much better body condition of the species in the estuary as compared with the reservoir (Newrkla and Duncan 1984; Amarasinghe and Sriya 2002).

Success of small pelagic freshwater clupeids

The small freshwater clupeid species are flexible and opportunistic feeders, which feed very efficiently on a whole range of food organisms from very small (ca. 0.05 mm) up to relatively large (up to 10 mm) ones and range from slow moving species to fast moving species (Duncan 1999; Ariyaratne et al. 2008). It is therefore expected that clupeids

would be always more successful in terms of abundance than fish species from riverine origin. However, this is not always the case.

Clupeids are not successful in Sri Lankan reservoirs. The facultative freshwater clupeid, *E. fluviatilis*, mainly inhabits coastal marine habitats and estuaries (Pethiyagoda 1991) and is found only in two Sri Lankan reservoirs, both well connected by a river to the sea, Parakrama Samudra and Rajanganaya reservoirs (Newrkla and Duncan, 1984; Amarasinghe and Sriya 2002). *E. fluviatilis* is however, able to build up a stable and abundant locally reproducing population in Parakrama Samudra (Newrkla and Duncan 1984; Ariyaratne et al. 2008), which is a pure freshwater reservoir. Hence, after colonising a particular reservoir they may be quite successful. However, in comparison with an estuarine population mainly feeding on large copepods, the individuals belonging to the enclosed freshwater population mature at a smaller size and have a poorer body condition (Amarasinghe and Sriya 2002). This suggests that food conditions are comparatively poor in the freshwater reservoir. Apparently, small food items such as rotifers are not so profitable as larger microcrustacean zooplankton items such as copepods (Duncan 1983, 1999; Amarasinghe and Sriya 2002).

In Thailand, commercial fish catches show that in only three of the twelve reservoirs the freshwater clupeid *C. aesarnensis* yields are substantially contributing to the total fish catch, i.e. Sirindhorn (65%), Sirikit (30%), Ubolratana (15% of total catch) (EGAT 1991). However, *C. aesarnensis*, although from marine origin has adapted itself to riverine conditions and is generally present in all major river systems in Thailand. Since local markets are often not available for *C. aesarnensis*, this species is not exploited in most reservoirs. This is probably the reason why this fish species was only reported from a few reservoirs. This clupeid species has most likely a more general distribution than what appears from the published records.

In Lake Taal, there was until recent times a very successful fishery on *S. tawilis* (annual catch 440 kg ha⁻¹ yr⁻¹, relative yield 79%) (Baluyut 1999). This species is certainly successful in Lake Taal, but is absent in other Philippine waterbodies.

In conclusion, freshwater clupeids are not successful in the Philippines (one lake only), and neither in Sri Lanka (only 2 reservoirs), but they are successful in Thailand where they inhabit all major

river systems and probably most reservoirs linked to the river systems.

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