Response of Zooplankton Population to Contrasting Environmental Conditions in a Shallow Mesotrophic Reservoir

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ABSTRACT

Changes in the zooplankton population in shallow, mesotrophic Ubolratana Reservoir were monitored during 2019-2022, years with contrasting environmental conditions of severe drought and flood events. In the six sampling occasions, water storage volume (WSV) was 13 %, 19 %, 58 %, 36 %, 110 %, and 56 % of capacity. Correlations between hydrological and water quality factors and zooplankton densities were analyzed for a better understanding of the drivers of zooplankton production and to enable further development of management approaches. In this study, comparatively low densities of zooplankton were observed during severe drought. The density increased with gradual increases of inflow (INF) and WSV. During mid-rainy season of 2021, the densities of copepods, cladocerans, rotifers and protozoans increased to high levels, with maximums of 13,179 ind·L^{-1}, 2,883 ind·L^{-1}, 3,940 ind·L^{-1} and 7,401 ind·L^{-1}, respectively. In contrast, the levels were decreased during high flood conditions (110 % of capacity). In addition, zooplankton density had a highly significant positive relationship ($p<0.01$) with INF and significant positive relationships ($p<0.05$) with WSV and density of small-sized protozoans. Copepod and rotifer densities in the lacustrine zone also had significant positive relationships ($p<0.05$) with total suspended solids (TSS), while they had significant negative relationships ($p<0.05$) with retention time (RT). Accordingly, it is possible that increases in zooplankton abundance can occur with conditions of comparatively high INF, WSV, and small-size protozoan density. In contrast, habitats with high RT during flood were not as suitable for zooplankton. Overall, the results implied the need to control INF, WSV, and RT for preventing deterioration in the abundance of zooplankton during environmental changes. These findings can be further applied for developing suitable management strategies for conservation of fishery-related resources of the mesotrophic reservoir ecosystem.

Keywords: Drought, Flood, Inflow, Reservoir ecosystem, Water quality, Zooplankton

INTRODUCTION

Zooplankton are a crucial food source for various aquatic animals. Their abundance and growth rate have been revealed to play a vital role in determining of the survival and growth of juvenile and zooplanktivorous fishes (Li and Chen, 2020). Most of the zooplankton feed upon suspended organic material, either phytoplankton or detritus. Thus, the zooplankton are involved in both the grazing and detrital chains, particularly since some may consume bacteria (Payne, 1986). In general, increases in temperature (Wolfinbarger, 1999), nutrients (Feuchtmayr *et al*., 2010), and phytoplankton (Striebel *et al*., 2012) enhance zooplankton abundance through a bottom-up mechanism. Zooplankton abundance and composition in many reservoir ecosystems are impacted by chemical parameters (Vincent *et al*., 2012). In the lacustrine system of Lake Okeechobee, Florida, historically low water

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Received 22 September 2022 / Accepted 19 November 2022

levels were associated with dramatic changes in zooplankton (Havens *et al*., 2007). Chaparro *et al*. (2011) reported that year-long zooplankton abundance was higher during a drought-caused low water period in a South American floodplain lake.

In the coming century, climate change may continue to increase the variability, frequency, and severity of impacts from both drought and flood phenomena (Naz *et al*., 2018). Climate change can alter hydrological and ecological regimes (Arora and Boer, 2001; Johnson *et al*., 2009) and thus may influence bottom-up processes that regulate zooplankton. Such environmental changes in habitat structure can impact seasonal dynamics of calanoid copepod populations (Winder *et al*., 2009) and induce remarkable cascading effects in pelagic food web systems (Jeppesen *et al*., 2010; Nickus *et al*., 2010). Depending on the future eco-hydrological regime, zooplankton can, thus, considerably decrease or increase in aquatic systems. Understanding the mechanisms and key factors driving spatial and temporal variability will be essential to managing aquatic ecosystems in a period of climate variation (Williamson *et al*., 2021).

Reservoirs are important for fishery production and provide a wide array of benefits to surrounding communities (Dodds and Whiles, 2010; Asawamanasak and Meksumpun, 2022). Nevertheless, during the hydrological variation induced by climate change, successional events are not consistent from year to year. Temporal variation in availability and abundance of food resources in reservoir ecosystems is, thus, important (Gliwicz and Pijanowska, 1989). Ubolratana Reservoir is the most productive reservoir in the northeastern region of Thailand (Thanasomwang, 2013; Muangsringam *et al*., 2021). The reservoir oscillates between drought and flood conditions depending on inflow quantity (Asawamanasak and Meksumpun, 2022; EGAT, 2022; Mengchouy and Meksumpun, 2022). In this study, we hypothesized that functions of hydrological factors, water quality, and related food resources in the reservoir during changing conditions would follow bottom-up processes and translate into higher zooplankton abundance compared to drought conditions. Understanding zooplankton response and drivers from this study will be useful for evaluating the zooplankton population changes, and in turn, for the development of conservation management of fishery-related resources of mesotrophic reservoir ecosystems.

MATERIALS AND METHODS

Study area

The Ubolratana Reservoir is located in the northeastern part of Thailand (Figure 1). It has surface area of 410 km^2 and maximum water storage volume of 2,431 million m^3 (EGAT, 2022). The reservoir has average mean depth of 5.5 m and receives water from the Phong and Phaniang rivers in the northern region, and from the Choen River in the southern region. A previous study by Mengchouy and Meksumpun (2022) reported that an area in the center of the reservoir (along the Phong River channel) was in mesotrophic condition, with moderate nutrient levels of 1.69-15.87 µM dissolved inorganic nitrogen and 0.02-0.82 µM orthophosphate phosphorus. The climate of the whole area is influenced by two tropical monsoons: the southwest monsoon from May to October (rainy season), and the northeast monsoon from November to April (dry season) (Ingthamjitr *et al*., 2009).

In this study, hydrological data (water storage volume and inflow) were obtained from the Electricity Generating Authority of Thailand (EGAT, 2022). Water storage volume of the reservoir during 2018-2022 fluctuated noticeably. During 2018-2020, the water storage volume was lower than the prescribed “minimum storage volume” (580 million m^3) of the reservoir. Contrastingly, during 2021, the water storage volume remarkably increased to 110 % of reservoir capacity (Figure 2).

Study of zooplankton

Sampling of zooplankton was carried out six times during 2020-2022: June 2020 (early rainy season), September 2020 (mid-rainy season), January 2021 (dry season), September 2021 (mid-rainy season), November 2021 (dry season), and March 2022 (dry season). During these months, the water storage volume of the reservoir was 13 %, 19 %, 58 %, 36 %, 110 %, and 56 % of capacity, respectively. The previous study by Mengchouy and Meksumpun (2022) indicated that the reservoir can be separated into three eco-hydrological zones. Accordingly, one surveyed site (UB1) was set up in the riverine zone, two surveyed sites (UB2 and UB3) were set up in the transition zone, and four surveyed sites (UB4, UB5, UB6 and UB7) were set up in the lacustrine zone of the reservoir (Figure 1).

On each sampling occasion, three shallow habitats (70 cm water depth) separated by a 20-m interval were investigated within each site. Samples of zooplankton were collected from surface water (0-30 cm water depth), whereby one hundred liters of water were filtered through 22-µm mesh of a plankton net and preserved with 4% formaldehyde solution. Zooplankton identification was conducted under light microscope (Model CHK/SA0333, Olympus) according to Sanoamuang (1998), Wongrat (2000), Sanoamuang and Savatenalinton (2001) and Dang *et al*. (2015).

In addition, three sizes of zooplankton were separated under light microscope (small size; <250 µm, medium size; 250-500 µm, and large size; >500 µm) by using a micrometer. Abundance of zooplankton was reported in the units of ind·L^{-1}.

Study of water quality and collection of hydrological parameters

At each sampling site, water temperature and dissolved oxygen were measured at 15 cm below the surface water using a multi-parameter YSI probe (Model 600QS). Total suspended solid (TSS) and chlorophyll *a* (Chl-*a*) of the water column were also analyzed. Water samples for TSS were passed through GF/C glass-fiber filter, and freeze-dried for the measurement of dry weight per volume of filtered water. The chlorophyll *a* was analyzed by spectrophotometric method (Parsons *et al*., 1984).

In addition, total storage volume and inflow of the riverine zone were from Electricity Generating Authority of Thailand (EGAT, 2022). Storage volumes of sampling sites in each sampling time were determined from water depth and related topographical information, using Surfer Version 13 according to Mengchouy (2020). On each sampling

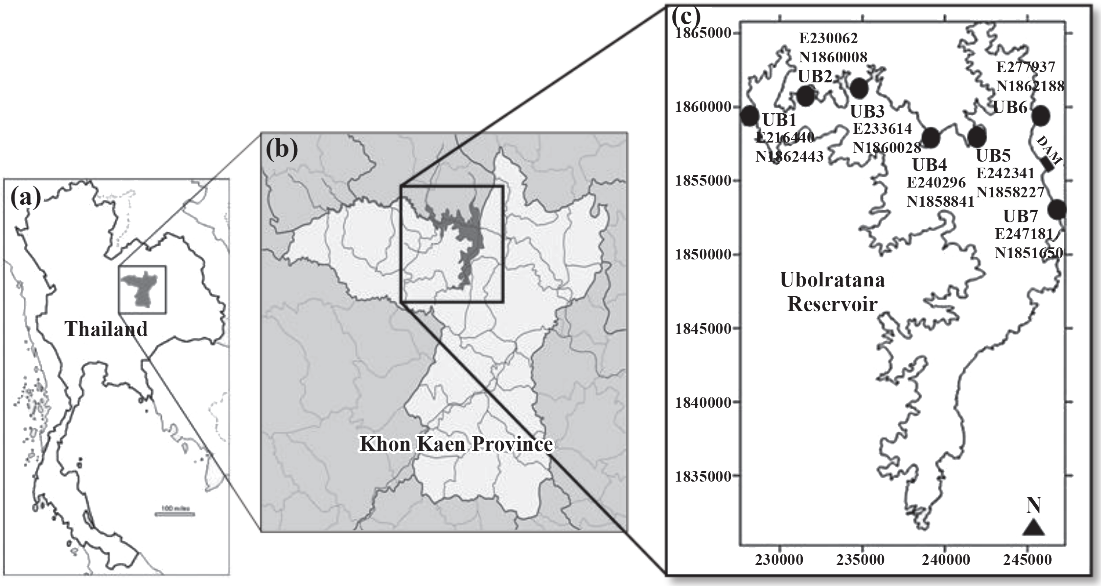

Figure 1. Surveyed sites along shoreline areas of Ubolratana Reservoir: riverine zone (UB1), transition zone (UB2, UB3), and lacustrine zone (UB4, UB5, UB6 and UB7); (a) map of Thailand; (b) map of Khon Kaen Province; (c) boundary of Ubolratana Reservoir.

occasion, inflow of the riverine surveyed site (UB1) was calculated from measurements from the prior six days. Based on the reservoir topography and the longitudinal distance from UB1, inflows of the transition (UB2 and UB3) and lacustrine (UB4, UB5, UB6, and UB7) survey sites were then evaluated to be about 70 %, 60 %, 20 %, 10 %, 2.5 %, and 1 % of UB1, respectively.

Data analysis

Descriptive statistics (means and standard deviations) were calculated to depict changes over sampling periods. Differences in parameters among sampling periods and locations were evaluated by paired sample T-test ($p<0.05$). Correlations between densities of zooplankton and various water parameters were analyzed using Spearman's rank correlation coefficient ($p<0.05$) using statistical software (SPSS 27, Windows evaluation version).

RESULTS

Changes in hydrological and water quality parameters

The water storage volume of the Ubolratana Reservoir during 2018-2022 is depicted in Figure 2. From 2018 to August 2020, monthly water storage volume gradually decreased to levels lower than the prescribed "minimum storage volume" of the reservoir (EGAT, 2022). Very low precipitation and inflows apparently caused this decrease in water storage volume (TMD, 2022).

Increases of inflow occurred during the mid-rainy season of 2020 and 2021. Accordingly, the water storage volume dramatically increased and fluctuated (Figure 2). High peaks of water storage were found during November 2020 and 2021 (1,589 million m^3 and 2,678 million m^3, respectively). In November 2021, the volume became higher than the prescribed "maximum storage volume" (2,431 million m^3) of the reservoir (EGAT, 2022).

During 2018-2022, climate impacts creating both drought and flood events were shown to alter reservoir hydrological regimes. The hydrological factors and water quality parameters of the seven surveyed sites are depicted in Table 1. The results indicated high variation of all parameters. The riverine and transition zones showed comparatively higher inflow (INF) and total suspended solids (TSS). The highest TSS (1,783 $mg \cdot L^{-1}$) and INF (24.1 million $m^3 \cdot day^{-1}$) were noted in sites UB1 and UB2, respectively. In contrast, the lacustrine sites reflected comparatively lower INF and TSS, but comparatively higher water storage volume (WSV), retention time (RT), and chlorophyll *a* (Chl-*a*).

Among the three zones, only WSV was significantly different ($p<0.05$, df = 5), while INF, TSS, RT, and Chl-a were not significantly different ($p>0.05$). In addition, when considering changes

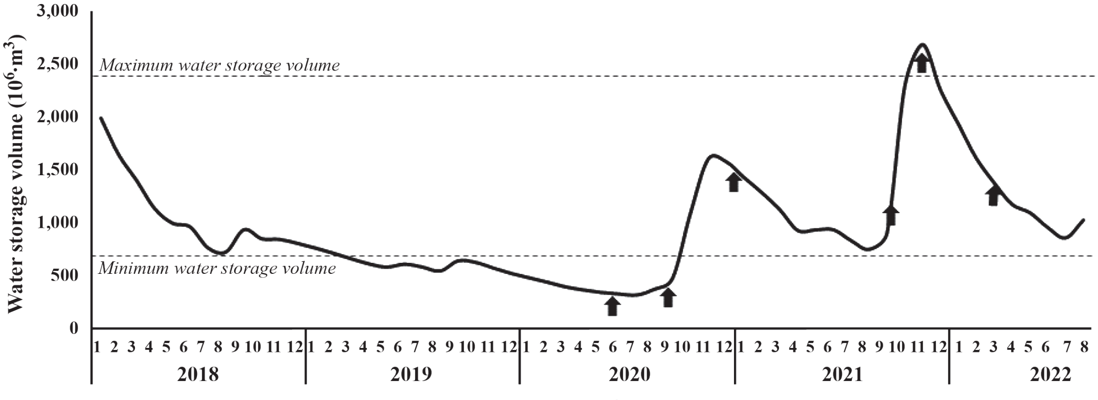

Figure 2. Water storage volume of the Ubolratana Reservoir during 2018-2022 (source: EGAT, 2022) (Arrows = sampling events).

Table 1. Hydrological factors and water quality parameters (INF = inflow, million m^3·day^{-1}; WSV = water storage volume, million m^3; RT = retention time, day; TEM = water temperature, °C; DO = dissolved oxygen, mg·L^{-1}; TSS = total suspended solids, mg·L^{-1}; Org-TSS = organic TSS, mg·L^{-1} and Chl-*a* = chlorophyll *a*, µg·L^{-1}) in the riverine zone (UB1), transition (UB2, UB3) and lacustrine (UB4, UB5, UB6 and UB7) zones of Ubolratana Reservoir during 2020-2022.

Hydrological and water quality parameters	**Sampling sites**						
	Riverine	**Transition**		**Lacustrine**			
	UB1	**UB2**	**UB3**	**UB4**	**UB5**	**UB6**	**UB7**
INF	0.1-18.5	1.7-24.1	0.1-13.8	0 .5-6.9	0.3-3.4	0.1-0.9	0.0-0.3
(million m^3·day^{-1})	(7.0±8.6)	(12.06±10.1)	(6.9±5.8)	(4.01±3.24)	(1.7±1.4)	(0.4±0.4)	(0.2±0.1)
WSV	0.1-0.6	9.2-81.4	9.2-81.4	11.0-96.6	6.8-60.3	2.7-24.1	0.8-7.2
(million m^3)	(0.3±0.2)	(34.0±26.7)	(34.0±26.7)	(45.2±32.7)	(25.2±19.8)	(10.1±7.9)	(3.0±2.4)
RT	0.01-6.08	1.22-22.65	2.14-39.63	5.08-94.02	6.35-117.53	10.16-188.06	7.62-141.04
(Day)	(1.57±3.00)	(7.36±10.23)	(12.88±17.90)	(37.71±48.97)	(38.20±53.09)	(61.13±84.94)	(45.85±63.70)
TEM	25.5-31.8	26.4-36.4	25.6-38.7	23.5-33.7	24.4-34.2	21.2-33.0	23.7-32.1
(°C)	(28.3±2.4)	(30.9±3.6)	(31.9±4.7)	(28.4±3.7)	(29.3±3.5)	(28.1±4.0)	(27.4±3.3)
DO	1.5-7.6	4.7-7.3	5.1-10.7	0.9-5.4	4.9-8.6	1.9-7.7	1.6-7.7
(mg·L^{-1})	(5.8±2.2)	(6.1±1.0)	(6.8±2.1)	(4.3±1.9)	(7.2±1.4)	(5.9±2.1)	(4.5±2.3)
TSS	8.8-1,783.0	5.1-280.4	7.3-162.3	13.1-52.9	6.8-49.2	8.2-59.6	3.6-31.9
(mg·L^{-1})	(457.6±689.0)	(86.1±109.4)	(54.2±62.5)	(31.3±16.5)	(20.9±15.9)	(23.5±19.2)	(16.3±10.8)
Org-TSS	1.6-230.2	3.5-45.0	3.1-48.6	5.1-44.5	4.6-40.7	4.8-34.6	2.1-25.1
(mg·L^{-1})	(61.1±87.7)	(16.8±16.7)	(18.3±19.1)	(21.3±16.2)	(16.1±14.1)	(14.7±11.9)	(11.7±9.0)
Chl-*a*	1.3-15.4	1.1-17.3	3.4-50.5	5.7-25.6	9.4-77.9	11.1-85.7	2.0-72.5
(µg·L^{-1})	(6.3±5.2)	(10.7±6.5)	(18.3±17.5)	(16.8±9.7)	(36.6±27.4)	(32.4±26.9)	(25.3±25.7)

between rainy and dry seasons, a significant difference ($p<0.05$, df = 2) of TSS was found for the transition zone sites. During the dry season, significant differences ($p<0.05$, df = 2) in WSV between the riverine and transition zone, and between the transition and lacustrine zones were also found.

In this study, average water temperatures of each station ranged between 27.4 and 31.9 °C (Table 1). Such ambient levels are suitable for the growth of zooplankton (Dodds and Whiles, 2010; Olds *et al*., 2014). Average dissolved oxygen concentrations (DO; 4.3-7.2 mg·L^{-1}) were also normal for mesotrophic reservoirs (García *et al*., 2002). The DO occasionally decreased to low levels in some lacustrine sites (i.e., UB4, UB7) during the high flood period in November 2021. In addition, during the entire study period, Chl-*a* of the sites in the lacustrine zone frequently increased to levels >25 µg·L^{-1}. The highest peak of Chl-*a* found in the lacustrine zone was remarkably high (about 90 µg·L^{-1}). Related bottom-up processes (Striebel *et al*., 2012) should enhance nutrient regeneration and phytoplankton growth in particular zones of the reservoir ecosystem. Such phenomena may imply spatial variation among the surveyed sites.

In the lacustrine zone of the reservoir, INF had a highly significant positive relationship ($p<0.01$) with WSV, a significant positive relationship ($p<0.05$) with TSS, and a significant negative relationship ($p<0.05$) with RT. The WSV was determined to have a significant negative relationship ($p<0.05$) with Chl-*a*, while the factor of TEM had a highly significant positive relationship ($p<0.01$) with Chl-*a*. Such relationships may imply that phytoplankton in the lacustrine ecosystem can be stimulated during comparatively lower WSV and higher TEM conditions of the reservoir.

Changes in composition and density of zooplankton

In this study, zooplankton in the Phyla Arthropoda, Rotifera, and Protozoa were examined from the Ubolratana Reservoir (Table 2). The copepods and nauplius copepods (Class Maxillopoda) were the dominant zooplankton that could be found in every zone of the reservoir ecosystem. The copepod densities of the riverine, transition, and lacustrine zones were in the ranges of 20-7,216 ind·L^{-1}, 124-7,109 ind·L^{-1}, and 222-7,806 ind·L^{-1}, respectively. Comparatively low density in the riverine zone (20 ind·L^{-1}) was observed only during a high inflow period (mid-rainy season; September 2021).

In this study, the densities of cladocerans, rotifers and protozoan were lower than those of copepods (Table 2). The cladoceran genera *Daphnia* and *Diaphanosoma* were recorded in all zones and had higher densities than other cladoceran genera. Their densities were highest (2,402 and 2,883 ind·L^{-1}, respectively) in the lacustrine zone, during mid-rainy season (September 2021) when WSV was comparatively low (Figure 2). In addition, cladoceran genus *Bosminopsis* was frequently encountered in the riverine zone of the reservoir, while the cladoceran genus *Daphnia* and rotifer genus *Brachionus* were common in all zones. The highest density (3,940 ind·L^{-1}) of *Brachionus* was documented in the lacustrine zone during mid-rainy season of 2019.

The densities of rotifer genera *Polyarthra*, *Lecane* and *Filinia* were comparatively lower than those of *Brachionus*. In addition, the protozoans were present in all zones. Nevertheless, comparatively higher protozoan densities were recorded in the lacustrine zone of the reservoir. In the lacustrine zone during September 2021, the density of *Difflugia*, a dominant large-sized protozoan, was highest (7,401 ind·L^{-1}).

Densities of zooplankton categorized by size as S (<250 µm), M (250-500 µm), and L (>500 µm) are depicted in Table 3. In this study, the size of copepods ranged from S to L because of contribution from the nauplii copepods, which were <250 µm. The most common sizes of cladocerans were M and L, while those of rotifers were S and M. The protozoans were generally the smallest, with most individuals <250 µm. The results indicated that among sites, the sizes of zooplankton were not significantly different ($p>0.05$). Nevertheless, small-size cladoceran genera, including the genus *Macrothrix* (Family Macrothricidae) (Table 2), was found in the riverine and lacustrine sites of the reservoir, where the levels of Chl-*a* were comparatively low (Table 1). Such an occurrence can imply good-quality habitats during some of the survey events (Loughheed and Chow-Fraser, 2002).

Considering the contribution of zooplankton biomass in a reservoir food chain, the copepod and cladoceran populations were of interest because they have been revealed to contribute substantially to secondary production (Table 3). Accordingly, temporal changes of total copepods and total cladocerans that occurred with the fluctuating environmental conditions during 2020-2022 were monitored and analyzed (Figure 3).

When compared to the fluctuations of the hydrological regime due to the drought of 2019-2020 to the flood event during 2021-2022 (Figure 2), the copepod (Figure 3a) and cladoceran (Figure 3b) populations displayed comparatively low and stable densities during the drought period (the 1st and 2nd sampling occasions). Increases of cladoceran densities were noted during the 3rd sampling occasion (Figure 3b), when the WSV was higher (Figure 2). In contrast, total copepod densities in almost study sites remained relatively unchanged, except for the riverine site (UB1), where the density increased.

During the mid-rainy season of 2021, apparent increases of INF were observed although WSV was still low (Figure 2). Both total copepod and cladoceran densities increased sharply by about 10-100 times, and their densities were highest (17,247 and 2,277 ind·L^{-1}, respectively) during the 4th sampling occasion (Figure 3a and 3b, respectively). The environmental conditions during that period appeared most suitable for copepod and cladoceran growth. Unfortunately, high flooding occurred during October 2021 to January 2022 and caused negative impacts to the zooplankton populations.

Table 2. Zooplankton taxa found in the riverine, transition and lacustrine zones in Ubolratana Reservoir during 2020-2022.

Taxa		Group/Genus	Density (ind·L^{-1})		
			Riverine	Transition	Lacustrine
Phylum Arthopoda					
Copepod	Class Maxillopoda	Copepod	20-7,216	124-7,109	222-7,806
		Nauplii copepod	15-5,110	1,364-4,009	81-13,179
Cladocerans	Class Branchiopoda				
	Family Bosminidae	*Bosminopsis*	0-280	0-31	0-13
	Family Chydoridae	*Camptocercus*	0-1	-	-
		Leberis	0-1	0-28	-
	Family Daphniidae	*Daphnia*	11-623	35-834	99-2,402
		Ceriodaphnia	0-10	0-5	-
	Family Macrothricidae	*Macrothrix*	3-60	-	0-64
	Family Moinidae	*Moina*	0-81	0-34	0-43
	Family Sididae	*Diaphanosoma*	0-489	0-287	0-2,883
Phylum Rotifera	Class Monogononta				
	Family Brachionidae	*Brachionus*	23-957	52-1,162	138-3,940
		Keratella	0-74	0-70	0-198
		Anuraeopsis	0-52	0-81	0-20
	Family Trichotriidae	*Macrochaetus.*	-	0-47	-
	Family Lecanidae	*Lecane*	7-211	0-282	13-395
	Family Notommatidae	*Monommata*	0-28	0-14	0-30
		Cephalodella	-	-	0-5
	Family Trichocercidae	*Trichocerca*	0-12	-	-
	Family Gastropodidae	*Ascomorpha*	0-29	0-50	0-3
	Family Asplanchnidae	*Asplanchna*	0-94	0-33	0-82
	Family Synchaetidae	*Polyarthra*	0-328	0-381	0-495
	Family Testudinellidae	*Testudinella*	0-92	0-21	0-74
		Filinia	0-165	0-237	2-425
	Family Trochosphaeridae	*Trochosphaera*	0-95	-	0-22
Phylum Protozoa	Class Sarcodina				
	Family Amoebidae	*Amoeba*	0-63	0-23	0-52
	Class Lobosa				
	Family Arcellidae	*Arcella*	6-322	0-639	54-406
	Family Difflugiidae	*Difflugia*	12-2,581	22-3,551	315-7,401
	Family Centropyxidae	*Centropyxis*	10-290	2-543	68-1,031
	Class Filosia				
	Family Euglyphidae	*Euglypha*	4-175	1-15	5-162
	Class Ciliatea				
	Family Holophryidae	*Holophyra*	0-46	0-54	0-17
	Family Prorodontidae	*Prorodon*	-	0-3	-
		Prorodonteres	-	0-1	-
		Coleps	0-3	0-8	0-540
	Family Spathidiidae	*Spatidium*	0-2	0-8	0-7
		Amphileptus	-	0-105	-
	Family Parameciidae	*Paramicium*	0-49	0-66	0-91
	Family Tintinnididae	*Tintinnopsis*	3-228	0-229	1-225
	Family Tracheliida	*Paradileptus*	0-16	0-1	-

Table 3. Abundance of each size class of copepods, cladocerans, rotifers, and protozoans (S: small size; M: medium size; L: large size) in the riverine (UB1), transition (UB2, UB3) and lacustrine (UB4, UB5, UB6 and UB7) zones of Ubolratana Reservoir during 2020-2022.

Density (ind·L^{-1})		**Sampling sites**						
		Riverine	**Transition**		**Lacustrine**			
		UB1	**UB2**	**UB3**	**UB4**	**UB5**	**UB6**	**UB7**
Total copepods	S	0-4,193	49-2,291	66-4,858	28-9,372	6-4,615	94-5,333	71-4,336
	M	1-1,475	26-650	28-1,945	51-4,943	4-1,585	46-2,539	21-1,580
	L	0-788	4-516	0-1,361	0-2,932	0-2,140	11-2,542	30-955
Cladocerans	S	0-238	0	0-53	0	0-23	0	0-10
	M	1-369	0-572	0-397	51-640	3-328	10-1,229	0-270
	L	0-218	0-137	0-181	9-874	0-691	0-1,048	0-269
Rotifers	S	0-317	0-504	0-143	0-723	0-1,517	0-511	0-172
	M	0-369	31-775	15-675	78-637	6-451	0-1,705	0-462
	L	0	0	0-30	0	0	0	0
Protozoans	S	16-1,063	36-4,033	43-2,785	402-3,689	32-1,487	57-3,232	262-1,003
	M	0-6	0-106	0-34	0-35	0-454	0-33	0-39
	L	0	0	0	0	0	0	0

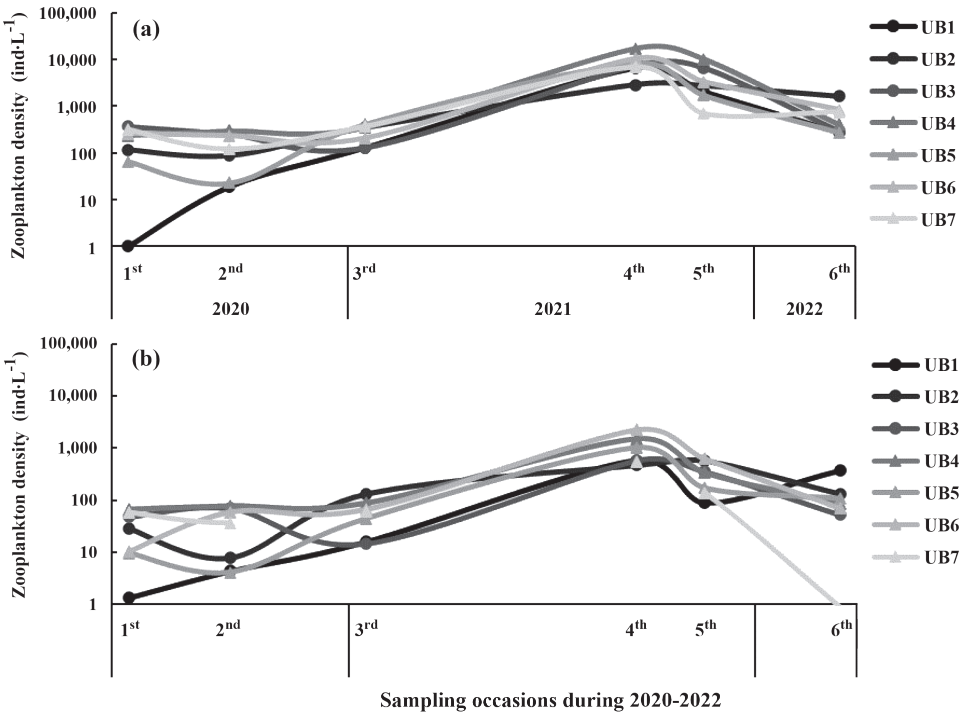

Figure 3. Density of zooplankton as (a) total copepods and (b) cladocerans of the studied sites (UB1-UB7) in Ubolratana Reservoir during 2020-2022 (1st = June 2020; 2nd = September 2020; 3rd = January 2021; 4th = September 2021; 5th = November 2021; 6th = March 2022).

During the highest peak of WSV in the flood event (November 2021; the 5th sampling occasion), the densities of total copepods and cladocerans in most sites were reduced to about 10 % of previous levels. Such deterioration of zooplankton abundance during the high flood event was likely due to the remarkable decrease of DO levels (Table 1) in the lacustrine sites.

Zooplankton and related environmental factors

Correlations between environmental factors and density of each size class of copepods, cladocerans, rotifers, and protozoans of the riverine and transition zones are shown in Table 4. In the riverine and transition zones, the density of all sizes

Table 4. Correlation coefficients between abundance of zooplankton and environmental factors of the riverine and transition zones and the lacustrine zone of Ubolratana Reservoir during 2020-2022 (PRO$_S$: small-size protozoans; other abbreviations are explained in Table 1).

Zooplankton density		**Environmental Factors**								
		INF	**WSV**	**RT**	**TEM**	**DO**	**TSS**	**Org-TSS**	**Chl-*a***	**PRO$_S$**
		Riverine and transition zones								
Copepods (ind•L^{-1})	S	**0.804****	**0.518***	-0.224 ^{ns}	-0.002 ^{ns}	0.010 ^{ns}	-0.283 ^{ns}	-0.212 ^{ns}	0.251 ^{ns}	**0.853****
	M	**0.811****	0.434 ^{ns}	-0.287 ^{ns}	0.227 ^{ns}	0.107 ^{ns}	-0.118 ^{ns}	-0.020 ^{ns}	0.453 ^{ns}	**0.746****
	L	**0.748****	0.405 ^{ns}	-0.245 ^{ns}	-0.040 ^{ns}	0.028 ^{ns}	-0.146 ^{ns}	0.079 ^{ns}	0.130 ^{ns}	**0.668****
	Total	**0.776****	**0.492***	-0.231 ^{ns}	0.151 ^{ns}	0.081 ^{ns}	-0.200 ^{ns}	-0.098 ^{ns}	0.418 ^{ns}	**0.806****
Cladocerans (ind•L^{-1})	S	-	-0.022 ^{ns}	-	0.149 ^{ns}	0.149 ^{ns}	-0.138 ^{ns}	-0.433 ^{ns}	0.278 ^{ns}	-0.065 ^{ns}
	M	**0.818****	0.193 ^{ns}	-0.168 ^{ns}	0.260 ^{ns}	0.138 ^{ns}	-0.119 ^{ns}	0.039 ^{ns}	0.255 ^{ns}	0.468 ^{ns}
	L	0.437 ^{ns}	0.048 ^{ns}	-0.275 ^{ns}	0.146 ^{ns}	-0.013 ^{ns}	0.078 ^{ns}	-0.004 ^{ns}	0.290 ^{ns}	**0.567***
	Total	**0.818****	0.381 ^{ns}	-0.294 ^{ns}	0.166 ^{ns}	0.141 ^{ns}	-0.214 ^{ns}	-0.210 ^{ns}	0.401 ^{ns}	**0.812****
Rotifers (ind•L^{-1})	S	-0.148 ^{ns}	0.198 ^{ns}	0.281 ^{ns}	-0.266 ^{ns}	0.215 ^{ns}	-0.329 ^{ns}	**-0.536***	-0.098 ^{ns}	0.142 ^{ns}
	M	**0.811****	**0.564***	-0.175 ^{ns}	0.208 ^{ns}	0.272 ^{ns}	-0.335 ^{ns}	-0.271 ^{ns}	**0.531***	**0.719****
	L	-	0.281 ^{ns}	-	-0.094 ^{ns}	0.000 ^{ns}	-0.211 ^{ns}	-0.328 ^{ns}	0.023 ^{ns}	0.023 ^{ns}
	Total	**0.818****	**0.532***	-0.112 ^{ns}	0.135 ^{ns}	0.321 ^{ns}	-0.411 ^{ns}	-0.458 ^{ns}	**0.554***	**0.746****
Protozoans (ind•L^{-1})	S	**0.818****	**0.596****	-0.252 ^{ns}	0.001 ^{ns}	-0.160 ^{ns}	-0.259 ^{ns}	-0.285 ^{ns}	0.304 ^{ns}	1.000 ^{ns}
	M	**-0.597***	-0.106 ^{ns}	0.560 ^{ns}	-0.159 ^{ns}	0.089 ^{ns}	-0.200 ^{ns}	-0.221 ^{ns}	-0.060 ^{ns}	-0.321 ^{ns}
	Total	0.441 ^{ns}	**0.475***	0.042 ^{ns}	-0.171 ^{ns}	0.039 ^{ns}	-0.400 ^{ns}	-0.449 ^{ns}	0.331 ^{ns}	**0.862****
		Lacustrine zone								
Copepods (ind•L^{-1})	S	**0.654****	0.410 ^{ns}	-0.500 ^{ns}	-0.228 ^{ns}	-0.270 ^{ns}	0.114 ^{ns}	-0.008 ^{ns}	-0.284 ^{ns}	**0.868****
	M	**0.611***	0.208 ^{ns}	-0.511 ^{ns}	0.212 ^{ns}	-0.254 ^{ns}	**0.489***	0.305 ^{ns}	0.020 ^{ns}	**0.826****
	L	0.511 ^{ns}	0.193 ^{ns}	**-0.521***	-0.101 ^{ns}	-0.212 ^{ns}	0.295 ^{ns}	0.190 ^{ns}	-0.024 ^{ns}	**0.684****
	Total	**0.607***	0.329 ^{ns}	**-0.521***	-0.113 ^{ns}	-0.251 ^{ns}	0.229 ^{ns}	0.054 ^{ns}	-0.195 ^{ns}	**0.880****
Cladocerans (ind•L^{-1})	S	-0.062 ^{ns}	-0.101 ^{ns}	0.124 ^{ns}	-0.057 ^{ns}	-0.015 ^{ns}	-0.260 ^{ns}	-0.229 ^{ns}	-0.105 ^{ns}	-0.120 ^{ns}
	M	0.511 ^{ns}	0.328 ^{ns}	-0.475 ^{ns}	-0.038 ^{ns}	-0.365 ^{ns}	0.353 ^{ns}	0.261 ^{ns}	-0.180 ^{ns}	**0.732****
	L	**0.554***	**0.489***	-0.507 ^{ns}	-0.057 ^{ns}	-0.166 ^{ns}	0.213 ^{ns}	0.099 ^{ns}	-0.227 ^{ns}	**0.761****
	Total	**0.532***	**0.446***	-0.489 ^{ns}	-0.043 ^{ns}	-0.258 ^{ns}	0.264 ^{ns}	0.148 ^{ns}	-0.231 ^{ns}	**0.780****
Rotifers (ind•L^{-1})	S	0.385 ^{ns}	0.141 ^{ns}	-0.490 ^{ns}	0.070 ^{ns}	0.017 ^{ns}	0.203 ^{ns}	0.039 ^{ns}	0.137 ^{ns}	0.335 ^{ns}
	M	0.493 ^{ns}	0.186 ^{ns}	**-0.557***	0.155 ^{ns}	-0.398 ^{ns}	**0.476***	0.339 ^{ns}	-0.103 ^{ns}	**0.651****
	Total	**0.546***	0.381 ^{ns}	**-0.575***	-0.074 ^{ns}	-0.340 ^{ns}	0.224 ^{ns}	-0.030 ^{ns}	-0.174 ^{ns}	**0.829****
Protozoans (ind•L^{-1})	S	**0.714****	**0.508***	-0.361 ^{ns}	-0.112 ^{ns}	-0.377 ^{ns}	0.259 ^{ns}	0.034 ^{ns}	-0.248 ^{ns}	1.000
	M	-0.364 ^{ns}	0.067 ^{ns}	0.489 ^{ns}	-0.145 ^{ns}	0.218 ^{ns}	-0.308 ^{ns}	-0.209 ^{ns}	-0.213 ^{ns}	-0.195 ^{ns}
	Total	**0.696****	**0.547****	-0.311 ^{ns}	-0.134 ^{ns}	-0.314 ^{ns}	0.232 ^{ns}	0.012 ^{ns}	-0.246 ^{ns}	**0.989****

Note: ** Correlation is significant at the 0.01 level (2-tailed); * Correlation is significant at the 0.05 level (2-tailed); ^{ns} Correlation is not significant ($p<0.05$).

of copepods, small-size cladocerans, total cladocerans, small-size rotifers and small-size protozoans had highly significant positive relationships ($p<0.01$) with INF.

The density of small-size copepods, total copepods, medium-size rotifers, total rotifers and total protozoans also had significant positive relationships ($p<0.05$) with WSV, while small-size protozoans had a highly significant positive relationship ($p<0.01$) with WSV. Moreover, the density of all sizes of copepods, total copepods, total cladocerans and rotifers had highly significant positive relationships ($p<0.01$) with small-size protozoans. In addition, the density of small-size rotifers and total rotifers had significant positive relationships ($p<0.05$) with Chl-*a*.

In the lacustrine zone (Table 4), besides the relationships with INF, WSV, and small-size protozoans, density of large-size copepods, total copepods, medium-size rotifers and total rotifers had significant negative relationships ($p<0.05$) with RT. The density of medium-size copepods and rotifers also had significant positive relationships ($p<0.05$) with TSS.

DISCUSSION

In this study, zooplankton abundance gradually increased (Figure 3) after the severe drought during 2018-2020 had passed (Figure 2). Nevertheless, there were other temporal changes in zooplankton abundance in the studied period. The highest abundance of zooplankton was found during the low-water period in mid-rainy season of 2021. Copepod abundance at Uboratana Reservoir (Figure 3a) is similar to that found in eutrophic habitats such as Valle de Bravo Reservoir (Mexico) and Lake George (Africa). The abundance is much higher than that found in the mesotrophic Lake Sybaya (South Africa). It is, however, lower than that of hypereutrophic habitats of Salto Grande Reservoir (SP, Brazil) (García *et al*., 2002; Santos-Wisniewski and Rocha, 2007; Olds *et al*., 2014). In addition, abundance of cyclopoid copepods was higher than that of calanoid copepods, in all seasons. Such a pattern is commonly observed for tropical reservoir ecosystems (Santos-Wisniewski and Rocha, 2007). Reproduction in copepods is usually sexual, with generation time of 20-30 days. The number of copepod generations per year can, thus, reach 15 generations in tropical hypertrophic lacustrine areas (Dodds and Whiles, 2010). The results of this study have revealed that the copepod population increased along with the increase of inflow and availability of small protozoa (Table 4). Such increases in abundance of copepods can be likely enhanced by a warmer growing period combined with fluctuations in food resource (i.e., protozoa) availability. Previous studies also reported that in eutrophic reservoirs, standing crops of copepod zooplankton can be enhanced by providing appropriate habitats and food resources during low-water conditions (Martin *et al*., 1981; Olds *et al*., 2014).

Cladocerans are normally filter-feeders on suspended living and detrital particles. The filtering mechanism of the cladocerans is very effective in retaining a wide range of particles (from 1-50 μm), and some species have the ability to survive on bacterial suspensions alone, although normally they would consume phytoplankton and detritus as well. Accordingly, the small-size cladocerans had no significant positive relationships ($p<0.05$) with the small-size protozoans (Table 4). Compared to the copepods, planktonic cladocerans have comparatively shorter life cycle under favorable conditions of temperature and food. Abundance of the cladocerans, thus, apparently fluctuated along with the environmental changes (Figure 3b). Under suitable conditions allowing frequent molting, the cladoceran eggs produce the next generation within a few weeks. Rapid increases also reflect high reproductive potential associated with asexual reproduction (Dodds and Whiles, 2010). Abundance of cladocerans is considered to be influenced by availability of suitable phytoplankton and suspended detritus (Dejenie *et al*., 2012). Nevertheless, during drought, when water depth was low, there were apparent cyanobacterial blooms, and the zooplankton community shifted towards greater relative abundance of copepods compared to cladocerans (Figure 3). A negative relationship between abundance of *Daphnia* in the zooplankton community and abundance of cyanobacteria was observed elsewhere (Dejenie *et al*., 2012). Daphnia also showed a negative relationship with turbidity in low-water conditions (Olds *et al*., 2014). Fish abundance was found to have a significant relationship with cladoceran abundance during the rainy season (Dejenie *et al*., 2012). During greatly reduced water volume periods, both top-down and bottom-up factors can favor copepods over cladocerans (Gaohua *et al*., 2017).

Change in cladoceran densities should reflect degraded habitats of the reservoir marginal areas. The plant-associated cladocerans such as chydorid and macrothricid cladocerans have been depicted as common in good-quality water resources, while pollution-tolerant cladocerans (e.g., *Brachionus*, *Moina*) can dominate deteriorated habitats (Loughheed and Chow-Fraser, 2002). The study by Castilho-Noll *et al*. (2010) also revealed that littoral habitats with higher macrophyte diversity had higher cladoceran richness than those with low macrophyte diversity. In this study, the drought conditions in the reservoir during the previous 2-3 years caused long-term deterioration of aquatic plants along the marginal habitats. The density of chydorid and macrothricid cladocerans were, thus, recorded in very low levels (Table 2).

The rotifers are suspension feeders, drawing fine particulate matter towards the mouth. Rotifers can increase in abundance under favorable food and temperature conditions. In this study, rotifers were in all zones at comparatively lower densities than the copepods and cladocerans (Tables 2-3). The highest rotifer density was found during the low-water period in mid-rainy season of 2021. The abundance of rotifers depends on many conditions and may reflect trophic status (Sanoamuang and Savatenalinton, 2001). In the Pasak Jolasid Reservoir (Thailand), diversity of zooplankton species tended to be high during high-water conditions (October) (Jithlang and Wongrat, 2006). In a mountain lacustrine habitat of Czech Republic, high flood events were found to increase species diversity of rotifers (Gabaldon *et al*., 2017). In an oligotrophic reservoir of Spain, drought events caused an increase in rotifer abundance. Nevertheless, the rotifer population can be replaced by the return of calanoid copepods when water levels return to normal (Villar-Argaiz *et al*., 2002).

Protozoa are an important component of planktonic systems covering a range of trophic conditions, and are dominant in many lacustrine habitats (Pace and Orcutt, 1981). Nevertheless, protozoa are rarely included in research on freshwater zooplankton populations. This is mainly because copepods, cladocerans, and rotifers are suggested to be the most important taxa in terms of biomass, grazing, and nutrient pathways (Makarewicz and Likens, 1979; Porter *et al*., 1979). As a general trend, nevertheless, small-size zooplankton (<250 µm; i.e., protozoa) are more tolerant than large-size zooplankton (>500 µm; i.e., copepods) to different forms of environmental stress. Size diversity of small-size zooplankton, thus, was comparatively lower (Table 3). Possible mechanisms to explain this phenomenon include the ability to recover after stress with short regeneration time (Havens and Hanazato, 1993). In addition, it seems that protozoan abundance can increase with increasing eutrophy. Pace and Orcutt (1981) revealed that densities of ciliate protozoans were about 10^2-10^4 ind·L^{-1} in oligotrophic habitats, and increased to about 10^3-10^5 ind·L^{-1} in eutrophic habitats. In Ubolratana Reservoir, the highest density (7,401 ind·L^{-1}) was observed in the eutrophic lacustrine site (Table 3), where the levels of chlorophyll *a* were comparatively high (Table 2). The small-size protozoans in each reservoir zone should serve as appropriate food sources for other zooplankton groups. In this study, the density of copepods, cladocerans and rotifers had highly significant positive relationships ($p<0.01$) with the density of small-size protozoans. Nevertheless, their density had no positive relationship with Org-TSS (Table 4). Therefore, various micro-organisms have been revealed to play important roles in the "microbial loop" (Horne and Goldman, 1994) of in the mesotrophic reservoir ecosystem.

In this study, two contrasting regions can be identified. One includes the riverine and transition regions, and the other is the lacustrine region of the reservoir. Accordingly, the responses of zooplankton populations were different (Table 4). Our findings were similar to the study of Casanova *et al*. (2009), in that abundance of zooplankton was higher in the regions with higher physico-chemical stability. Connectivity was found to affect the limnological stability, which was also related to seasonality. Accordingly, calm regions were associated with high zooplankton abundance. Conversely, instable regions in rainy seasons (or during higher inflow conditions) can decrease biomass and elevate diversity values. Physical/chemical variables among lacustrine habitats that have been linked with resource availability, and correlated with the micro-zooplankton biomass include temperature (+), water depth (-), and the water retention time of systems (+) (Yan, 1986). Hering *et al*. (2010), moreover, reported that flow regime and channel morphology can also be decisive factors for riverine invertebrates and fish. Such evidence coincided with our present results. In this study, densities of both copepods and cladocerans had highly significant positive relationships ($p<0.01$) with INF (Tables 4).

During the high flood event of the reservoir ecosystem (Figure 3; in the 5th sampling occasion), nutrient limitation and decreased phytoplankton abundance may have induced the starvation of zooplankton (George *et al*., 1990; Olds *et al*., 2014). Dissolved inorganic nitrogen and phosphorus had an indirect impact on zooplankton abundance and size by influencing the abundance of phytoplankton (Noges *et al*., 2003; Beklioglu and Tan, 2008; Li *et al*., 2022). George (2000) reported that *Daphnia* abundance was decreased due to food limitation. During high discharge events, increased flow rates moving water through the reservoir can also reduce zooplankton abundance (Beaver *et al*., 2013).

The results also indicated that density of most zooplankton groups had no significant relationship with Chl-*a* (Tables 4). This may imply the impacts from increasing dominance of cyanobacteria in response to environmental variation (Shatwell *et al*., 2008; Paerl and Huisman, 2009; Wagner and Adrian, 2009). Cyanobacteria can thrive under environmental variation and outcompete other phytoplankton, in part due to their buoyancy regulation and good performance under increased temperatures (Robarts and Zohary, 1987). In this study, the water storage volume of Ubolratana Reservoir during 2018-2022 reflected contrasting conditions caused by drought and flood events during the study (Figure 2). Over the past 56 years of reservoir operation, the water storage volume was lowest in 2020, as a result of significantly decreased inflow into the reservoir (EGAT, 2022).

The decreased inflow can impact water quality in the reservoir, cause water stratification, and increase water temperature and transparency-factors that influence the growth of potentially toxic cyanobacteria (Paerl, 2014). Accordingly, toxin-producing cyanobacteria can be found more often during drought conditions (Berg and Sutula, 2015). A previous study reported that drought conditions of a reservoir could trigger *Cylindrospermopsis* blooms (Bouvy *et al*., 2000). During the dry season of 2019, high density of *Cylindrospermopsis* was similarly observed in the transition and lacustrine zones of Ubolratana Reservoir (Mengchouy and Meksumpun, 2022). Such an occurrence indicates that drought conditions are suitable for the growth of potentially toxic cyanobacteria (Mowe *et al*., 2015; Moura *et al*., 2018). Furthermore, increased cyanobacteria abundance does not favor herbivorous zooplankton because cyanobacteria are poor-quality food for zooplankton (Wilson *et al*., 2006) and their filaments can clog feeding apparatus of filter-feeding zooplankton (Porter and McDonough, 1984). Cyanobacteria, moreover, can be toxic for several consumers (Hansson *et al*., 2007).

In addition, reservoir ecosystems are structured both by their nutrient base, such as total internal and external nutrient loading, as well as by the types of top predators present. The trophic cascade here, thus, is the result of the top-down and bottom-up processes by which we can explain many population changes. Large zooplankton dominate when zooplanktivorous fish are absent, but are soon eliminated if predators are introduced (Dodson, 1974). In one study, zooplanktivorous fish led to a dramatic shift from large-bodied crustacean zooplankton (length >1 mm) to smaller species less subject to fish predation (Northcote, 1988). Therefore, spatial changes of zooplankton abundance can also be altered with changes of zooplanktivorous fish in the reservoir ecosystem. In this study, as with previous studies (i.e., Yan, 1986; Hering *et al*., 2010; Beaver *et al*., 2013; Gaohua *et al*., 2017), changes of zooplankton in the reservoir ecosystem reflect complex relationships between various physicochemical and biological factors that vary over time. Thus, thorough sampling in representative zones of the reservoir ecosystem are recommended for further analysis of multi-functional impacts from environmental factors.

CONCLUSION

During contrasting environmental conditions caused by drought and flood events in 2018-2022, densities of zooplankton in Ubolratana Reservoir ecosystem fluctuated temporally. Densities of zooplankton increased gradually along with increases of INF and WSV in 2020. Then, during the low-water period in mid-rainy season of 2021, the densities of total copepods, cladocerans, rotifers and protozoans increased to high levels, with maximums of 13,179 ind·L^{-1}, 2,883 ind·L^{-1}, 3,940 ind·L^{-1}, and 7,401 ind·L^{-1}, respectively. Thereafter, the densities were observed to decrease when the high flood event in 2021 occurred, possibly due to decreased DO. In the riverine and transition zones of the reservoir, density of zooplankton had significant positive relationships with INF, WSV, and small-size protozoans. In the lacustrine zone, besides significant positive relationships with INF, WSV, and small-size protozoans, the densities of copepods and rotifers also had significant positive relationships with TSS and significant negative relationships with RT. Nevertheless, zooplankton density had no positive relationship with Org-TSS. Accordingly, increases in zooplankton density of the riverine and transition zones of the reservoir can occur at comparatively high INF and WSV, while increases in density of the lacustrine zone sites can occur at comparatively high INF, WSV, and TSS. During continuous flood conditions, in contrast, areas with higher RT were not suitable for zooplankton. Additionally, habitat conditions with comparatively high small-size protozoan density are suitable for the nourishment of zooplankton. The "microbial loop", thus, has been revealed to be of importance in the mesotrophic reservoir ecosystem.

Overall, this study has explained functions of hydrological factors and water quality that impact zooplankton abundance. The results imply the need to control hydrological drivers to prevent deterioration in abundance of zooplankton due to changes of the reservoir's environmental conditions. In addition, an understanding of trends of change in zooplankton biomass can be useful for developing suitable conservation management of fishery-related resources of the mesotrophic reservoir ecosystem. Further studies should assess the impacts of zooplanktivorous fish populations and of surrounding land use for mitigation of zooplankton fluctuations. Ecological models relating to the impacts of inflows and water storage volumes, together with other related water and habitat parameters, should also be developed and evaluated further.

ACKNOWLEDGEMENTS

This study was supported by the National Research Council of Thailand, the Graduate School of Kasetsart University, the Kasetsart University Research and Development Institute, and the Department of Fishery Biology, Faculty of Fisheries, Kasetsart University. The authors acknowledge Dr. Urairathr Nedtharnn for her kind recommendation in data analysis. Comments from anonymous reviewers were much appreciated. Deep thanks are also due to all members of the Sediment and Aquatic Environment Research Laboratory, the Department of Fishery Biology, for their kind cooperation in field surveys and encouragements.

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