RESEARCH PAPER

Annual variation in biomass and the community structure of crustacean zooplankton over 5 years in Lake Toya, Japan

Syuhei Ban · Wataru Makino · Hiroyuki Sakano · Hiroyuki Haruna · Hiroshi Ueda

Abstract The biomass and population dynamics of crustacean zooplankton were determined in oligotrophic Lake Toya in Japan over 5 years from May 1992 to May 1997. In 1992 and 1993, zooplankton biomass was up to 4.3 g dry weight m^{-2}, whereas it decreased to <1 g dry weight m^{-2} after 1994. This extreme change in biomass was associated with the succession of dominant species from larger ones, such as *Daphnia longispina* and *Cyclops strenuus* (*s. lat.*), to smaller ones, such as *Eubosmina tanakai* and *Bosmina longirostris*. Consequently, this biomass change seemed to cause an increase in the chlorophyll *a* concentration in the euphotic zone and a decline in lake transparency. Because the birth rates of the dominant species were somewhat higher after 1994, the decline in the populations of larger crustaceans seemed to depend more on their rate of death rather than rate of birth, and this higher death rate is not considered to be attributed to food shortage. Although these results strongly suggest a top-down cascading effect of fish predation upon crustaceans, annual catches of two commercially important planktivorous fish species have also decreased in the lake, coincidentally with decreases in zooplankton biomass. This may be attributable to fishing regulations that prohibit catching smaller fish, implying that such smaller fish affect zooplankton and phytoplankton, as well as lake transparency.

Keywords Top-down control · Crustacean zooplankton · Annual variation · Planktivorous fish · Oligotrophic lake

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S. Ban · W. Makino · H. Sakano · H. Haruna · H. Ueda
Faculty of Fisheries, Hokkaido University, 3-1-1 Minato-machi, Hakodate, Hokkaido 041-8611, Japan

Present Address:
S. Ban (✉)
School of Environmental Science, University of Shiga Prefecture, 2500 Hassaka-cho, Hikone, Shiga 522-8533, Japan
e-mail: ban@ses.usp.ac.jp

Present Address:
W. Makino
Graduate School of Life Science, Tohoku University, Aramaki Aza Aoba, Sendai, Miyagi 980-8578, Japan

Present Address:
H. Sakano
Fisheries Agency, Ministry of Agriculture, Forestry and Fisheries of Japan, 1-2-1 Kasumigaseki, Chiyoda-ku, Tokyo 100-8907, Japan

Present Address:
H. Haruna · H. Ueda
Field Science center for northern biosphere, Hokkaido University, Kita 11, Nishi 10, Kita-ku, Sapporo 060-0811, Japan

Introduction

The abundance and composition of zooplankton species in a lake are largely determined by the balance of potential prey productivity (bottom-up control) and predation pressure from various organisms in the habitat (top-down control) (e.g., Carpenter et al. 2001; Yoshida et al. 2003). In general, phytoplankton production in an individual lake is rather stable interannually as long as there is no severe anthropogenic disturbance, such as eutrophication (e.g., Wetzel 2001) and/or global warming affecting primary productivity in a lake during the recent years (O'Reilly et al. 2003; Michelutti et al. 2005; Tadonleke 2010). Annual variation of zooplankton biomass and community structure in a lake has been often shown to be more effectively influenced by top-down rather than bottom-up forces. For example, a

pronounced reduction in biomass and average body size of lacustrine zooplankton in response to the introduction of planktivorous fish has been repeatedly observed as larger zooplankton species are selectively preyed upon by the planktivorous fish (e.g., Brooks and Dodson 1965; Zaret 1980; Kerfoot and Sih 1987).

In Japan, lacustrine sockeye salmon (*Oncorhynchus nerka*) and pond smelt (*Hypomesus transpacificus nipponensis*) have been artificially introduced into many natural lakes and reservoirs since the end of nineteenth century for the sake of commercial fisheries (Tokui 1964; Shiraishi 1960). Because both species are typical visually oriented planktivores (e.g., Motoda 1950), attention has been paid to the prey–predator interaction between these fish species and zooplankton, as well as to the competitive interactions between the two fishes (Tokui 1960; Shiraishi 1960). Previous studies have reported that the annual catch of lacustrine sockeye salmon in an oligotrophic lake declined or fluctuated after pond smelt was introduced into the lake (Tokui 1960). In Lake Towada, both the annual catch of lacustrine sockeye salmon and the zooplankton community structure fluctuated significantly after an accidental introduction of pond smelt in the mid-1980s (Takamura et al. 1999). After this introduction, the replacement of lacustrine sockeye salmon by pond smelt as the dominant planktivore was associated with a shift in the community structure of zooplankton from larger *Daphnia* and *Acanthodiaptomus* species to smaller *Bosmina* and rotifers (Takamura et al. 1999), and vice versa (Takamura et al. 2001). However, it is not sufficient to understand only the relationship between the shift in zooplankton community structure and the introduction of fish, because information on the foraging behavior of the fish and the population dynamics of their prey species is limited. Further detailed information on the relationship between the two planktivorous fish species and responses of the food web structure in a lake will be needed to assess the sustainability of the lake's ecosystem and to manage economic activity, including fisheries, surrounding the lake.

Lake Toya is an oligotrophic caldera lake located at an altitude of 84 m in central Hokkaido, the northernmost island of Japan (COD, 0.7 mgO$_2$ L^{-1}; TN, 0.22 mgN L^{-1}; TP, <0.003 mgP L^{-1}), having 179 and 116.3 m of maximum and average depth, respectively, and 70.44 km^2 of surface area (Hokkaido 2005). Neither lacustrine sockeye salmon nor pond smelt are native to the lake (Motoda 1950); both species were artificially introduced in the early twentieth century (Ohno and Ando 1932; Tokui 1964). In addition, local fishermen continue to release both fish species into the lake every year, whereas the annual catches of both species show extreme year-to-year variation (Sakano et al. 1996). The annual catches of lacustrine sockeye salmon and pond smelt comprise most of the total fish catch in the lake (Sakano

1999), and these two fish species are the dominant planktivores in the lake. Although these fish may affect zooplankton populations and consequently the lake's ecosystem, few studies on zooplankton and its interaction among them have been performed. Population dynamics and foraging behavior of the two fish species has been studied elsewhere (Sakano 1999; Sakano et al. 2000, 1996). In this study, we determined seasonal and year-to-year variation in biomass of crustacean zooplankton and in population dynamics of the dominant crustacean species over 5 years from May 1992 to May 1997 and compared the variation with the annual catch of each species. We discuss the effect of crustacean zooplankton on phytoplankton biomass, lake transparency, and the two planktivorous fish species in the lake.

Methods

Field survey

Field observations were made at approximately 10-day intervals from spring to autumn (the growing season of zooplankton) and at monthly intervals in winter at Station 1 (about 170 m deep) in Lake Toya (42°36′N, 140°51′E) over 5 years from 27 May 1992 to 29 May 1997. Because the lake is never fully covered with ice (Motoda 1950), observations can be made in winter. Station location and detailed lake morphometry are described elsewhere (Makino et al. 1996). Zooplankton was collected by a vertical net haul from a depth of 100 m with a conical plankton net (diameter, 30 cm; mesh size, 0.1 mm) fitted with a flow meter. Zooplankton samples were immediately fixed with 5 % sugar formalin. Water samples used for measuring chlorophyll *a* concentration were collected at nine depths (0, 10, 20, 30, 40, 60, 80, 100, and 120 m) with a 6-L Van Dorn bottle. Chlorophyll *a* concentration in the <50-μm fraction, the size range on which crustacean zooplankton efficiently feed (Sterner 1989), was measured fluorometrically (Parsons et al. 1984). Concentrations of plankton in this size range account for >80 % of the total chlorophyll *a* concentration in the lake (Nakano and Ban 2003). Water temperature was measured at 1-m intervals with a thermistor thermometer (Toho Dentan Ltd.) from a depth of 50 m to the surface. Transparency depth (Z_{sd}) was measured with a 30-cm diameter Secchi disk, and the depth of the euphotic zone (Z_{eu}) was calculated using the equation $Z_{eu} = 2.7 Z_{sd}$ (Wetzel 2001).

Measurement for abundance and biomass of crustacean zooplankton

In the laboratory, zooplankton species were identified, and five cladoceran speceis—*Daphnia longispina*, *Daphnia*

galeata, *Eubosmina tanakai*, *Bosmina longirostris*, and *Holopedium gibberum*—and a single copepod species of *Cyclops strenuus* (s. lat.) were counted under a binocular microscope at 40× magnification. These six species were the dominant crustacean zooplankton in terms of biomass and >98 % of total zooplankton biomass during the study period. *E. tanakai* (see Kotov et al. 2009) and *C. strenuus* (s. lat.) (Ishida 2002) were formerly identified as *Bosmina coregoni* (Makino et al. 1996) and either *C. strenuus* (Makino and Ban 1998) or *Cyclops* sp. (Makino and Ban 2000), respectively. For each crustacean species, the number of males, females, egg-bearing females, eggs, and individuals in each developmental stage was also counted. The total length, excluding the tail spine, of 40 individuals for each cladoceran species collected on each occasion was measured under a microscope with a digital micrometer (Mitutoyo Digi-Matic) at 100× magnification to calculate body weight. To calculate crustacean biomass, equations of the length-to-weight relationship for each cladoceran species (Table 1) and individual dry weight for each developmental stage of copepods (Table 1) were used. Additionally, body length of adult female copepods with no caudal ramus was also measured using the same procedure as for cladocerans in order to compare female body size among crustaceans.

To obtain equations for the length-to-weight relationship of cladocerans and mean individual body weight for each developmental stage of copepod, zooplankton was collected monthly by a vertical net haul from a depth of 100 m

to the surface and immediately fixed with 2.5 % glutaraldehyde solution (Kimmerer and McKinnon 1986). This was done from May 1993 to July 1994. Between 100 and 600 individuals of each cladoceran species and of each copepod developmental stage were sorted from the zooplankton samples. For cladocerans, total length, excluding the tail spine, was measured by the same procedure as described above before drying. A batch of specimens from each species and stage was rinsed with distilled water and immediately transferred to a preweighed aluminum pan and weighed with an electro balance (Mettler UM-3, sensitivity is 0.1 µg) after drying at 60 °C for 24 h.

The abundance of each zooplankton species is represented as the mean number of individuals per liter (ind. l^{-1}) throughout the 0- to 100-m water column. Biomass was calculated from the dry body weight of each zooplankton species harvested on each occasion, integrated by the number of each species throughout the 0- to 100-m water column, and represented as grams dry weight per square meter.

Estimation for instantaneous birth rate

To estimate the instantaneous birth rate (b, day^{-1}) of the three dominant species [*C. strenuus* (s. lat.), *D. longispina*, and *E. tanakai*], the egg ratios (E) were calculated from number of the eggs (B) and females (N) using an equation (Edmondson 1968),

$$E = B/N.$$

For the copepod species, the number of adult females was used. The variable b was calculated using the following equations (Paloheimo 1974):

$$b = \ln(1 + E/D)$$

$$D = \exp\left[\ln c_1 + \ln T + c_2(\ln T)^2\right],$$

where D and T represent embryonic development time in each species (days) and ambient water temperature (°C), respectively. The constants c_1 and c_2 for each species were obtained from Bottrell et al. (1976). Mean water temperature at the water column depth at which 80 % of the integrated number of each zooplankton species was distributed was used for the calculation. The vertical distribution of each zooplankton species at each occasion was determined using a vertical series of samples collected both during the day and at night (Makino 1998).

Fish catch data

In Lake Toya, two planktivorous fish species, lacustrine sockeye salmon and pond smelt, are commercially fished, and their fry and eggs, respectively, are artificially

Table 1 Equation for length–weight relationship in five cladocerans and body weight of each developmental stage in *Cyclops strenuus* (s. lat.) occurring in Lake Toya

Species	Sex and stage	Equation
Daphnia longispina		$W = \exp(2.9254\ln L - 18.5939)$
D. galeata		$W = \exp(2.9254\ln L - 18.5939)$
Bosmina longirostris		$W = \exp[3.0395\ln(L/1000) + 3.0896]$[a]
Eubosmina tanakai		$W = \exp(3.1568\ln L - 18.6735)$
Holopedium gibberum		$W = \exp(2.7598\ln L - 16.7818)$
Cyclops strenuus (s. lat.)	Male	$W = 2.5742$
	Female	$W = 4.6058$
	C5	$W = 3.5989$
	C4	$W = 2.3676$
	C3	$W = 1.5632$
	C2	$W = 0.871$
	C1	$W = 0.5371$
	Nauplius	$W = 0.2085$

W body dry weight (µg) of each species, L length (µm) of each species
[a] From Bottrell et al. (1976)

reintroduced every year. Data from 1992 to 1997 on the annual catch and release of these two planktivorous fishes were obtained from the Lake Toya Fisheries Cooperative (unpublished data; Sakano et al. 1996; Matsuishi et al. 2002).

Statistical analyses

Spearman's rank correlation analysis was performed between chlorophyll *a* concentration in the euphotic zone and transparency depth during the study period, and between total crustacean biomass and either chlorophyll *a* concentration or transparency depth during the stagnation period (from June to Novemver) in each year studied to examine the relationship between crustaceans, phytoplankton, and transparency depth. Rank correlation analysis was selected due to its robustness and large skewness of data. The relationship between temperature or chlorophyll *a* concentration and instantaneous birth rate in each species of the three dominant crustaceans, namely, *C. strenuus* (*s. lat.*), *D. longispina*, and *E. tanakai* during the study period were also analyzed by Spearman's rank correlation analysis. Partial correlation analysis was also performed to check the influence of temperature on the relationship between chlorophyll *a* concentration and birth rate. The year-to-year variation in average temperature, chlorophyll *a* euphotic zone concentration, transparency depth, total crustacean biomass, and instantaneous birth rate of the dominant crustaceans during the stagnation period was assessed by one-way analysis of variance (ANOVA).

A post hoc test was then conducted using Scheffe's method when the ANOVA indicated significant differences. Temporal trends in body size of individuals in *D. longispina* populations were also tested by Spearman's rank correlation between the percentage of large daphnids (body length >1 mm), which corresponds to the adult stage in the field (Makino et al. 1996), and the number of days beginning from 1 January 1992. As we observed, large changes in these percentages, especially during winter (January–April), we tested for interannual differences in *D. longispina* body size in winter between the years 1993 and 1995 using Welch's ANOVA and Tukey–Kramer's honestly significant difference (HSD) post hoc test. Correlation analysis between the annual catch of the two planktivorous fishes and average zooplankton biomass during the stagnation period were used to evaluate the relationship between fish catch and zooplankton levels.

Results

Environmental valuables

Water temperature increased at the lake surface in May, and thermal stratification was established from June to November every year during the study period over 5 years from 27 May 1992 to 29 May 1997 (Fig. 1a). The thermocline developed at 10–20 m from June to August and deepened to 30 m by November. Lake water was

Fig. 1 Vertical profile of water temperature (**a**) and seasonal changes in transparency depth (**b**) at Station 1 in Lake Toya from May 1992 to May 1997. *Shaded area* represents stagnation period from June to November (see text)
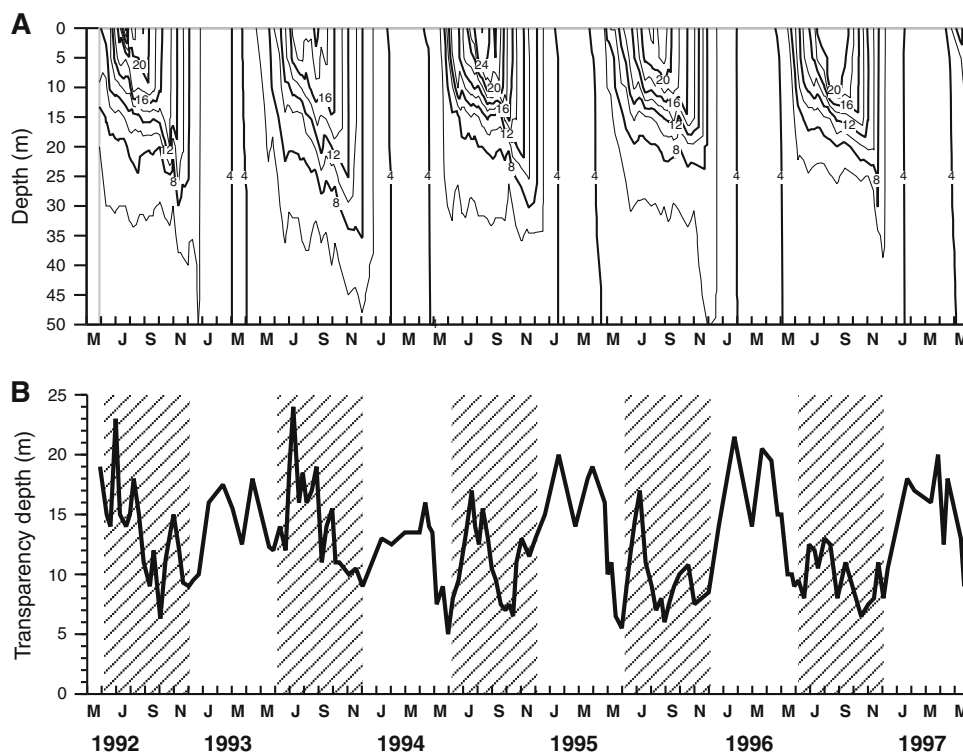
completely isothermal at 4 °C from January to April, which is the mixing period. The water temperature varied from 3 °C to 25 °C in the epilimnion during the study period, whereas it was relatively stable, <6 °C, at depths >40 m. Transparency depth increased regularly just after the thermocline developed and during the mixing period every year and varied from 6 to 24 m (Fig. 1b). The increase in spring transparency exceeded 20 m in 1992 and 1993 but did not reach 16 m after 1994; winter transparency increased to 18 m before 1993 but was >20 m after 1995. This temporal variation in transparency depth was negatively correlated with chlorophyll a concentration in the euphotic zone (Spearman's correlation analysis, $r_s = -0.52$, $n = 82$, $P < 0.0001$). Mean transparency depth during the stagnation period was >13 m in 1992 and 1993 but decreased to approximately 10 m after 1994 (Table 2). Consequently, the euphotic zone during this period was >35 m in 1992 and 1993 but approximately 27 m after 1994. Mean water temperatures in the euphotic

zone, however, did not vary significantly among years (Table 3).

Average chlorophyll a concentration in the euphotic zone fluctuated greatly, from 0.2 to 2.7 µg L^{-1}, during the study period, whereas the average value throughout the entire water column was relatively stable (Fig. 2a). The phytoplankton biomass indicated as chlorophyll a concentration was vertically restricted in the euphotic zone during the stagnation period each year (Fig. 2b). In 1995, when extremely high values were recorded, the values were restricted to the zone above 30 m. Annual mean concentration in the euphotic zone during the stagnation period increased after 1994 and was significantly higher in 1995 and 1996 than before 1994 (Tables 2, 3).

Body size of the dominant crustaceans

In terms of body length, *D. longispina* was the largest crustacean zooplankton in the lake, followed by *D. galeata*,

Table 2 Average water temperature above a depth of 30 m, chlorophyll a concentration in the euphotic zone, transparency depth, crustacean zooplankton biomass, and instantaneous birth rates of

Cyclops strenuus (*s. lat.*), *Daphnia longispina*, and *Eubosmina tanakai* during the growing season from June to November at Station 1 in Lake Toya among the 5 years studied

| Parameter	Species	Year				
		1992	1993	1994	1995	1996
Temperature (°C)		11.4 (1.9)	11.9 (1.6)	12.3 (1.9)	11.9 (1.8)	10.7 (1.9)
Chlorophyll a (µg L^{-1})		0.6 (0.2)	0.6 (0.2)	0.9 (0.2)	1.4 (0.7)	1.0 (0.3)
Transparency depth (m)		13.2 (3.8)	14.9 (4.0)	11.1 (3.0)	9.8 (3.0)	10.0 (2.2)
Total zooplankton biomass (g dry-weight m^{-2})		1.6 (0.9)	2.0 (1.1)	0.6 (0.4)	0.5 (0.3)	0.8 (0.6)
Birth rate (day^{-1})	*C. strenuus* (*s. lat.*)	0.019 (0.007)	0.014 (0.011)	0.011 (0.010)	0.016 (0.007)	0.034 (0.021)
	D. longispina	0.031 (0.027)	0.030 (0.014)	0.088 (0.040)	0.122 (0.040)	–
	E. tanakai	0.025 (0.010)	0.028 (0.033)	0.075 (0.027)	0.055 (0.038)	0.074 (0.043)

Numbers in parentheses represent standard deviation

Table 3 Results of analysis of variance (*ANOVA*) of each parameter among the five years from 1992 to 1996. When *ANOVA* indicated significant difference, post-hoc test by Scheffe's method was conducted. Figures in most right column represent each of the 5 years

Parameter	Species	ANOVA			Post-hoc test by Scheffe's method*
		df	F	p	
Temperature (°C)		4, 77	1.7	0.16	
Chlorophyll a (µg L^{-1})		4, 77	15.4	< 0.01	<u>95 96 94 92 93</u>
Transparency depth (m)		4, 76	7.0	< 0.01	<u>93 92 94 95 96</u>
Total zooplankton biomass (g dry-weight m^{-2})		4, 77	12.7	< 0.01	<u>93 92 96 94 95</u>
Birth rate (day^{-1})	*C. strenuus* (*s. lat.*)	4, 77	8.3	< 0.01	<u>96 92 95 93 94</u>
	D. longispina	3, 60	27.7	< 0.01	<u>95 94 92 93</u>
	E. tanakai	4, 71	9.6	< 0.01	<u>94 96 95 93 92</u>

* Significant differences are not scored by the same line at $p < 0.05$
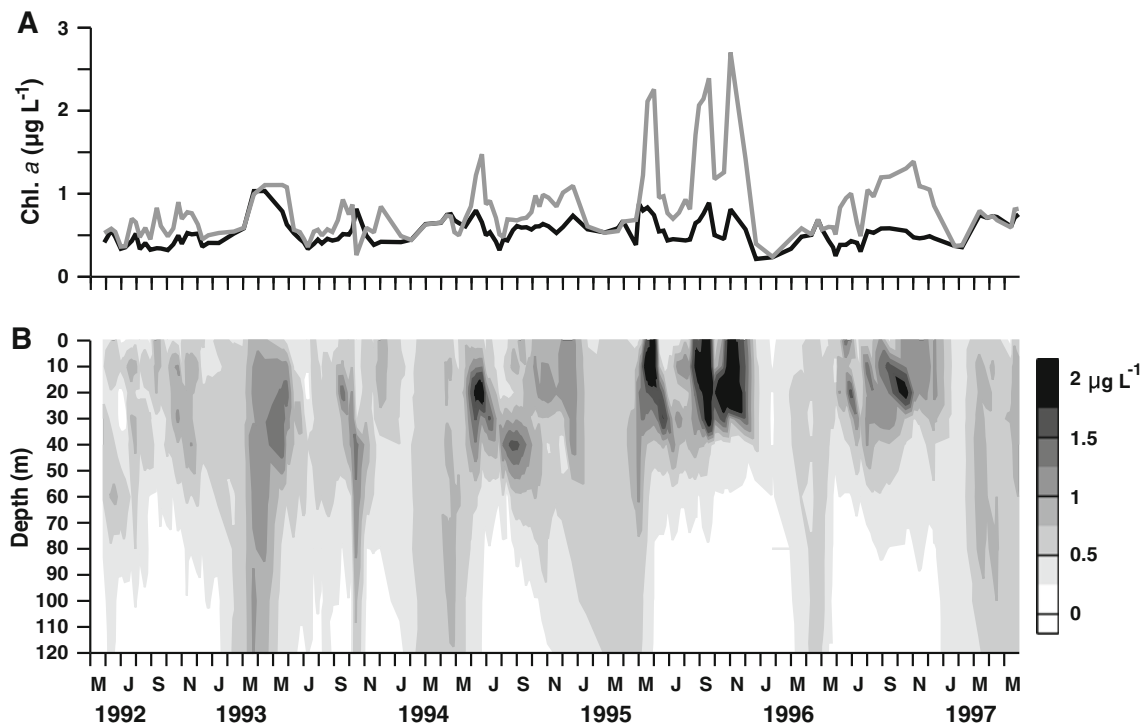
Fig. 2 Seasonal changes in average chlorophyll *a* concentration throughout a 0- to 120-m water column (*black line*) and within a euphotic zone (*gray line*) (**a**), and vertical distribution of chlorophyll *a* concentration (**b**) at Station 1 in Lake Toya from May 1992 to May 1997

Table 4 Average body length with range from minimum to maximum in six dominant crustacean zooplankton species occurring in Lake Toya

Species name	No. of animals measured	Body length (mm)		
		Average	Maximum	Minimum
D. longispina	2864	1.54	1.86	0.91
D. galeata	359	1.46	1.76	1.00
H. gibberum	1263	1.24	1.70	0.40
C. strenuus (*s. lat.*)	6424	1.12	1.46	0.92
E. tanakai	3981	0.67	0.87	0.52
B. longirostris	1606	0.46	0.62	0.34

H. gibberum, *C. strenuus* (*s. lat.*), and *E. tanakai* (Table 4). The smallest species was *B. longirostris*. Seasonal variation in body size of the dominant crustaceans was minimal, except for *D. longispina*, the body length of which declined during the study period. Percentages of adult daphnids in the population of >1 mm in body length gradually decreased throughout the study period (Spearman's rank correlation analysis, $n = 76$, $r_s = -0.46$, $P < 0.0001$), especially in winter. Percentage of adults found from January to April was around 80 % in 1993, 30 % in 1994, and <20 % in 1995. Average daphnid body length from January to April was significantly larger in 1993 than in either 1994 or 1995 (Table 5).

Crustacean zooplankton biomass

Crustacean zooplankton biomass varied seasonally and annually (Fig. 3). It increased in June and then decreased after September and was extremely low during winter each year, except for the first winter in 1992–1993. Therefore, the period during which biomass increased was designated as the growing season, which was almost the same duration as the stagnation period (Fig. 1). In 1992 and 1993, biomass reached 4.3 g dry weight m^{-2}. From 1994 to 1996, it remained at low levels, approaching 1.0 g dry weight m^{-2}, which was only one quarter of the biomass measured in 1992. The mean biomass during the growing seasons after

Table 5 Comparison of body size of *Daphnia longispina* occurring from January to April over 3 years (1993, 1994, 1995), with analysis of variance (*ANOVA*) and post hoc test by Tukey–Kramer's honestly significant difference (HSD)

Year	Species	Body length (mm)		Post hoc test by Tukey–Kramer's HSD*
		Mean	(*n*, SE)	
1993	*D. longispina*	1.19	(200, 0.02)	a
1994	*D. longispina*	0.90	(73, 0.04)	b
1995	*D. longispina*	0.86	(77, 0.04)	b
	Results of *ANOVA*			
	$df = 2, 164.7; F = 44.99; P < 0.0001$			

The variables *n* and SE in parentheses represent the number of animals measured and standard error, respectively

* Statistically significant between different letters at $P < 0.05$

1994 was significantly lower than that measured in 1992 and 1993 (Tables 2, 3). In the first winter, biomass levels were somewhat lower, by 0.1–0.5 g dry weight m^{-2} but decreased to <0.1 g dry weight m^{-2} in the second winter and further to <0.05 g dry weight m^{-2} after the third winter.

Spearman's rank correlation analysis showed that crustacean biomass during the growing season was positively correlated with transparency depth ($n = 82$, $r_s = 0.42$, $P < 0.0001$) and negatively with mean chlorophyll *a* concentration in the euphotic zone ($n = 82$, $r_s = -0.72$, $P < 0.0001$).

Composition of dominant crustaceans

Species composition also changed during the study period (Fig. 3). In 1992 and 1993, the most dominant species was *D. longispina*, followed by *E. tanakai* and *C. strenuus* (*s. lat.*). In 1994, *C. strenuus* (*s. lat.*) and *H. gibberum* dominated, accounting for >80 % of total crustacean zooplankton biomass, but levels of *D. longispina* and *E. tanakai* did not increase to the same degree. In 1995,

E. tanakai was the most dominant species, accounting for almost 100 % of the total crustacean biomass, but the numbers of the other cladocerans and the copepod species did not increase. *B. longirostris* was not detected until September 1995, then increased in numbers in June 1996 to become the most dominant species during the growing season. This succession of dominant species was correlated with body size: the largest, *D. longispina*, disappeared first and was followed by *C. strenuus* (*s. lat.*), and finally, *E. tanakai* was replaced by the smallest species, *B. longirostris*.

Population dynamics of the dominant species

C. strenuus (*s. lat.*) gradually increased in number from 1992 to 1993 but declined in 1994, then remained at a very low level, <0.5 ind. L^{-1}, after 1995 (Fig. 4). In contrast, its egg ratio increased during summer each year and reached nearly the same annual maximum (close to 0.5 eggs female^{-1}) except for 1996, when the egg ratio increased to >1 egg female^{-1}. In both 1992 and 1993, *D. longispina* increased each summer, to >6 ind. L^{-1} in
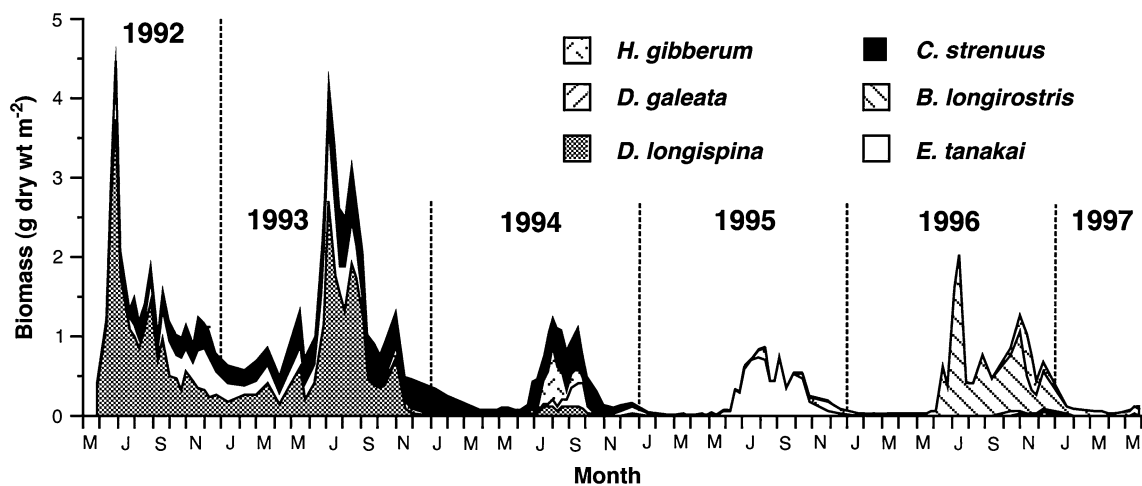
Fig. 3 Seasonal changes in zooplankton biomass at Station 1 in Lake Toya from May 1992 to May 1997

Fig. 4 Seasonal changes of abundance (*solid lines*) and egg ratio (*circles*) of six dominant crustaceans at Station 1 in Lake Toya from May 1992 to May 1997
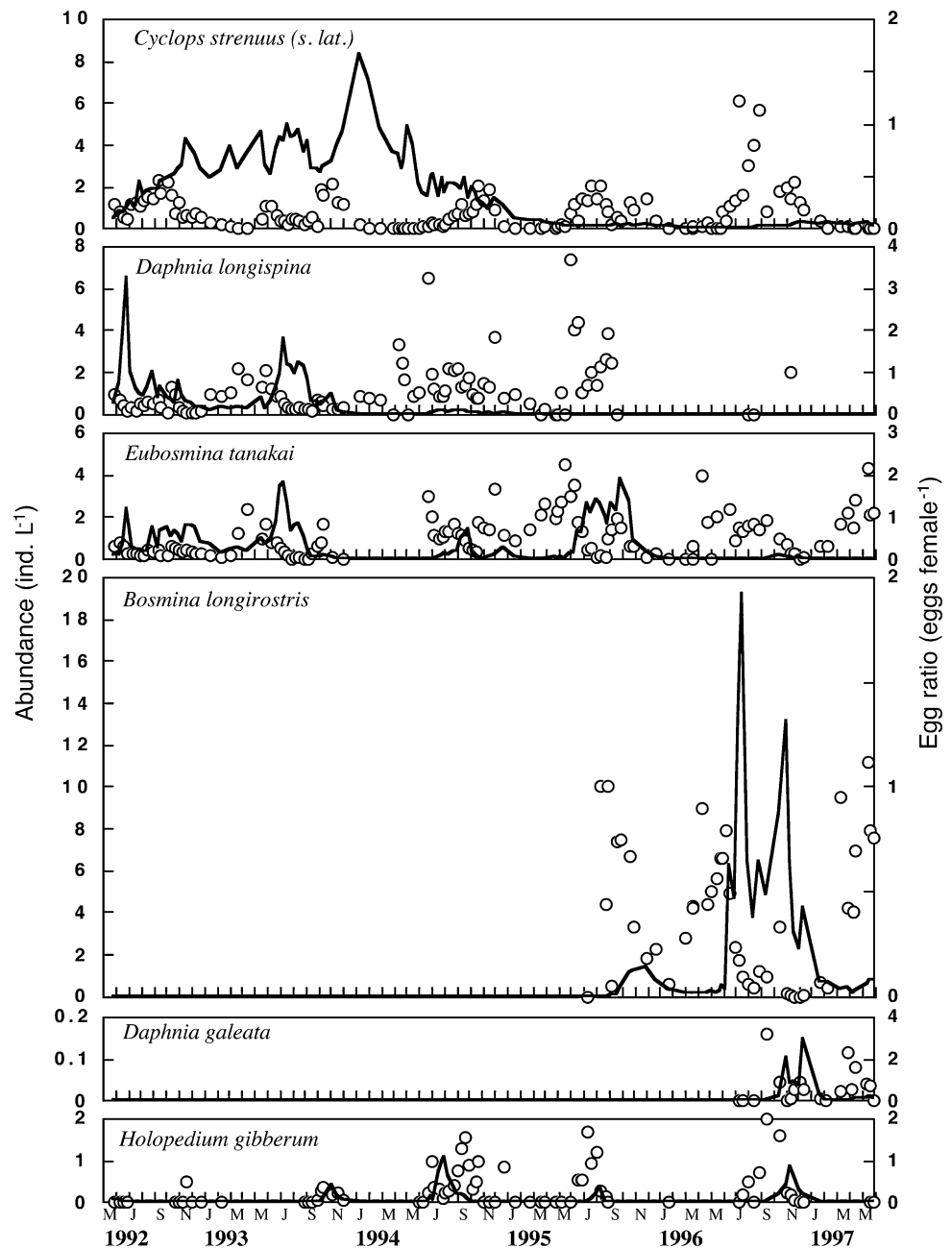
1992. However, this species did not exceed 0.01 ind. L^{-1} in 1994 and almost disappeared after the middle of September in 1995, although its egg ratio after 1994 increased to >3 eggs female^{-1}, or 2- to 3-fold greater than the egg ratio observed in 1992 and 1993. *E. tanakai* also increased each summer until 1995 but thereafter became very scarce. Egg ratios of this species varied seasonally and reached higher values after 1994 compared with those before 1993. *B. longirostris* increased abruptly after September 1995 and reached a maximum of 19.2 ind. L^{-1} in July 1996. *D. galeata* was not detected until June in 1996, but its numbers increased slightly after November 1996.

H. gibberum regularly increased once a year but did not reach 1 ind. L^{-1}, though the timing of the increase varied from year to year.

Instantaneous birth rates of the three dominant crustaceans, *C. strenuus* (*s. lat.*), *D. longispina*, and *E. tanakai* changed seasonally each year and were positively correlated with both ambient water temperature and chlorophyll *a* concentration in the euphotic zone (Table 6). Partial correlation coefficient between chlorophyll *a* concentration and birth rate, however, was 0.02, 0.63, and 0.33 in *C. strenuus* (*s. lat.*), *D. longispina,* and *E. tanakai*, respectively, suggesting the birth rate of *C. strenuus*

Table 6 Spearman's rank correlation coefficient between ambient temperature and chlorophyll *a* concentration in the euphotic zone and birth rate for each three crustacean species, *Cyclops strenuus* (s. lat.), *Daphnia longispina*, and *Eubosmina tanakai*, from Lake Toya during the study period from 27 May 1992 to 29 May 1997

Species	Number	Ambient temperature	Chlorophyll *a* concentration in euphotic zone
Cyclops strenuus (s. lat.)	134	0.72**	0.21*
Daphnia longispina	96	0.40**	0.50**
Eubosmina tanakai	115	0.29**	0.48**

* $P < 0.05$, **$P < 0.01$
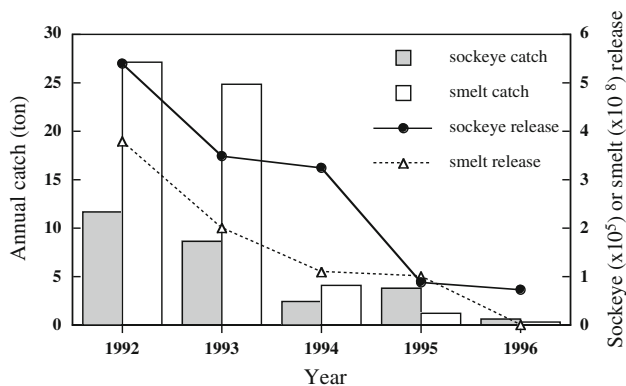
Fig. 5 Annual catch and release of lacustrine sockeye salmon (*Onchorhynchus nerka*) and pond smelt (*Hypomesus transpacificus nipponensis*) from Lake Toya from 1992 to 1996

(s. lat.) may depend on temperature alone. There were no significant differences in average instantaneous birth rates calculated during the growing season among first 4 years in the copepod and first 2 years in the two cladocerans. The average birth rates in *C. strenuus* (s. lat.) were 0.011–0.019 day^{-1} from 1992 to 1995 and 0.034 day^{-1} in 1996 (Table 2). There was no significant difference in birth rates over the first 4 years, but these rates were significantly higher (2.5 fold) in 1996 (Table 3), despite a declining population density after 1994 (Fig. 4). In *D. longispina* and *E. tanakai*, the average birth rates after 1994 were also significantly higher than those in 1992 and 1993 (Tables 2, 3). No calculation for *D. longispina* was performed in 1996 because it was not detected in plankton samples. These results strongly suggest that declining population levels of the three dominant species may not be attributable to decreasing birth rates but rather to increasing death rates.

Fish catch

In Lake Toya, the annual catch of both lacustrine sockeye salmon and pond smelt showed a decreasing trend throughout the study period (Fig. 5). The annual catch of these two species was large in 1992 and 1993 but declined severely after 1994. The number of pond smelt and sockeye

salmon released also decreased from year to year due to a lower catch of adult females from which eggs were obtained. Finally, no release was made for pond smelt in 1996. The annual catch of these two species was positively correlated with average zooplankton biomass during the growing season ($n = 5$, $r = 0.81$ and 0.94 for sockeye salmon and pond smelt, respectively).

Discussion

During the growing season in Lake Toya, extreme decreases in crustacean zooplankton biomass were accompanied by increasing chlorophyll *a* concentration during the study period from 27 May 1992 to 29 May 1997. According to Hokkaido (2005), total phosphorus was consistently near the detection limit throughout the water column and showed no increasing trend during the period of this study. Therefore, the increasing trend in phytoplankton biomass may not be related to nutrient loading into the lake. On the other hand, many previous studies have shown that large cladocerans, especially daphnids, can efficiently remove sestonic substances, including phytoplankton, from the waters (Horn 1981; Horn and Horn 1995; Kasprzak et al. 1999; Vanni and Temte 1990). In Lake Toya, crustacean biomass, consisting mostly of large *D. longispina* and *C. strenuus* (s. lat.) species, was correlated negatively with average chlorophyll *a* concentration in the euphotic zone and correlated positively with transparency depth. Therefore, the crustaceans might regulate phytoplankton biomass and consequently lake transparency through their feeding, because transparency seemed to depend on phytoplankton biomass. This type of top-down regulation has been reported for many other lakes and ponds (Lampert 1978a; Vanni and Temte 1990; Takamura et al. 1999), except for some lakes in which phosphate is extremely limiting, such as in the Canadian Shield lakes (Elser et al. 1998). These results and the literature imply that increases in chlorophyll *a* concentration in the euphotic zone and decreases in transparency during the growing season after 1994 may be attributable to reduced biomass levels of the dominant crustacean species.

We found a pronounced year-to-year succession in species composition, accompanied by biomass reduction in crustacean zooplankton, which declined in 1994, and its community structure shifted from one dominated by the larger species, *D. longispina* and *C. strenuus* (*s. lat.*) in 1992 and 1993, to one dominated by the smaller species, *E. tanakai* in 1995, and finally by the smallest species, *B. longirostris*, which replaced *E. tanakai* in 1996. Our results for zooplankton population dynamics revealed that even in the "collapsed" species, such as *D. longispina* and *C. strenuus* (*s. lat.*), the instantaneous birth rates during the growing season in low zooplankton biomass years (after 1994) were comparable with those in high zooplankton biomass years (1992–1993). Instantaneous birth rates of zooplankton are generally influenced by ambient temperature and species interaction with bottom-up forces, such as food limitation due to the tight relationship between egg production and food concentration (Lampert 1978b). In this study, seasonal variation in instantaneous birth rates of the two dominant cladoceran species depended on both ambient temperature and concentrations of chlorophyll *a* of <50 μm, which represents a proxy value for potential food available for the crustaceans, although that in the copepod was correlated with ambient temperature alone. Furthermore, neither average temperature nor average chlorophyll *a* concentration during the growing season had decreased during the low zooplankton biomass years. These results suggest that species succession in the lake from larger to smaller could not be explained by bottom-up forces. Birth rates for zooplankton can also be reduced by parasite infection (Yan and Larsson 1988), but based on the external morphology of zooplankton collected from the lake, we found no evidence of such infection.

A declining trend in body size during the study period was found for the largest species, *D. longispina*. Mean body size and percentage of adult-sized individuals in the population decreased during the study period, especially in winter. Reduction in the average body size of zooplankton can be caused by selective feeding by visually oriented predators, such as planktivorous fish, namely, by top-down forces (Brooks and Dodson 1965; Zaret 1980), although predation by fish in winter should be less frequent due to low temperatures (Bartell and Kitchell 1978; Hairston et al. 1983). Jeppesen et al. (2004) compared the effect of predation by fish on the body size of cladocerans in winter with that in spring, summer, and autumn in 34 lakes over 8–9 years. The authors suggested that the impact of fish predation on cladoceran body size was as strong in winter as in the other three seasons. Low turnover rates due to low temperatures and food concentrations would therefore keep the average body size of cladocerans on the smaller end of the size range during winter if fish were abundant (Jeppesen et al. 2004).

Analyzing stomach contents of lacustrine sockeye salmon and pond smelt from Lake Toya showed that they selectively fed on larger prey, such as *D. longispina*, in the high zooplankton biomass years (Sakano 1999). Other studies also show selective feeding on larger zooplankton by lacustrine sockeye salmon (Eggers 1978; Kaeriyama et al. 1992; Scheuerell et al. 2005) and pond smelt (Shiraishi 1957; Tomita and Hada 1966; Chang et al. 2005). However, the stomach content composition in lacustrine sockeye salmon switched to the smaller planktonic prey, such as *E. tanakai* and benthic gammarids and fish larvae after 1994, when larger prey were replaced by smaller ones (Sakano 1999). Because juvenile sockeye salmon consume less-preferred copepods depending on availability of preferred daphnids in Lake Washington (Scheuerell et al. 2005), such opportunistic feeding after 1994 may indicate that the density of daphnids falls below a threshold for detection by the fish. Therefore, decreases in body size of not only mixed crustacean communities but also single *D. longispina* species after 1994 indicate intensive predation pressure by the two fish species. This evidence, together no indication of reduced birth rates of crustaceans, as discussed above, collectively suggests that predation by lacustrine sockeye salmon and pond smelt has played an important role in eliminating larger crustaceans from the water column after 1994. This implies that these two commercially important fish species affect the lower trophic levels and ecosystem of Lake Toya.

Conversely, the annual catch of these two species is positively correlated with zooplankton biomass during the study period. Although this implies bottom-up control by zooplankton prey on fish populations, it should be noted that fish catch does not necessarily indicate fish stock in the lake. In Lake Toya, fishermen must use a gill net with mesh size >50 mm for sockeye salmon and a gill-net with mesh size >20 mm for pond smelt due to fishing regulations; therefore, fish smaller than those mesh sizes cannot be caught. Juvenile sockeye and young-of-the-year (YOY) pond smelt are never caught with gill nets of these mesh sizes (Sakano 1999). Our previous report for the lake showed that body size of both sockeye salmon and pond smelt, except for age 0 pond smelt, decreased with decreasing zooplankton biomass from 1993 to 1997 (Sakano et al. 2000). Specific growth rates of 0+ sockeye salmon, estimated using back-calculated length with scale radius, also decreased with decreasing zooplankton biomass until 1995 (Sakano et al. 2000). Fish growth was thought to be associated with diminution of zooplankton biomass, and these smaller fishes are not expected to be caught with gill nets of the size fishermen are permitted use. Therefore, the lower annual catches in the low relative to the high zooplankton biomass years may be attributable to an increasing abundance of these smaller fish, which could not be caught using gill nets.

The specific growth rates of sockeye salmon in the second- and third-year classes also decreased with decreasing zooplankton biomass until 1995 but thereafter tended to increase (Sakano et al. 2000). The older sockeye salmon ate unidentified fish larvae and small pond smelts rather than zooplankton in low zooplankton biomass years, and larger individuals ate primarily fish prey, particularly small pond smelts (Sakano et al. 2000). This dietary shift from zooplankton to fish may be due not only to decreasing populations of large planktonic prey but also to increasing numbers of young and smaller fish, mostly YOY pond smelt, as the growth rate of sockeye salmon older than the second-year class recovers (Sakano 1999).

Bioenergetic models of fish growth in several lakes and oceans show that as an age class, younger fish consume more prey than older ones. In Lake Michigan, larval and YOY alewives have been shown to account for 50 % of total annual zooplankton consumption by alewives (Hewett and Stewart 1989). YOY herrings (*Clupea harengus*) are also more important planktivores than the yearlings in the Baltic Sea (Rudstam et al. 1992). Arrhenius and Hansson (1993) estimated that larval and YOY herrings accounted for 45 % of total zooplankton consumption by herring in the Baltic Sea. In Lake Toya, both juvenile sockeye salmon and YOY pond smelt are caught less often by gill nets, as described above. Increasing numbers of these small fish may cause declining zooplankton biomass and consequently reduced growth of both species. These less-frequently caught smaller fish might join the planktivore population in the following year as planktivores. Sakano (1999) estimated population ingestion rates by lacustrine sockeye salmon and pond smelt in Lake Toya using a bioenergetic model and gross growth efficiency, respectively, from 1993 to 1996, and suggested that population ingestion rates of YOY pond smelt remained high, even in 1994 and 1995 when population ingestion rates of 1+ pond smelt and any age class of sockeye salmon decreased. The low population ingestion rate of both species, including YOY pond smelt, in 1996 may partly explain sporadic increases in populations of large *D. galeata* in October and December 1996. No artificial release of pond smelt occurred in 1996, and the stock of YOY pond smelt seemed to decrease only in 1996. Hossain et al. (2010) estimated ecosystem functions in Lake Toya using Ecopath with Ecosim software and showed that pond smelt were the most dominant animal in terms of biomass, perhaps influencing the dynamics of organisms at both lower and higher trophic levels in the lake.

According to our results from zooplankton biomass and population dynamics, a top-down cascading effect of these two planktivorous fish species in Lake Toya was expected. However, fish catch data did not necessarily indicate top-down control by the fish on zooplankton biomass. This inconsistency may be attributed to fishing regulations designed for fishermen to prevent catching smaller fish, which implies that the smaller fish, particularly YOY pond smelt, affect zooplankton, phytoplankton, and transparency in the lake.

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