HOKKAIDO UNIVERSITY

Title	Annual variation in biomass and the community structure of crustacean zooplankton over 5 years in Lake Toya, Japan
Author(s)	Ban, Syuhei; Makino, Wataru; Sakano, Hiroyuki et al.
Citation	Limnology, 14(1), 59-70 https://doi.org/10.1007/s10201-012-0387-3
Issue Date	2013-01
Doc URL	https://hdl.handle.net/2115/51918
Rights	The original publication is available at www.springerlink.com
Type	journal article
File Information	Lim14-1_59-70.pdf



Hokkaido University Collection of Scholarly and Academic Papers : HUSCAP

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

Syuhei Ban[1], Wataru Makino[2], Hiroyuki Sakano[3], Hiroyuki Haruna[4], Hiroshi Ueda[4]

Faculty of Fisheries, Hokkaido University, 3-1-1 Minato-machi, Hakodate, Hokkaido 041-8611, Japan

1) Present address, School of Environmental Science, University of Shiga Prefecture, 2500 Hassaka-cho, Hikone, Shiga 522-8533, Japan

2) Present address, Graduate School of Life Science, Tohoko University Aramaki Aza Aoba, Sendai, Miyagi 980-8578, JAPAN

3) Present address, National Research Institute of Fisheries Science, Fisheries Research Agency, Ueda, Nagano 386-0031, Japan

4) Present address, Field Science center for northern biosphere, Hokkaido University, Kita 11, Nishi 10, Kita-ku, Sapporo 060-0811, Japan

Running head, Top-down induced annual variation of zooplankton

Corresponding author, Syuhei Ban (ban@ses.usp.ac.jp)

Abstract

Biomass and population dynamics of crustacean zooplankton were investigated in Lake Toya, oligotrophic caldera lake in Japan, during five years from 1992 to 1997. Zooplankton biomass increased in summer with increasing water temperature every year, and varied annually even if temperature and food conditions did not change so much. In 1992 and 1993, zooplankton biomass reached up to > 4 g dry-wt m^{-2}, while it declined below 1 g dry-wt m^{-2} after 1994. This extreme change of the zooplankton biomass depends on succession of three dominant species from large ones, such as *Daphnia longispina* and *Cyclops* cf. *sibiricus*, to small ones, such as *Eubosmina longispina* and *Bosmina longirostris*. Analyzing population dynamics of the dominant crustaceans demonstrates that the year-to-year variation in the abundance is related to the death rate but not birth rate. Since chlorophyll *a* concentrations within the euphotic zone and the birth rates of each species were rather higher in low zooplankton biomass years, the higher death rates after 1994 is not considered to be attributed to food shortage. Two planktivorous fish, lacustrine sockeye salmon (*Oncorhynchus nerka*) and pond smelt (*Hypomesus transpacificus nipponensis*), were artificially introduced every year for the sake of commercial fisheries in the lake. Although the two fishes are expected to be the most important predator for the large crustaceans, *D. longispina* and *C.* cf. *sibiricus*, which are actually fed on by the two fishes, the annual catch of the fishes was positively correlated to the average biomass of the crustaceans during summer season. This conflicting result is considered to be attributed to less catch of the fishes with fishing regulation for a gill net used by fishermen due to lowering the growth rate of the fishes in the low zooplankton biomass years. Proliferation of young and/or small fishes, including young-of-the-year pond smelt, which cannot be caught with the gill net may play an important role for eliminating the large crustaceans. Our results suggest that excessively artificial introduction of planktivorous

fish, especially pond smelt, limits the zooplankton production in oligotrophic lake such as Lake Toya, subsequently decreasing the growth rate of the fish, and that this negative feed-back finally enhances lowering the annual fish catch.

Introduction

Top-down control has been well known phenomena in various ecosystems, influencing community structure, population dynamics and behavior of organisms in lower trophic levels (Paine 1966, 1969, Carpenter and Kitchell 1993). In the aquatic ecosystems, many previous studies have demonstrated that planktivorous fish affects structure and dynamics of zooplankton communities through the size-selective predation (Brooks and Dodson 1965, Zaret 1980, Kerfoot and Sih 1987). Although the bottom-up control also plays an important role for understanding the structure and composition of freshwater communities (Lampert 1985, Sterner and Elser 2002), predation is still an important driving force for changing the food-web and the ecosystem, especially in the environments to which top predators are introduced accidentally (e.g., alewife in Connecticut lakes in Brooks and Dodson 1965) and artificially (e.g., Nile perch in Lake Victoria in Ligtvoet and Witte 1991).

In Japan, artificial introduction of two typical planktivorous fishes, lacustrine sockeye salmon (*Oncorhynchus nerka*) and pond smelt (*Hypomesus transpacificus nipponensis*), had been made in a lot of natural lakes and reservoirs from the end of 19th century for the sake of commercial fisheries (Shiraishi 1960, Tokui 1964). These two fishes are considered to be potential competitors (Tokui 1960, Sakano 1999). Although Tokui (1960) has been pointed out that introduction of pond smelt to oligotrphic lakes in which sockeye salmon already colonized leads reduction of the sockeye salmon production four decades ago, there is a few study for the effects of these voracious planktivores on zooplankton communities and lake ecosystem. Recently, Takamura *et al.* (1999) analyzed long-term data sets for fish catch, zooplankton biomass and lake transparency in oligotrophic Lake Towada, where lacustrine sockeye salmon has been introduced from the beginning of 20th century, and showed that introduction of pond smelt after 1980's shifts the zooplankton community structure from

large grazers, i.e. *Daphnia* and *Acanthodiaptomus,* to small ones, i.e. *Bosmina* and rotifers, and then enhance phytoplankton biomass, subsequently lowering the lake transparency. This suggests that simultaneous introduction of these two planktivorous fishes to an oligotrphic lake extremely affects the lake ecosystem, but information is limited and it is still open question.

Lake Toya is oligotrophic caldera lake located in central Hokkaido, northern island of Japan, and both lacustrine sockeye salmon and pond smelt live together from early 20th century (Ohno and Ando 1932, Tokui 1964). Both fishes are not native species in the lake, and have never colonized before the first introduction of them into the lake (Motoda 1950). Both the two fishes are artificially introduced every year for the sake of commercial fisheries. Cumulative data sets for the annual catch of the two fishes show extreme year-to-year variation (Sakano *et al.* 1996). Detailed analyses for the diet and population dynamics of the two fishes in Lake Toya presented elsewhere (Sakano 1999, Sakano *et al.* 2001, Sakano *et al.* in prep.).

In the present study, we investigate annual variation of biomass and population dynamics of crustacean zooplankton during five years from 1992 to 1997, and discuss effect of two planktivorous fishes on zooplankton biomass and the species composition, and effect of the negative feedback to the fish production in the lake.

Materials and Methods

Zooplankton was collected at regularly ca. 10 days interval by a vertical net haul from 100 m to the surface with a conical plankton net (diameter, 30cm; mesh size, 0.1mm) fitted with a flow meter at St. 1 (ca. 170 m deep) in Lake Toya (42˚36' N, 140˚51' E) during five years from 27 May 1992 to 29 May 1997. A location of the station and detailed morphometry of

the lake have been described elsewhere (Makino *et al.* 1996). The animals collected were immediately fixed with 5% sugar formalin. Water samples for measuring chlorophyll *a* concentration were collected from 9 depths (0, 10, 20, 30, 40, 60, 80, 100 and 120m) with a 6-L Van-Dorn bottle. Chlorophyll *a* concentration of < 50-μm fraction, in the size range which crustacean zooplankton efficiently feed on (Sterner 1989), was measured fluorometrically (Parsons *et al.* 1984). Practically, the concentrations of this size range mostly account for > 80% of total chlorophyll *a* concentration in this lake (Nakano and Ban 2003). Water temperature was measured at 1m interval with a thermister thermometer (Toho Dentan Ltd.) from 50 m to the surface. Transparency depth (Z_{sd}) was measured with a 30-cm diameter Secchi disk, and depth range of the euphotic zone (Z_{eu}) was calculated with an equation of $Z_{eu} = 2.7*Z_{sd}$ (Wetzel 2001).

In the laboratory, zooplankton species was identified and counted under a binocular microscope at magnification of 40x. In crustacean zooplankton, male, female, egg-bearing female and the eggs were also counted. Total length not including tail spin of each 40 individuals in the cladocerans collected at each occasion was measured under a microscope with a digital micrometer (Mitutoyo Digi-Matic) at a magnification of 100x in order to estimate the body weight. To estimate the biomass of the zooplankton, equations of length-weight relationship for each cladoceran species (Table 1), and individual dry weight for each rotifer species (Bottrell *et al.* 1976) and for each stage of the copepod (Table 1) were used. To obtain the equations of length-weight relationship for cladocerans and mean individual body weight for each stage of the copepod, zooplankton was collected monthly with a vertical net haul and then fixed with 2.5% glutaraldehyde solution (Kimmerer and McKinnon 1986) from May 1993 to July 1994. Cumulative number of 100-600 individuals of each crustacean species were sorted from the zooplankton samples. For the cladocerans, the

total length without tail spin was measured with the same procedure as described above before dried. The specimens were rinsed with distilled water, and immediately transferred to pre-weighed aluminum pan, after dried at 60˚C for 24 h, weighed with an electro balance (Mettler UM-3, sensitivity is 0.1µg).

Abundance of each zooplankton species represented as mean individual numbers per liter (ind. l^{-1}) throughout the 0-100 m water column. Biomass was calculated from the body dry weight of each zooplankton species occurred at each occasion and integrated number of each species throughout the 0-100 m water column, and represented as gram dry weight per square meter (g dry-wt m^{-2}).

To evaluate the population dynamics of the crustacean zooplankton, egg ratio (E) was calculated from number of the egg (B) and female (N) using an equation (Edmondson 1968),

$$E = B/N.$$

For the copepod, number of adult female was used. Instantaneous birth (*b*) and death rates (*d*) were calculated from following equations (Paloheimo 1974),

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

$$D = \exp [\ln a + \ln T + c (\ln T)^2],$$

$$d = b - r,$$

where D, T, and *r* represent embryonic development time (days), ambient temperature (˚C) and instantaneous rate of population growth for each species, respectively. Constants of *a* and *c* for each species were referred from Bottrell *et al.* (1976). The average temperature in the depth of which 80% of each zooplankton species throughout the water column were distributed was used for the calculation. The vertical distribution of each zooplankton species were determined monthly at both day and night (Makino 1998).

In Lake Toya, two planktivorous fishes of lacustrine sockeye salmon (*Oncorhynchus*

nerka) and pond smelt (*Hypomesus transpacificus nipponensis*) are caught commercially, and both the eggs and fry are artificially introduced every year, respectively. Data for annual catch and number of release of the two planktivorous fishes from 1992 to 1997 were obtained from Lake Toya Fisheries Cooperative.

Year-to-year variations on mean temperature, mean chlorophyll *a* concentration, mean transparency depth, total zooplankton biomass and the life history parameters of the dominant crustaceans during growing season, i.e. from June to November (see Results), were tested with one-way analysis of variance (ANOVA). Multiple comparison was then conducted using Scheffe's method, when ANOVA indicated significant difference among the five years. Correlation analysis was made between annual fish catch of the two planktivorous fishes and mean zooplankton and *Daphnia* biomass in the growing season every year during the study period, in order to evaluate the relationship between two planktivorous fishes and zooplankton.

Results

Water temperature increased at the surface in May and thermal stratification was established from June to November every year during the study period (Fig. 1A). The thermocline developed at 10-20 m in June to August and shifted downward to 30 m by November. The lake water was completely isothermal from January to April. Water temperature varied from 3 to 25˚C in the epilimnion, while it was relatively stable, < 6˚C, at deeper than 40 m throughout the study period. Year-to-year variation of the mean water temperature above 30 m depth was small and not significantly different among the five years (Table 2). Transparency depth varied seasonally from 5 to 20 m (Fig. 1B). It tended to be shallower in spring and autumn than in summer and winter. It exceeded 20 m in June before 1994, but

after that it never reached 18 m, though it tended to increase in June every year. Mean transparency depth during the stratification period, therefore, was > 13 m in 1992 and 1993, but decreased to ca. 10 m after 1994 (Table 2). Consequently, euphotic zone also varied seasonally, being 15-30 m in spring and autumn, and up to 60 m in summer and winter.

Mean chlorophyll *a* concentrations throughout the water column were relatively stable with low level at 0.2-1.0 µg l^{-1} during the study period, although the mean concentrations in the euphotic zone more fluctuated and increased up to 2.7 µg l^{-1} in 1995 (Fig. 2A). Chlorophyll *a* concentrations were relatively higher above 50 m during the stratification period, while homogeneous during the mixing period every year (Fig. 2B). In 1995, when the extreme high values were recorded, it was restricted above 30 m. A large year-to-year variation of the chlorophyll *a* concentration in the euphotic zone was found during the stratification period, and it was significantly higher in 1995 and 1996 than before 1994 (Table 2).

In Lake Toya, five cladoceran (*Daphnia longispina, D. galeata, Eubosmina longispina, Bosmina longirostris* and *Holopedium gibberum*) and single copepod (*Cyclops* cf. *sibiricus*) species were dominant zooplankton in biomass during the study period. *E. longispina* and *C.* cf. *sibiricus* were formerly identified as *Bosmina coregoni* (Makino *et al.* 1996) and *Cyclops strenuus* (Makino and Ban 1998) or *Cyclops* sp. (Makino and Ban 2000), respectively. Tanaka (2000) reexamined specimens collected from several lakes and ponds in Hokkaido and emphasized that all the specimens previously identified as *B. coregoni* in Japan should be referred as *E. longispina*. Einsle (1996) suggested that distribution of *C. strenuus* was restricted in Europe, and recent taxonomic studies for Japanese cyclopoids showed that *C.* cf. *sibiricus* would be more appropriate nomenclature for the copepod formerly identified as *C. strenuus* in Japan (Ishida 2002a, b).

The biomass of these six species accounted for mostly 100 % of total zooplankton biomass (Fig. 3). Other cladocerans and rotifers were very scarce and do not contribute the biomass. The zooplankton biomass varied seasonally and annually. It increased in June and decreased after September, being extremely low during winter every year except for the first winter. In 1992 and 1993, it reached up to > 4 g dry-wt m^{-2}. In the first winter, depression of the biomass was not so much, 0.5-1.0 g dry-wt m^{-2}, but became severely after second winter. The biomass dropped down to < 0.1 g dry-wt m^{-2} in the second winter and < 0.05 g dry-wt m^{-2} after third winter. In 1994 to 1996, summer increase was restricted at low level, around 1.0 g dry-wt m^{-2}, being 1/4 of the biomass in 1992. The mean summer biomass after 1994 was significantly lower than in 1992 and 1993 (Table 2). Species composition also changed from year to year (Fig. 3). In 1992 and 1993, the most dominant species was *D. longispina*, followed by *E. longispina* and *C.* cf. *sibiricus*. In 1994, *C.* cf. *sibiricus* and *H. gibberum* dominated, accounting for > 80% of total zooplankton biomass, but *D. longispina* and *E. longispina* did not increase so much. In 1995, *E. longispina* was the most dominant species, accounting for mostly 100% of the zooplankton biomass, but other cladocerans and copepod did not increase. *B. longirostris* never been found until September 1995, but increased in June 1996, being most dominant zooplankton during the summer season. These results indicate that the year-to-year variation of the zooplankton biomass in Lake Toya depends on population size and succession of the each dominant species.

C. cf. *sibiricus* gradually increased in number from 1992 to 1993, but declined in 1994, then keeping very low levels of < 0.5 ind. l^{-1} after 1995 (Fig. 4). In contrast, egg ratio of this copepod showed similar seasonal trend every year and nearly same values of annual maximum in summer (ca. 0.5 eggs $female^{-1}$) except for that in 1997, when the egg ratio exceeded 1 egg $female^{-1}$. The egg ratios during summer season were not significantly

different among first four years between 1992 and 1995, being significantly higher in 1997 (Table 2). *D. longispina* increased in summer of 1992 and 1993, reached up to > 6 ind. l^{-1}. However, it did not increase over 0.01 ind. l^{-1} in 1994, and almost disappeared after 1995. The egg ratios varied seasonally and were significantly higher in 1994 and 1995 rather than in 1992 and 1993 during the summer season (Table 2). *E. longispina* also increased in summer every year until 1995, but thereafter disappeared. The egg ratio seasonally fluctuated and slightly increased after 1994 (see also Table 2). *B. longirostris* was never found until June 1995 but increased after September 1995, reached maximum of 19.2 ind. l^{-1} in July 1996. *D. galeata* was also never found until June 1996, but slightly increased in November 1996. *H. gibberum* regularly increased once a year, not reaching by 1 ind. l^{-1}, though the time varied from year to year.

In *C.* cf. *sibiricus*, seasonal pattern of the birth rates, which increased in summer but decreased in winter, was similar in each year (Fig. 5). The mean values during the summer season were almost the same every years from 1992 to 1995 and 2.5 times higher in 1996 (see also Table 2), in spite of declining the population density after 1994 (see Fig. 4). The death rates gradually increased from 1992 to 1996, though there were no significant differences among the years (Table 2) due to large variances. Also in *D. longispina*, both the birth and death rates were higher in 1994 and 1995 than in 1992 and 1993 (Table 2). After 1994, the death rates were frequently greater than the birth rates (Fig. 5). In *E. longispina*, the birth and death rates fluctuated but balanced until 1995, except for winter to spring in 1994 when it disappeared from the water column (see Fig. 4). Although no significant difference of the mean death rates during the summer season was found among the five years, the death rates outstripped the birth rates in late summer in 1995 to spring in 1996 (Fig. 5), and *E. longispina* thereafter declined. In the remaining three species, *B. longirostris, D. galeata* and

H. gibberum, the birth and death rates balanced throughout the period when the animals occurred in the water column, although the former two species occurred after 1995 (Fig. 5). These results suggest that year-to-year variation of the three dominant species, *C.* cf. *sibiricus*, *D. longispina* and *E. longispina*, is related to the death rates but not to the birth rates throughout the study period.

Annual catch of both pond smelt (*Hypomesus transpacificus nipponensis*) and lacustrine sockeye salmon (*Oncorhynchus nerka*) varied from year to year throughout the study period (Fig. 6). The annual catch of the two fishes was large in 1992 and 1993, but severely declined after 1994. Number of release for pond smelt and sockeye salmon also decreased from year to year, because of becoming less catch of adult females from which the eggs were obtained. Finally, no release was made for pond smelt in 1996. The annual catch of the two fishes considerably depended on average zooplankton biomass during summer season, especially *Daphnia* biomass (Fig. 7).

Discussion

In Lake Toya, zooplankton biomass showed year-to-year variation during the study period, and this variation was related to fluctuation of the biomass of the three dominant species, *Cyclops* cf. *sibiricus*, *Daphnia longispina* and *Eubosmina longispina*. According to the analysis of the population dynamics, annual variation in abundance of these three crustaceans depends on the death rate but not the birth rate. Both the chlorophyll *a* concentration and birth rate of the three crustaceans after 1994, that is low zooplankton biomass years, were the same as or the higher levels than those before 1993. These imply that phytoplankton as food does not seem to be limited amount for reproduction of them even in the low zooplankton biomass years and that the death rate is not related to food shortage.

Recent studies demonstrate that food quality also affect life history traits of zooplankton (Gulati and DeMott 1997). Elemental composition and lipid content of food particles play an important role for growth and reproduction of the grazers such as micro-crustaceans, but such a food quality influences species-specific. Daphnids have lower N:P ratio than copepods and bosminids do (Andersen and Hessen 1991, Hessen and Lyche 1991), and therefore demand more phosphorus (Urabe and Watanabe 1992, Elser and Urabe 1999), being more susceptible to phosphorus limited environments. Although we did not measure both nitrogen and phosphorus of the seston in the lake, total nitrogen: total phosphorus (TN:TP) ratio previously reported in Lake Toya (ca. 50, Hokkaido Research Institute for Environmental Pollution 1990) is greater than body N:P ratio of daphnids previously measured in European lakes (14-26 in Hessen and Lyche 1991). However, reproductive potential of all the three dominant crustaceans, *C.* cf. *sibiricus*, *E. longispina* and *D. longispina*, was the stable during the present study or rather higher in the low zooplankton biomass years. TN:TP ratio is not appropriate indicator for low phosphorus resource environment, but sestonic carbon: phosphorus (C:P) ratio in the lake may not exceed above the threshold for daphnid population growth (Urabe and Watanabe 1992). The food quality, therefore, did not affect their reproduction, and could not explain the annual variation of the abundance of the dominant crustaceans in Lake Toya.

Many previous studies demonstrate that planktivorous fish affects abundance and community structure of zooplankton through the size-selective predation (e.g. Brooks and Dodson 1965). Planktivorous fish is mostly visual oriented predator and selects a large and conspicuous prey (Zaret 1980). It has been shown that accidental introduction of alewife (*Alosa pseudoharengus*), which is exclusive planktivore, shifted the species composition of the zooplankton from large ones to small ones in Connecticut lakes (Brooks and Dodson

1965). Early works for role of fish predation on zooplankton communities generalize that the size of dominant zooplankton preys decreases with increasing fish densities (Brooks and Dodson 1965, Hall *et al.* 1970).

In Lake Toya, two planktivorous fishes, pond smelt and sockeye salmon, artificially introduced every year for the sake of commercial fisheries. In the present study, zooplankton biomass decreased from year to year, and the species composition varied annually. The dominant species succeeded from year to year; large species such as *D. longispina* (maximum body length, 1.9 mm) firstly declined, medium sized *C.* cf. *sibiricus* (maximum body length, 1.2 mm) secondly and small sized *E. longispina* (maximum body length, 0.9 mm) thirdly. Finally, after 1996 the smallest species of *Bosmina longirostris* (maximum body length, 0.6 mm) replaced *E. longispina*. Analyzing the stomach contents of the two fishes showed that the both fishes fed on the large preys, such as *D. longispina* and *C.* cf. *sibiricus*, during 1992 to 1993 when the zooplankton biomass was high, while switched to the smaller prey such as *B. longirostris*, *E. longispina* and benthic gammarids or fish larvae after 1994 when the large crustaceans declined (Makino 1998, Sakano 1999, Sakano *et al.* in prep.). These may imply that predation by such both planktivorous fishes plays an important role for eliminating the large crustaceans from the water column during the present study.

On the other hand, positive correlation between the annual catch of the two fishes and zooplankton biomass was found in the study period, though negative correlation between the biomass of zooplankton and planktivorous fish is more likely. In a minnow-dominated Canadian Shield, it has been shown that *Daphnia* failed to increase in spite of collapse of the minnow population by introduction of piscivorous northern pike (Elser *et al.* 1998). This failure to daphnid increase was explained by poor food quality as high sestonic C:P ratio for growth and reproduction of *Daphnia*. In Lake Toya, however, both food quantity and quality

does not seem to influence reproduction of the dominant crustaceans, as we mentioned above. In the present study, such conflicting results is considered to be related to fishing regulation for a gill net used by fishermen. In Lake Toya, fishermen have to use a > 50 mm-mesh size of the gill net for sockeye salmon and > 20 mm-mesh for pond smelt. Therefore, fishes smaller than this regulation are not caught. Juvenile sockeye and age 0 pond smelt are never caught with such mesh-size of the gill net. Our previous report in 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.* 2001). Weight-specific growth rate of sockeye salmon estimated using back-calculated length with scale radius also decreased with decreasing zooplankton biomass until 1995 (Sakano *et al.* 2001). These evidences suggest that lower annual catch of these fishes in the low zooplankton biomass years than in the high zooplankton biomass years may be attributed to lowering the growth rate of the fishes due to food shortage.

The weight-specific growth rate of sockeye salmon in the second and third year classes also decreased with decreasing zooplankton biomass from 1992 to 1995, but thereafter tended to increase (Sakano *et al.* 2001). The older aged sockeye salmon ate unknown fish larvae and young pond smelts rather than zooplankton in low zooplankton biomass years, and larger individuals ate more fish preys (Sakano *et al.* 2001, Sakano *et al.* in prep.). This diet shift from zooplankton to fish may be considered to be caused by not only decreasing the large crustaceans but also increasing the larval and young fishes, mostly pond smelts, because of recovering the growth rate of the older aged sockeye salmon.

Body size of young-of-the-year (YOY) pond smelt estimated using back-calculated length with otolith does not decline even in the low zooplankton biomass years, although that of age 1 pond smelt declined, suggesting enough amount of food items for the YOY pond

smelt but not for the age 1 (Sakano *et al.* 2001). It has been shown that the pond smelt larvae feeds on rotifers and small crustaceans such as *Bosmina* spp. in Lake Suwa (Yamagishi 1974), and small zooplankton species, such as *E. longispina* and *B. longirostris*, occurred at relatively large number even in the low zooplankton biomass years in Lake Toya. Whereas the age 1 pond smelt has been shown to prefer larger preys, such as *D. longispina* and *C.* cf. *sibiricus* in Lake Toya (Yoshida, unpublished data). Furthermore, number of release is three order higher in pond smelt than in sockeye salmon every year. These evidences imply that YOY pond smelt could survive even in the low zooplankton biomass years as much as in the high zooplankton biomass years and be more important predator for crustacean zooplankton in Lake Toya. Sporadic increase in relatively large *Daphnia galeata* in winter 1996, when no release of pond smelt due to no catch of the adult, supports this idea.

Bioenergetic model of fish growth in several lakes and oceans shows that younger fishes 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 herring (*Clupea harengus*) is also more important planktivore than the yearling in Baltic Sea (Rudstam *et al.* 1992). Arrhenius and Hansson (1993) estimated that larval and YOY herrings accounted for 45% of total consumption of zooplankton by herrings in Baltic Sea. In Lake Toya, neither juvenile sockeye salmon nor YOY pond smelt are caught by fisherman's gill net as described above. Increasing YOY pond smelt due to uncertain reason is considered to result in declining the zooplankton biomass and subsequently inhibiting to grow up as large body size of both sockeye salmon and pond smelt as it can be caught with fisherman's gill net. These uncaught small fishes might join the population in next year as planktivore.

In conclusion, large annual variation of zooplankton biomass depends on their death

rate rather than birth rate, and the death rate is considered to be derived from predation by small fishes, such as YOY pond smelt and smaller young sockeye salmon that could not be caught with fisherman's gill nets in the previous years. These evidences suggest that excessively artificial introduction of planktivorous fish in oligotrophic lake such as Lake Toya may limit zooplankton production, and subsequently reduce growth rate of the fish. This negative feed-back probably enhances lowering the annual fish catch.

Acknowledgments

This study was partially supported with Grant for Environmental Research Projects of the Sumitomo Foundation for SB. We thanks member of Plankton Laboratory, Hokkaido University, for assistance of the samplings.

References

Andersen, T. and Hessen, D.O. 1991. Carbon, nitrogen, and phosphorus content of freshwater zooplankton. Limnol. Oceanogr. **36**: 807-814.

Arrhenius, F. and Hansson, S. 1993. Food consumption of larval, young and adult herring and sprat in the Baltic Sea. Mar. Ecol. Prog. Ser., **96**: 125-137.

Bottrell, H.H., Duncan, A., Gliwigz, Z.M., Grygierek, E., Herzig, A., Hillbright-Ilkowska, A., Kurasawa, H., Larsson, P. and Weglenska, T. 1976. A review of some problems in zooplankton production studies. Norw. J. Zool., **24**: 419-456.

Brooks, J.L. and Dodson, S.I. 1965. Predation, body size, and composition of plankton. The effect of a marine planktivore on lake plankton illustrates theory of size, competition, and predation. Science, **150**: 28-35.

Carpenter, S.R. and Kitchell, J.F. 1993. The Trophic Cascade in Lakes. Cambridge University

Press, Cambridge.

Edmondson, W.T. 1968. A graphical model for evaluating the use of the egg ratio for measuring birth and death rates. Oecologia, **1**: 1-37.

Einsle, U. 1996. Copepoda: Cyclopoida. Genera Cyclops, Megacyclops, Acanthocyclops. SPB Academic Publishing, Amsterdam.

Elser, J.J., Chrzanowski, T.H., Sterner, R.W. and Mills, K.H. 1998. Stoichiometric constraints on food-web dynamics: A whole-lake experiment on the Calandian Shield. Ecosystems, **1**: 120-036.

Elser, J.J. and Urabe, J. 1999. The stoichiometry of consumer-driven nutrient recycling: theory, observations, and consequences. Ecology, **80**: 735-751.

Gulati, R.D. and DeMott, W. (*Editors*) 1997. The role of food quality for zooplankton. Freshwater Biol., **38**: 445-771.

Hall, D.J., Cooper, W.E. and Werner, E.E. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. Limnol. Oceanogr. **15**: 829-928.

Hessen, D.O. and Lyche, A. 1991. Inter- and intraspecific variations in zooplankton element composition. Arch. Hydrobiol., **121**: 355-363.

Hewett, S.W. and Stewart, D.J. 1989. Zooplanktivory by alewives in Lake Michigan: Ontogenetic, seasonal, and historical patterns. Trans. Am. Fish. Soc., **118**: 581-596.

Hokkaido Research Institute for Environmental Pollution 1990. Lakes and Marshes in Hokkaido. (In Japanese). Hokkaido Research Institute for Environmental Pollution, Sapporo.

Ishida, T. 2002a. Aspects on the planktonic copepods of inland waters. (In Japanese). Rikusui Seibutugaku-ho, **17**: 1-7.

Ishida, T. 2002b. Illustrated fauna of the freshwater cyclopoid copepods of Japan. (In Japanese). Bull. Biogeogr. Soc. Japan, **57**: 37-106.

Kerfoot, W.C. and Sih, A. 1987. Predation. Direct and Indirect Impacts on Aquatic Communities. University Press of New England, Hanover and London.

Kimmerer, W.J. and McKinnon, A.D. 1986. Glutaraldehyde fixation biomass of preserved plankton. J. Plankton Res., **8**: 1003-1008.

Lampert, W. 1985. Food limitation and the structure of zooplankton communities. Advances in Limnology. E. Schweizerbart'sche Verlagsbuchhandlung (Nagele u. Obermiller), Stuttgart.

Ligtvoet, W. and Witte, F. 1991. Perturbation through predator introduction: Effects on the food web and fish yields in Lake Victoria (East Africa). *In* Terrestrial and Aquatic Ecosystems: Perturbation and Recovery. *Edited by* O. Ravera. Ellis Horwood, New York. pp. 263-268.

Makino, W. 1998. Ecological studies on free-living cyclopoid copepod, *Cyclops strenuus*, in Lake Toya. (In Japanese). PhD thesis, Hokkaido University, Hakodate.

Makino, W. and Ban, S. 1998. Diel changes in vertical overlap between *Cyclops strenuus* (Copepoda; Cyclopoida) and its prey in oligotrophic Lake Toya, Hokaido, Japan. J. Mar. Syst., **15**: 139-148.

Makino, W. and Ban, S. 2000. Response of life history traits to food conditions in a cyclopoid copepod from an oligotrophic environment. Limnol. Oceanogr. **45**: 396-407.

Makino, W., Haruna, H. and Ban, S. 1996. Diel vertical migration and feeding rhythm of *Daphnia longispina* and *Bosmina coregoni* in Lake Toya, Hokkaido, Japan. Hydrobiologia, **337**: 133-143.

Motoda, S. 1950. Hokkaido kosho-shi. (In Japanese). Sci. Rep. Hokkaido Fish Hatchery, **5**:

1-96.

Nakano, A. and Ban, S. 2003. Microbial communities in oligotrophic Lake Toya, Japan. Limnology,

Ohno, I. and Ando, K. 1932. Toya-ko no masu ni tsuite. (In Japanese). Sake-masu Iho, **4**: 5-9.

Paine, R.T. 1966. Food web complexity and species diversity. Am. Nat., **100**: 65-75.

Paine, R.T. 1969. A note on trophic complexity and community stability. Am. Nat., **103**: 91-93.

Paloheimo, J.E. 1974. Calculation of instantaneous birth rate. Limnol. Oceanogr. **19**: 692-694.

Parsons, T.R., Maita, Y. and Lalli, C.M. 1984. A manual of chemical and biological methods for seawater analysis. Pergamon Press, Oxford.

Rudstam, L.G., Hansson, S., Johansson, S. and Larsson, U. 1992. Dynamics of planktivory in a coastal area of the northern Baltic Sea. Mar. Ecol. Prog. Ser., **80**: 159-173.

Sakano, H. 1999. Effects of interaction with congeneric species on growth of sockeye salmon, *Oncorhynchus nerka*, in Lake Toya. (In Japanese). PhD thesis, Hokkaido University, Hakodate.

Sakano, H., Ban, S., Kaeriyama, M., Ueda, H. and Shimazaki, K. 2001. The interaction between lacustrine sockeye salmon (*Oncorhynchus nerka*) and pond smelt (*Hypomesus nipponensis*) in relation to the decline of zooplankton biomass in Lake Toya, northern Japan. Verh. Internat. Verein. Limnol. **27**: 3881-3885.

Sakano, H., Kaeriyama, M., Ueda, H., Sakurai, Y. and Shimazaki, K. 1996. Growth pattern and age determination by scales of lacustrine sockeye salmon in Lake Toya. (In Japanese). Sci. Rep. Hokkaido Salmon Hatchery, **50**: 125-138.

Shiraishi, Y. 1960. The fisheries biology and population dynamics of pond-smelt, *Hypomesus*

olidus (Pallas). (In Japanese). Bull. Freshwater Fish. Res. Lab., **10**: 1-263.

Sterner, R.W. 1989. The role of grazers in phytoplankton succession. *In* Plankton Ecology. *Edited by* U. Sommer. Springer-Verlag, Berlin. pp. 107-170.

Sterner, R.W. and Elser, J.J. 2002. Ecological Stoichiometry. Princeton University Press, Princeton and Oxford.

Takamura, N., Mikami, H., Mizutani, H. and Nagasaki, M. 1999. Did a drastic change in fish species from kokanee to pond smelt decrease the secci disc transparency in the oligotrophic Lake Towada, Japan? Arch. Hydrobiol., **144**: 283-304.

Tanaka, S. 2000. A taxonomic revision of Japanese Bosminidae (Crustacea, Cladocera). (In Japanese). Toyamashi Kagaku-bunka-senta Kenkyu houkoku, **23**: 109-125.

Tokui, T. 1960. Studies on the kokanee salmon. III. Fluctuations in abundance of the spawning kokanee salmon of Lake Shikotsu, Hokkaido, Japan. (In Japanese). Sci. Rep. Hokkaido Fish Hatchery, **15**: 7-16.

Tokui, T. 1964. Studies on the kokanee salmon V. Transplantations of the kokanee salmon in Japan. (In Japanese). Sci. Rep. Hokkaido Fish Hatchery, **18**: 73-90.

Urabe, J. and Watanabe, Y. 1992. Possibility of N or P limitation for planktonic cladocerans: an experimental test. Limnol. Oceanogr. **37**: 244-251.

Wetzel, R.G. 2001. Limnology, Lake and river ecosystems. the 3rd edition. Academic Press, San Diego.

Yamagishi, H. 1974. On the ecology of the youngs of the pond smelt, *Hypomesus olidus* (Pallas) in Lake Suwa. Appendix. The relation of the progress of eutrophication in the lake to the annual catches of the pond smelt. (In Japanese). Japanese Journal of Ecology, **24**: 10-21.

Zaret, T.M. 1980. Predation and Freshwater Communities. Yale University Press, New

Haven and London.

Figure legends

Fig. 1. Vertical profile of water temperature (A) and seasonal changes of transparency depth (B) at St. 1 in Lake Toya from May 1992 to May 1997. Shaded area represents stratification period from June to November (see text).

Fig. 2. Seasonal changes of chlorophyll *a* concentration throughout a 0-120 m water column (black line) and within a euphotic zone (gray line) (A), and vertical distribution of chlorophyll *a* concentration (B) at St. 1 in Lake Toya from May 1992 to May 1997.

Fig. 3. Seasonal changes of zooplankton biomass at St. 1 in Lake Toya from May 1992 to May 1997.

Fig. 4. Seasonal changes of abundance (solid lines) and egg ratio (circles) in six dominant crustaceans at St. 1 in Lake Toya from May 1992 to May 1997.

Fig. 5. Seasonal changes of birth and death rates in six dominant crustaceans at St. 1 in Lake Toya from May 1992 to May 1997.

Fig. 6. Annual catch and release of lacustrine sockeye salmon (*Oncorhynchus nerka*) and pond smelt (*Hypomesus transpacificus nipponensis*) in Lake Toya from 1992 to 1996.

Fig. 7. Relationship between annual catch of two fishes (lacustrine sockeye salmon and pond smelt) and mean biomass of total crustaceans (A) and *Daphnia* spp. (B) in the summer season from June to November.

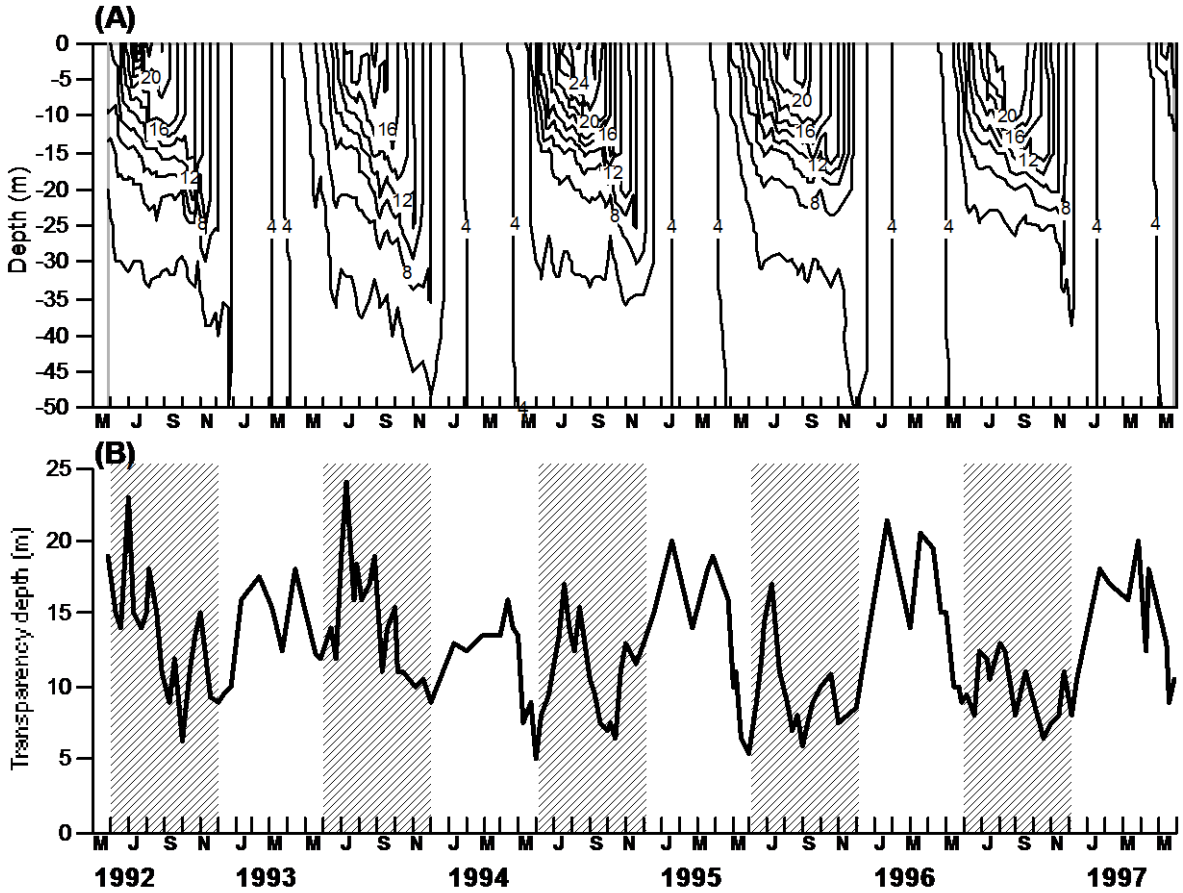

(A)
Depth (m)
0
-5
-10
-15
-20
-25
-30
-35
-40
-45
-50
M J S N J M M J S N J M M J S N J M M J S N J M M J S N J M M
(B)
Transparency depth (m)
25
20
15
10
5
0
1992
1993
1994
1995
1996
1997

Fig. 1

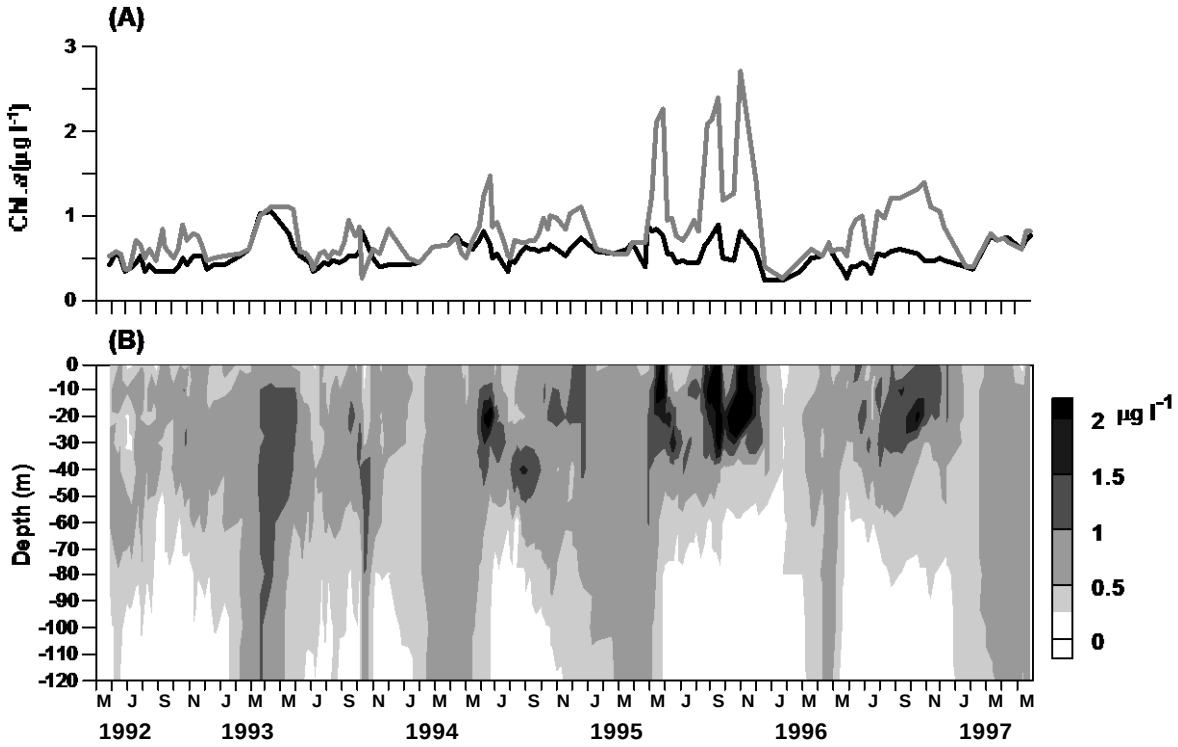

(A)
Chl.a (µg l-1)
3
2
1
0
(B)
Depth (m)
0
-10
-20
-30
-40
-50
-60
-70
-80
-90
-100
-110
-120
M J S N J M M J S N J M M J S N J M M J S N J M M J S N J M M
1992
1993
1994
1995
1996
1997
2 µg l-1
1.5
1
0.5
0

Fig. 2

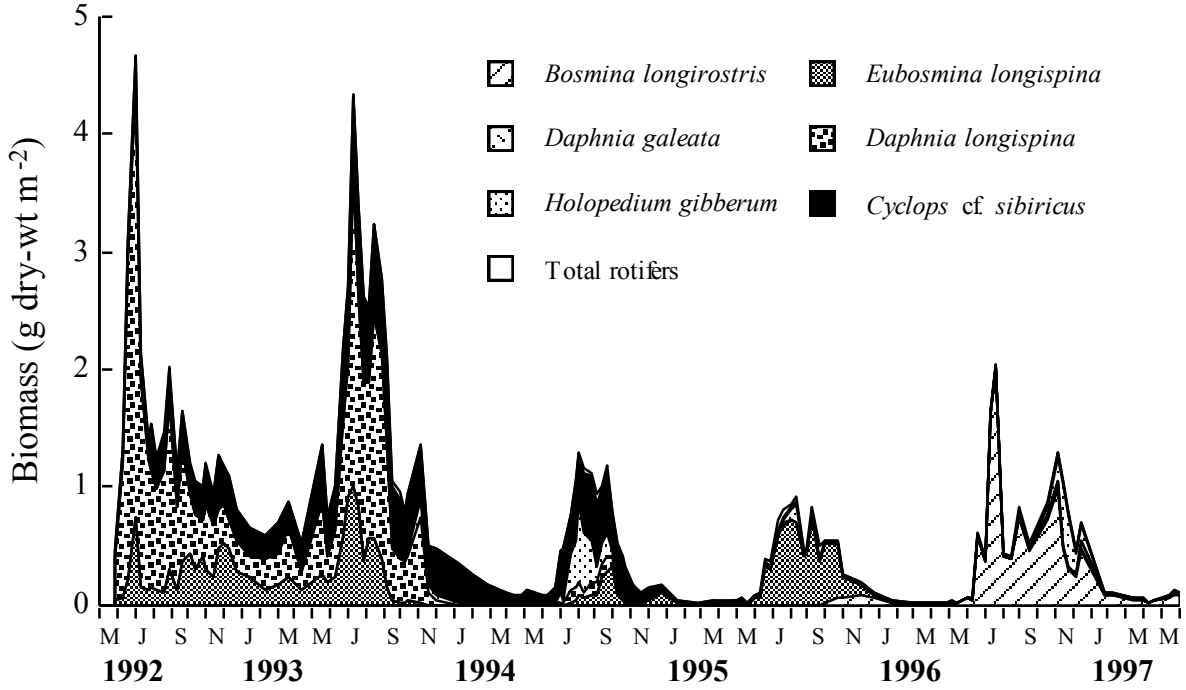

Biomass (g dry-wt m-2)
0
1
2
3
4
5
Bosmina longirostris
Daphnia galeata
Holopedium gibberum
Total rotifers
Eubosmina longispina
Daphnia longispina
Cyclops cf. sibiricus
M J S N J M M J S N J M M J S N J M M J S N J M M J S N J M M
1992
1993
1994
1995
1996
1997

Fig. 3

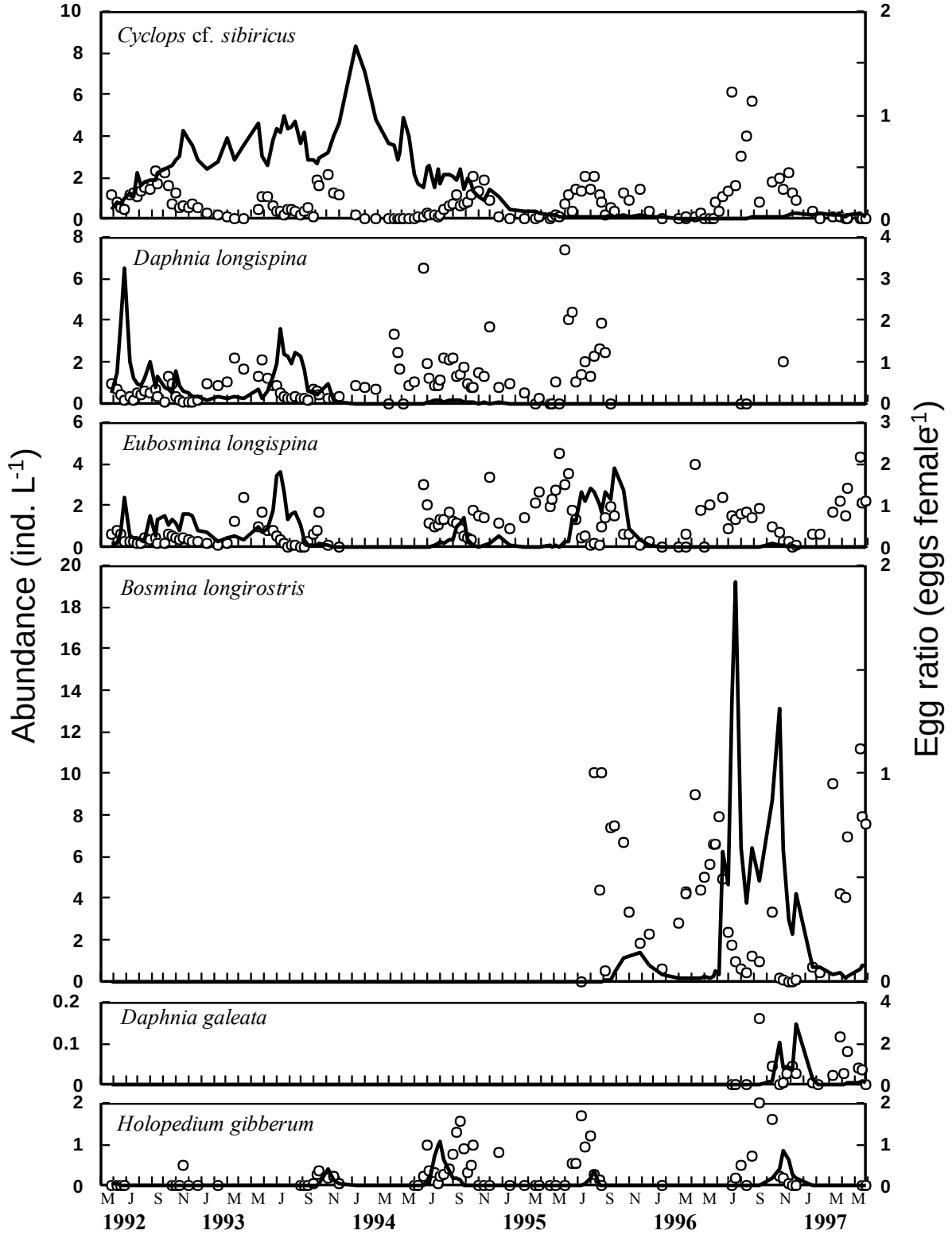

Cyclops cf. sibiricus
Daphnia longispina
Eubosmina longispina
Bosmina longirostris
Daphnia galeata
Holopedium gibberum
Abundance (ind. L-1)
Egg ratio (eggs female-1)
M J S N J M M J S N J M M J S N J M M J S N J M M J S N J M M
1992
1993
1994
1995
1996
1997

Fig. 4

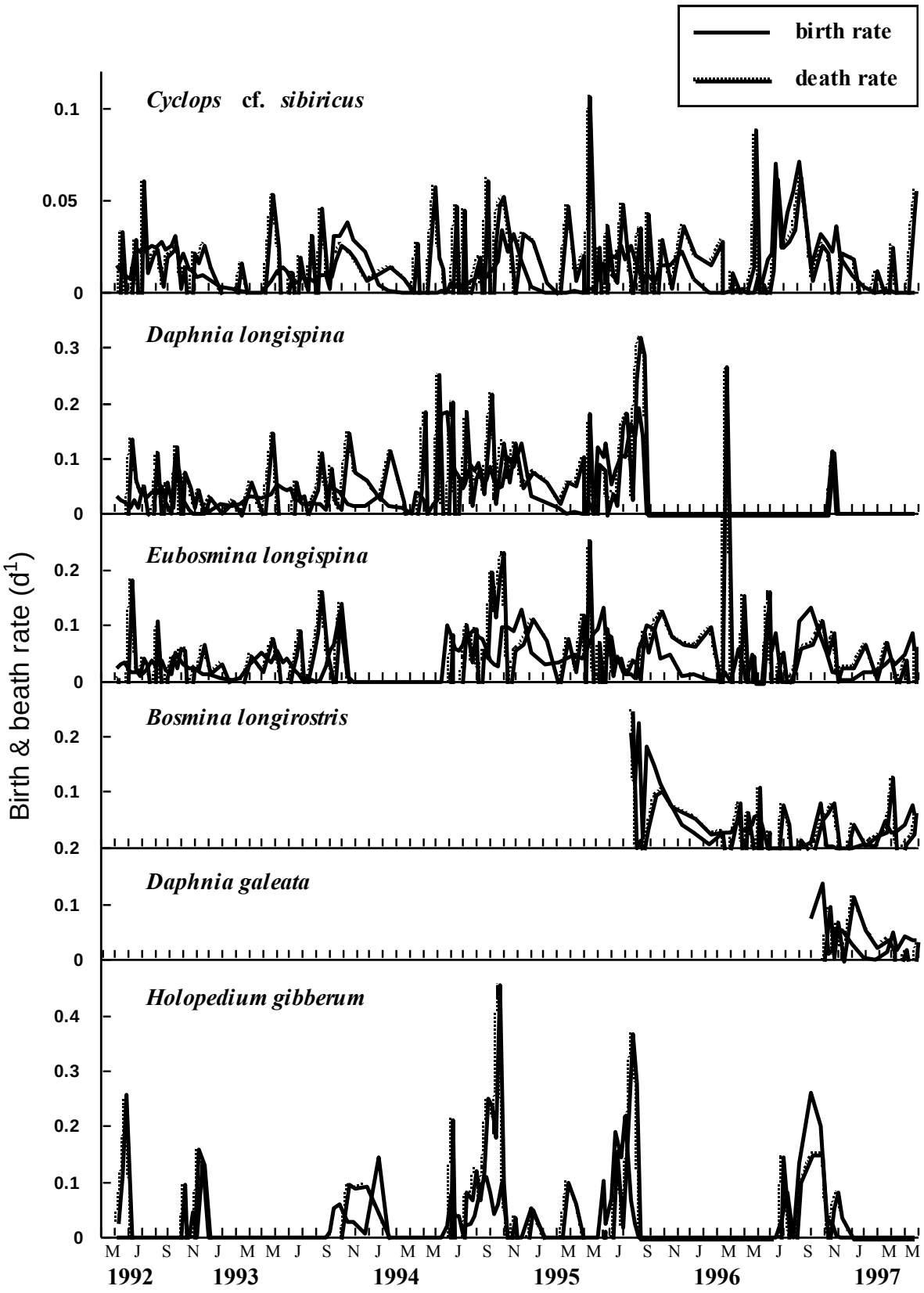

birth rate
death rate
Cyclops cf. sibiricus
Daphnia longispina
Eubosmina longispina
Bosmina longirostris
Daphnia galeata
Holopedium gibberum
Birth & beath rate (d-1)
0.1
0.05
0
0.3
0.2
0.1
0
0.2
0.1
0
0.2
0.1
0.2
0.1
0
0.4
0.3
0.2
0.1
0
M J S N J M M J S N J M M J S N J M M J S N J M M J S N J M M
1992
1993
1994
1995
1996
1997

Fig. 5

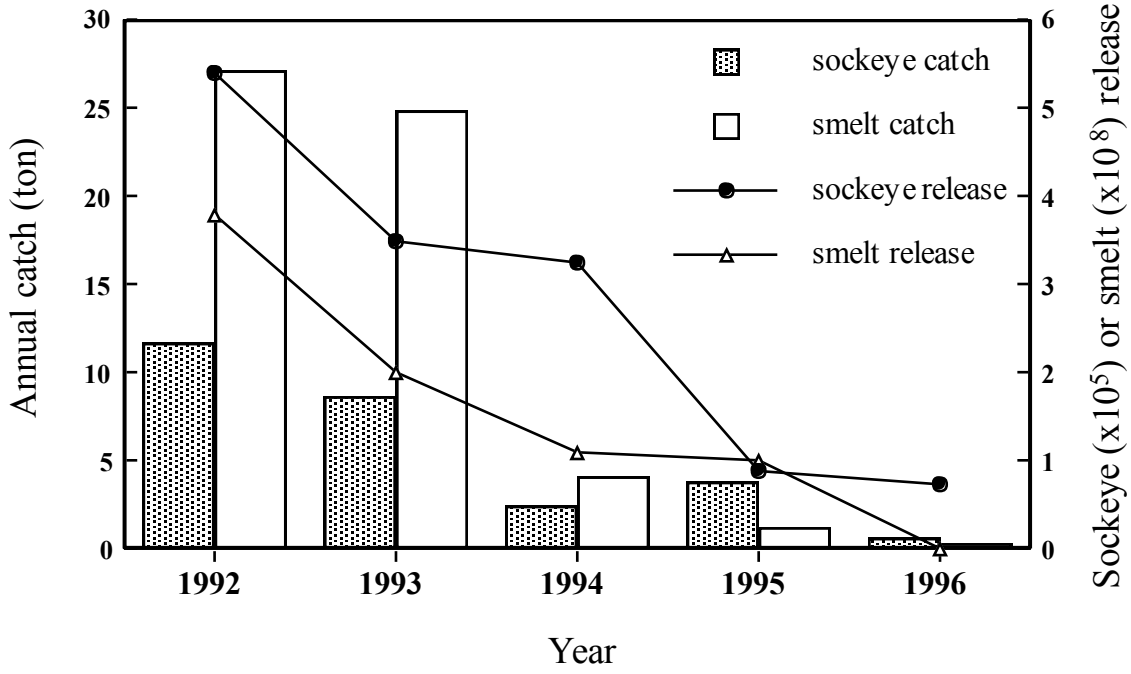

Annual catch (ton)
Sockeye (x10^5) or smelt (x10^8) release
Year
sockeye catch
smelt catch
sockeye release
smelt release
30
25
20
15
10
5
0
6
5
4
3
2
1
0
1992
1993
1994
1995
1996

Fig. 6

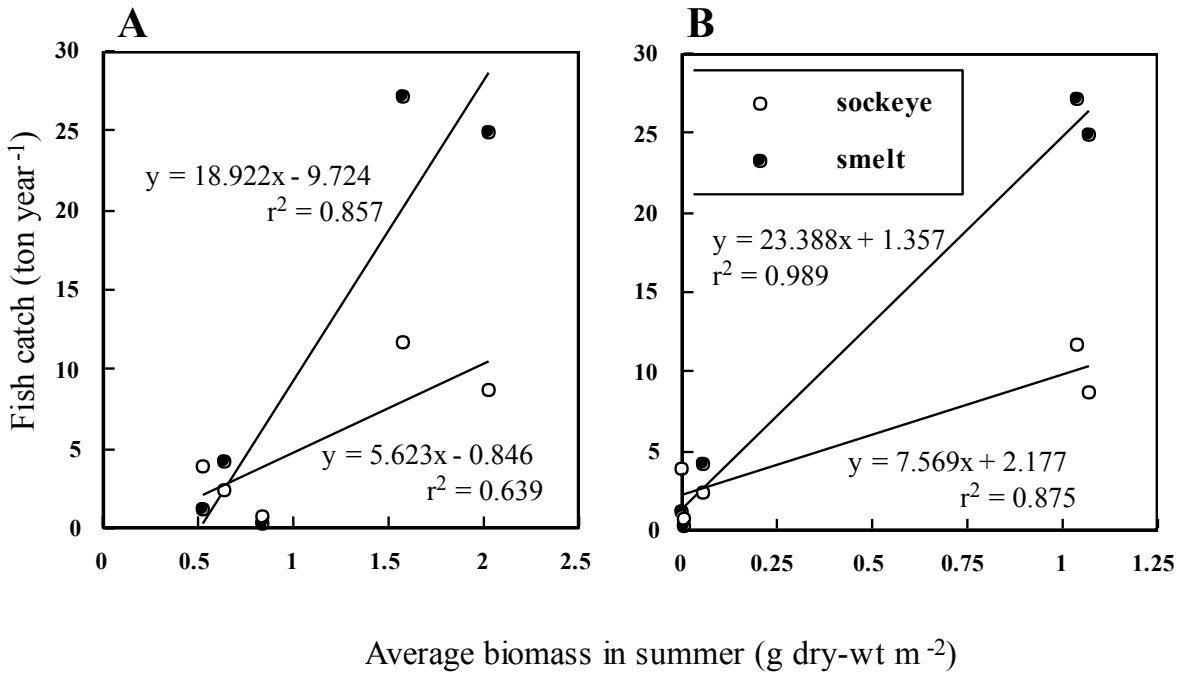

A
B
Fish catch (ton year-1)
y = 18.922x - 9.724
r2 = 0.857
y = 5.623x - 0.846
r2 = 0.639
y = 23.388x + 1.357
r2 = 0.989
y = 7.569x + 2.177
r2 = 0.875
sockeye
smelt
Average biomass in summer (g dry-wt m-2)

Fig. 7

Table 1. Equation of length-weight relationship in five cladocerans and body weight of each developmental stage in *Cyclops* cf. *sibiricus* occurred in Lake Toya. W and L represent body dry weight (μg) and length (μm) of each species.

Species name	Sex & stage	Equation
Daphnia longispina		W=exp(2.9254lnL-18.5939)
Daphnia galeata		W=exp(2.9254lnL-18.5939)
Bosmina longirostris		W=exp[3.0395ln(L/1000)+3.0896] [1)]
Eubosmina longispina		W=exp(3.1568lnL-18.6735)
Holopedium gibberum		W=exp(2.7598lnL-16.7818)
Cyclops cf. *sibiricus*	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

1) used an equation from Bottrel *et al*. (1976)

Table 2. Results of ANOVA and mean water temperature above 30 m depth, mean chlorophyll *a* concentration in the euphotic zone, mean transparency depth, total zooplankton biomass, and life history parameters (egg ratio, birth and death rates) of *Cyclops* cf. *sibiricus*, *Daphnia longispina* and *Eubosmina longispina* during the growing season (from June to November at St. 1 in Lake Toya among the five years studyed.

		year					ANOVA			Post hoc test*
Parameter	Sp. name	1992	1993	1994	1995	1996	*df*	*F*	p	by Scheffe's method
temperature		11.4 (1.9)	11.9 (1.6)	12.3 (1.9)	11.9 (1.8)	10.7 (1.9)	4, 77	1.69	0.161	
chlorophyll		0.61 (0.15)	0.58 (0.17)	0.85 (0.24)	1.39 (0.66)	1 (0.25)	4,77	15.38	< 0.0001	95 96 94 92 93
transparency depth		13.2 (3.8)	14.9 (4.0)	11.1 (3.0)	9.8 (3.0)	10 (2.2)	4, 76	6.95	< 0.0001	93 92 94 95 96
zooplankton biomass		1.58 (0.93)	2.03 (1.12)	0.64 (0.42)	0.53 (0.25)	0.84 (0.55)	4,77	12.7	< 0.0001	93 92 96 94 95
life histry parameters										
egg ratio	*C.* cf *sibiricus*	0.240 (0.110)	0.150 (0.130)	0.150 (0.120)	0.220 (0.120)	0.480 (0.360)	4, 77	8.29	< 0.0001	96 92 95 93 94
	D. longispina	0.230 (0.180)	0.220 (0.150)	1.210 (1.550)	1.260 (0.600)	---	3, 60	6.74	0.0005	95 94 92 93
	E. longispina	0.190 (0.090)	0.210 (0.230)	0.950 (1.170)	0.510 (0.480)	0.620 (0.330)	4, 75	4.46	0.0027	94 96 95 93 92
birth rate	*C.* cf *sibiricus*	0.019 (0.007)	0.014 (0.011)	0.011 (0.010)	0.016 (0.007)	0.034 (0.021)	4, 77	8.3	< 0.0001	96 92 95 93 94
	D. longispina	0.031 (0.027)	0.030 (0.014)	0.088 (0.040)	0.122 (0.040)	---	3, 60	27.67	< 0.0001	95 94 92 93
	E. longispina	0.025 (0.010)	0.028 (0.033)	0.075 (0.027)	0.055 (0.038)	0.074 (0.043)	4, 71	9.64	< 0.0001	94 96 95 93 92
death rate	*C.* cf *sibiricus*	0.009 (0.028)	0.011 (0.017)	0.011 (0.038)	0.013 (0.029)	0.020 (0.027)	4, 71	0.252	0.908	
	D. longispina	0.029 (0.064)	0.040 (0.049)	0.072 (0.085)	0.139 (0.119)	---	3, 60	4.84	0.004	95 94 93 92
	E. longispina	0.010 (0.079)	0.041 (0.063)	0.053 (0.102)	0.051 (0.045)	0.048 (0.083)	4, 70	0.93	0.45	

*) Significant differences are not scored by the same line at $p<0.05$.