

Primary Research Paper

Swimming behaviour of *Chironomus acerbiphilus* larvae in Lake Katanuma

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Abstract

We conducted a seasonal survey of the swimming behaviour of *Chironomus acerbiphilus* larvae in volcanic Lake Katanuma from April 1998 to December 2001. Swimming *C. acerbiphilus* density was much higher than other chironomid species in lakes. All *C. acerbiphilus* larvae (1st through 4th instars) swam, but the earlier instars (especially the 1st) had the greatest densities and fluctuations. First instars were never found in the benthic population. This result indicates that the 1st-instar larvae are planktonic. Low water temperature (below about 10 °C) resulted in the seasonal disappearance of swimming chironomid larvae. Chemical factors – oxygen depletion or presence of hydrogen sulfide – also restricted the distribution of swimming and benthic larvae. Larvae were distributed only in the oxygen-rich part of the lake bottom and swam only in the oxygen-rich layer of the water column. The density of older swimming *C. acerbiphilus* (3rd and 4th instars) tended to increase with increasing benthic larval densities. The chemical stress of oxygen depletion or presence of hydrogen sulfide during holomixis within and after the stratification period leads to conspicuous swimming behaviour of benthic *C. acerbiphilus* larvae. Almost all *C. acerbiphilus* larvae died on this occasion.

Introduction

Chironomid larvae are some of the most abundance benthic invertebrates in lentic waters such as lakes, ponds, and reservoirs. They often are part of the first consumer trophic level in aquatic ecosystems. Chironomid larvae are mostly herbivorous and/or detritivorous and are the major prey of predaceous macrofauna. Although chironomid larvae are generally sedentary benthos, swimming chironomid larvae are sometimes observed. Some species of chironomid larvae are planktonic in the 1st instar (Oliver, 1971; Davies, 1976a), and some show swimming behaviour even in later stages (Moon, 1940; Berg, 1950; Oliver, 1971; Davies, 1976a). Therefore, studies of chironomid larvae must include research on swimming behaviour if they are to address their dynamics, completely in an aquatic ecosystem.

There have been many reports of population dynamics of benthic chironomid larvae. However, few have described the population dynamics of swimming chironomid larvae or their swimming behaviour. Especially few are reports concerned with fluctuations in the density of swimming larvae, especially in lentic waters. In this study, we investigated the swimming behaviour of *Chironomus acerbiphilus* Tokunaga larvae in the strongly acidic Lake Katanuma, Japan.

Throughout Japan and the Kurile Islands, there are many acidic volcanic lakes. Lake Katanuma was once called the most acidic lake (pH 1.4) in the world (Yoshimura, 1934). Now the lake water has pH 2.2, on average, owing to high concentrations of sulfate produced by the oxidation of hydrogen sulfide, which emanates from fumaroles on the lake bottom.

No zooplanktonic or nektonic organisms exist in Lake Katanuma, but high densities of chironomid larvae (*C. acerbiphilus* Tokunaga) are found in sediment. *C. acerbiphilus* is notable as a species that survives in highly acidic, as well as hot, springs (Yamamoto, 1986). In Lake Katanuma, it is the only macrofaunal species distributed across the whole lake from the coastal to profundal zones, although several species of insect larvae have been found in shoreline sediments of the lake (Fujimatsu, 1938).

Chironomus acerbiphilus larvae build a tube around them and live in the substratum of Lake Katanuma. They are herbivorous and mainly eat benthic diatoms (Doi et al., 2001). Swimming is suggested to be characteristic of *C. acerbiphilus* larvae (Fukuhara, personal communication).

Yamagishi & Fukuhara (1971) suggested that swimming *Chironomus plumosus* (Linnaeus) larvae were easily preyed and comprised a major food source for pond smelts in Lake Suwa. The effects of predation by carnivorous fishes can make it difficult to study swimming behaviour of chironomid larvae in a lake. In Lake Katanuma, however, no carnivores that feed on chironomids are present. Therefore in Lake Katanuma we could investigate the swimming behaviour of

C. acerbiphilus larvae in the absence of carnivore effects. This seasonal survey of swimming behaviour of *C. acerbiphilus* larvae in Lake Katanuma was carried out to clarify the dynamics of its swimming behaviour in relation to environmental factors.

Study area

Lake Katanuma is a volcanic lake in northwestern Miyagi prefecture, Japan (38 °44' N, 140 °43' E; 306 m above sea level; surface area 1.24×10^5 m²; volume 6.89×10^5 m³; maximum depth 21 m) (Fig. 1). It is highly acidic (pH 2.0–2.2) and has no inflowing or outflowing streams. Sulfur-containing gases (such as hydrogen sulfide) and heat are supplied from fumaroles on the bottom of the lake (Satake, 1975; Sato, 1995).

Lake Katanuma is dimictic and covered by ice from January to mid-March. Inverse stratification occurs under the ice cover. After turnover in March, weak stratification develops with a thermocline at a depth of 3–5 m. Stratification is generally observed from April to late August. During the stratification period, oxygen-rich water with no hydrogen sulfide can be detected in the

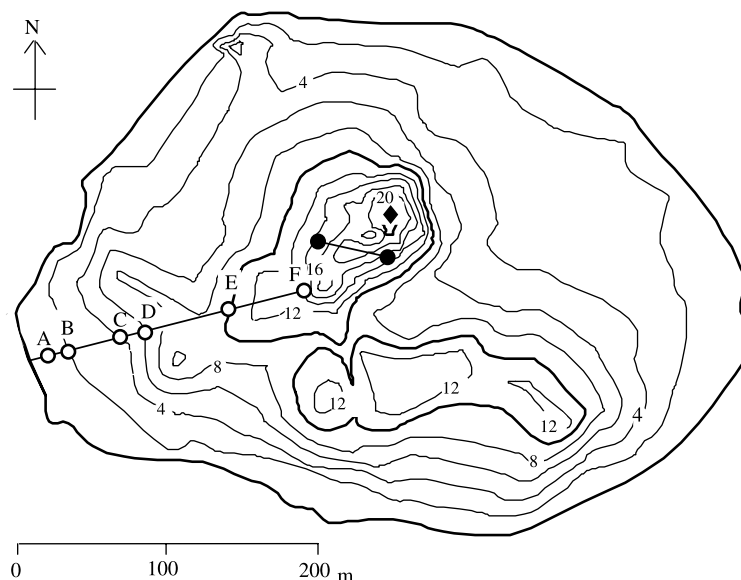


Figure 1. Bathymetric map of Lake Katanuma showing (○) sampling stations (A, B, C, D, E, and F) for swimming larvae collected by net and benthic larvae at 1, 2, 4, 6, 10, and 15 m depths, respectively. (●) Ends of the transect along which sediment traps were set to collect swimming larvae. (◆) Sampling point for water samples to determine water quality (20 m depth).

epilimnion, whereas in the hypolimnion oxygen is depleted and hydrogen sulfide accumulates.

The circulation period is from late August to December. At the start of circulation period, the entire water column is anoxic and in some years this condition persists for more than a few weeks. Then, oxygen returns to the water column and hydrogen sulfide disappears, completely. However, the dissolved oxygen condition is only 30–70% saturated during the circulation period.

In Lake Katanuma, occasional short-term holomixis is observed during unusually cold weather, and even during summer, when stratification is weak (little difference in water temperature between the epilimnion and hypolimnion) because of heat supplied by volcanic activity (Doi et al., 2001). On such occasions, oxygen depletion increases and hydrogen sulfide becomes detectable throughout the water column. The frequency and duration of short-term holomixis depends on interannual variations in weather conditions and volcanic heat flux (Shikano et al., 2004).

Materials and methods

Sampling was carried out biweekly from 1998 to 2001. Swimming and benthic *C. acerbiphilus*

larvae were collected from stations at different depths along a transect from the southeast edge to the center of the lake (Fig. 1). In 1998 and 1999, sampling was carried out by turns at all six stations (A, B, C, D, E, and F) and two stations (B and E). In 2000 and 2001, stations B, C, and E only were sampled.

Benthic larvae were collected using an Ekman-Birge grab ($0.15 \times 0.15 \text{ m}^2$). In 1998 and 1999, we collected three replicates at stations A, C, D, and F and five replicates at stations B and E. In 2000 and 2001, we collected five replicates at stations B, C, and E. Each grab sample was preserved in a collection bag without sieving.

Swimming larvae were collected by towing a net (opening diameter 30 cm, mesh size 0.075 mm) from the lake bottom to the surface. Five replicates were collected at all stations. In addition, to estimate the swimming depth of larvae, sediment traps (funnels 20 cm in diameter) were set near the center of the lake (Figs. 1 and 2) at six different depths (2, 4, 6, 8, and 10 m in 1998; these plus 0.5 m in 1999–2001). The traps were set for 4 or 5 days every 2 weeks from April to December.

All samples including grab samples were fixed in 4% neutralized formalin solutions immediately after collection. In the laboratory, the benthic larvae samples were washed onto a sieve (0.130 mm

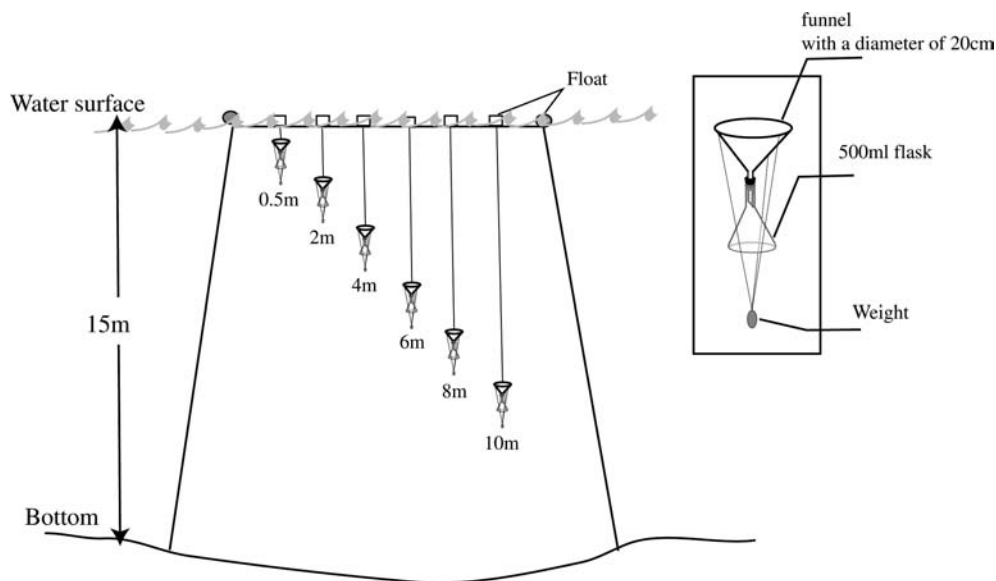


Figure 2. Sediment traps for collection of swimming larvae. Traps were set at six different depths (0.5, 2, 4, 6, 8, and 10 m).

mesh) and then removed. Benthic and swimming larvae were sorted under a stereomicroscope separated into four instars on the basis of head capsule width and preserved in 70% ethanol. In 2001, larval body length was measured with an eyepiece micrometer under the microscope at 8× magnification.

Water temperature was measured at the center of the lake with a U-22 water quality monitor (Horiba, Kyoto, Japan). At the same site, water samples were collected at seven depths (0, 1, 2, 4, 6, 10, and 15 m) with a Van Dorn water sampler (3 l). They were used to measure dissolved oxygen by Winkler's method. Water samples were transferred to BOD bottles and fixed immediately after collection in the Van Dorn samples.

Results

Benthic larvae comprised more than 80% of the total annual mean density of *Chironomus acerbiphilus*, although the percentage varied among years (Table 1).

Swimming larvae collected by nets included all four instars, but no pupae were collected. The 1st and 2nd instars comprised more than 40% of swimming larvae. In contrast, benthic larvae collected in grab samples were mainly 3rd and 4th instars, usually more than 90%; 1st-instar larvae were never found in benthic samples. Samples collected in sediment traps were mainly 4th instars.

Our results also showed percentages of benthic larvae to swimming larvae collected by net were much higher in 3rd and 4th instars than 1st and 2nd instars. This indicates that 1st and 2nd instar larvae tended to swim more than 3rd and 4th instar larvae.

Maximum and minimum body lengths of the benthic larvae and swimming larvae were 15.2 mm and 2.8 mm and 15.2 mm and 0.8 mm, respectively (Fig. 3). The minimum length of swimming larvae was equivalent to the size of just-hatched larvae.

Swimming larvae collected by net and trap showed similar seasonal variations in each of the 4 years (Fig. 4). No swimming larvae were collected from December to early April each year, when water temperature was below 10 °C. However, swimming larvae were found throughout the

warmer season (from April to November), but decreased in November, when water temperature dropped to between 10 and 15 °C (Fig. 4).

The seasonal pattern of occurrence of swimming larvae differed each year (Fig. 4). In 1998, swimming behaviour was observed continuously from April to November except in mid June. In 1999, swimming larvae were not collected until end of June, but thereafter through November fair numbers of swimming larvae were collected. In 2000, swimming larvae were only collected from May through August and in November. That year, September and October corresponded to the start of the circulation period. In 2001, swimming larvae were not collected until June; the early circulation period was from mid August through September.

When swimming larvae were not collected, the densities of benthic larvae were very low. On 24 July 1998, however, many swimming larvae but very few benthic larvae were collected.

We compared densities of swimming and benthic 3rd- and 4th-instar larvae which might be more influenced by over-crowding than smaller larvae (Fig. 5). Mean benthic larval densities were calculated only from stations in oxygen-rich zones (stations A and B above the thermocline during the stratification period; all stations during the circulation period), but the density of swimming larvae was determined by averaging across all stations, since swimming larvae can disperse easily throughout the lake. During the stratification period, swimming and benthic larval densities were significantly correlated (Fig. 5). The best fit of the regression was not exponential but linear. While during the circulation period, the correlation was not significant.

Swimming larvae comprised all four instars in all months (Fig. 6). First-instar larvae were most abundant overall (except on 24 July 1998 when most swimming larvae sampled were 3rd and 4th instars), but showed considerable fluctuation in number from month to month.

Figure 7 shows the number of swimming larvae collected in traps set at different depths in 1998. The number of swimming larvae collected corresponded with dissolved oxygen concentrations, such that during the stratification period, *C. acerbiphilus* larvae were collected only at depths above the thermocline. On 12 June, after

Table 1. Annual mean densities of benthic and swimming larvae (collected by net and trap) by instar

Instar	Swimming: net (ind. m ⁻²)					Benthic (ind. m ⁻²)					Swimming: trap (ind. trap ⁻¹ day ⁻¹)					
	1998	1999	2000	2001	1998	1999	2000	2001	1998	1999	2000	2001	1998	1999	2000	2001
1st	74.4 (32.4)	208.5(73.6)	36.9 (46.2)	15.9(24.4)	0(0)	0(0)	0(0)	0(0)	0.1 (0.4)	1.7 (1.5)	0.4 (1.4)	0.1 (1.1)	0.1 (0.4)	1.7 (1.5)	0.4 (1.4)	0.1 (1.1)
2nd	15.8 (6.9)	40.8 (14.4)	10.0 (12.5)	16.0 (24.6)	38.9 (2.5)	16.6 (1.5)	4.6 (0.7)	20.1 (1.7)	0.5 (1.3)	3.2 (2.8)	0.4 (1.3)	0.1 (1.9)	0.5 (1.3)	3.2 (2.8)	0.4 (1.3)	0.1 (1.9)
3rd	47.3 (20.6)	18.7 (6.6)	12.0 (15.0)	19.4 (29.8)	487.3 (31.3)	133.6 (12.1)	94.4 (14.5)	363.3 (30.6)	3.7 (10.6)	5.1 (9.4)	2.1 (7.6)	0.8 (11.1)	3.7 (10.6)	5.1 (9.4)	2.1 (7.6)	0.8 (11.1)
4th	92.0 (40.1)	15.3 (5.4)	20.9 (26.2)	13.8 (21.2)	1029.2 (66.1)	953.9 (86.4)	552.1 (84.8)	799.9 (67.5)	30.4 (87.8)	46.6 (86.3)	25.0 (89.7)	6.3 (86.0)	30.4 (87.8)	46.6 (86.3)	25.0 (89.7)	6.3 (86.0)
Total	229.5 (100.0)	283.3 (100.0)	79.9 (100.0)	65.2 (100.0)	1557.0 (100.0)	1104.1 (100.0)	651.1 (100.0)	1183.3 (100.0)	34.7 (100.0)	54.0 (100.0)	27.9 (100.0)	7.3 (100.0)	34.7 (100.0)	54.0 (100.0)	27.9 (100.0)	7.3 (100.0)

Values in parentheses are proportions of the total sample (%).

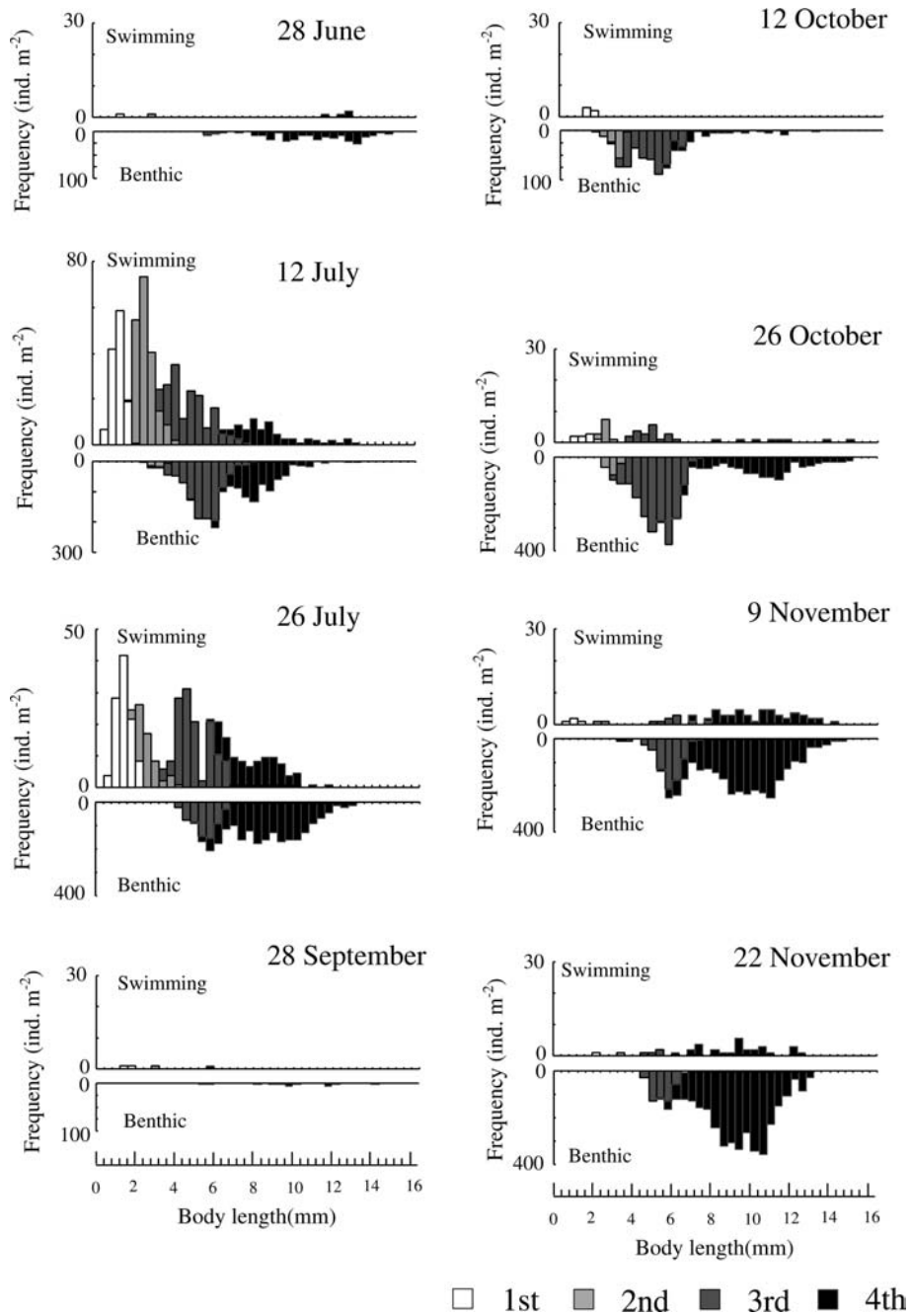


Figure 3. Distribution of body lengths by instar of swimming larvae collected by net and benthic larvae in 2001. No swimming larvae were collected from April to mid June, from August to late September, or in December.

holomixis had started, no dissolved oxygen was detected and no larvae at all were collected. However, on 24 July, short-term holomixis occurred and larvae were collected in the shallowest waters. During the circulation period (from September

to December), swimming larvae were collected throughout the water column. The number of swimming larvae collected tended to decrease with increasing depth during both the stratification and circulation periods.

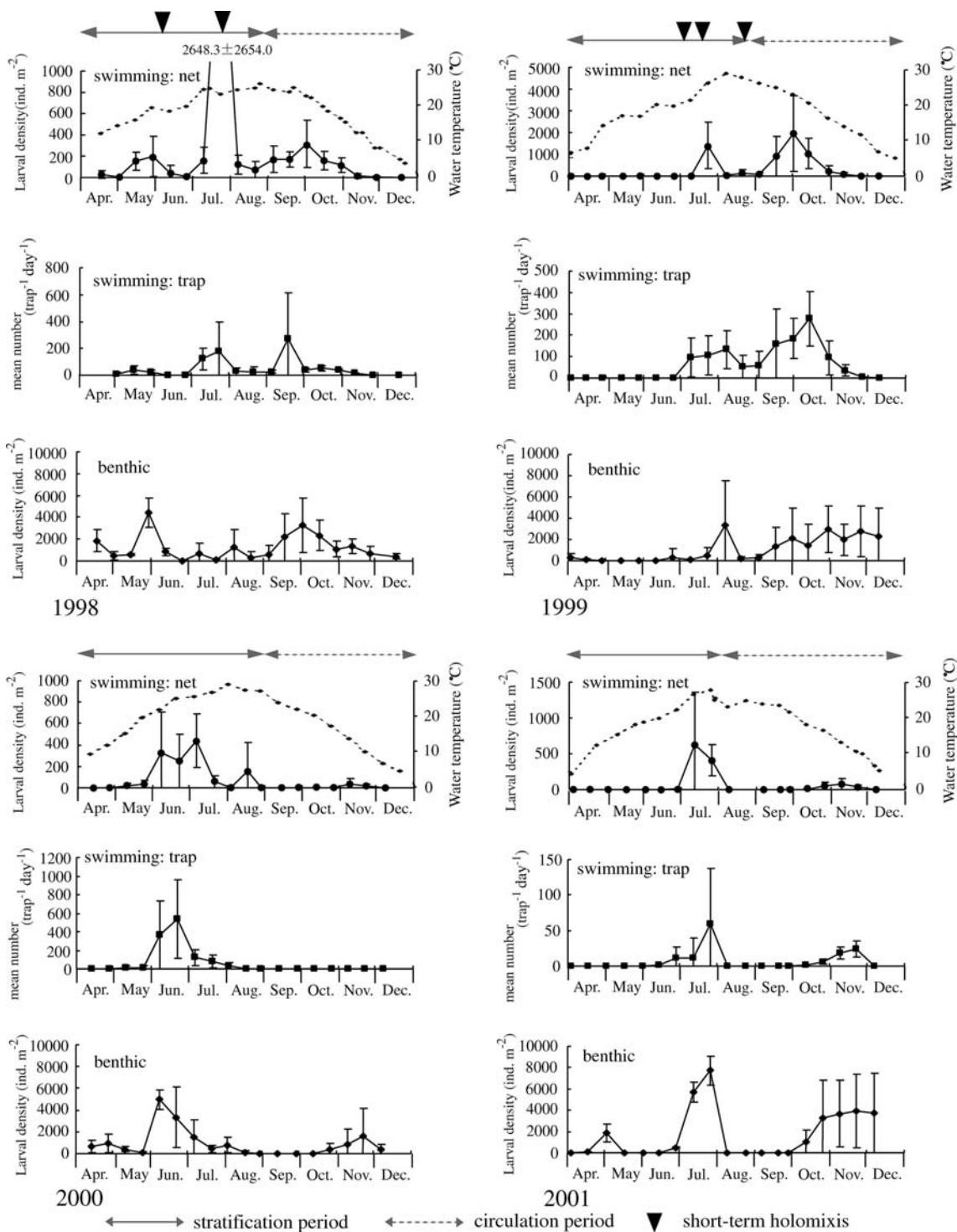


Figure 4. Seasonal changes in mean density of swimming larvae collected by nets (top panels), mean number of larvae collected per trap per day (middle panels), and mean density of benthic larvae (bottom panels) in 1998, 1999, 2000, and 2001. Seasonal changes in surface water temperature at the center of Lake Katunuma are shown by the dashed lines. Vertical bars show ± 1 S.D. For swimming larvae collected by traps and benthic larvae, we used the samples collected from oxygen-rich areas only.

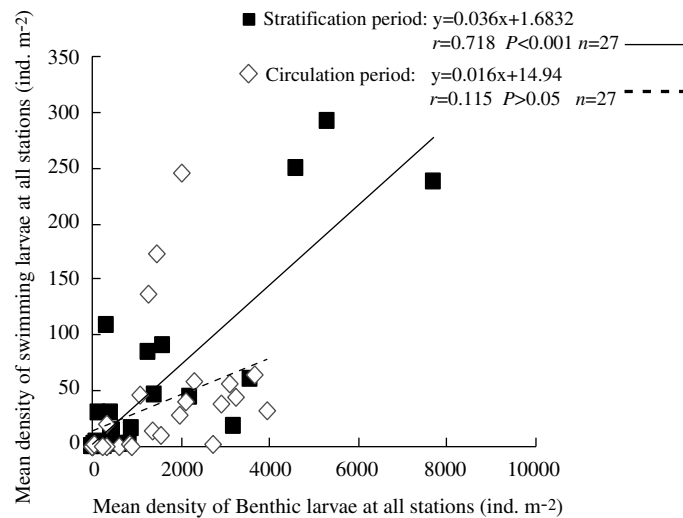


Figure 5. Correlation between mean densities per unit area of swimming and benthic 3rd- and 4th-instar larvae. Mean benthic larval density was calculated from stations A and B during the stratification period and from all stations during the circulation period. We used data from May to November and excluded data from the period during which benthic larvae were not collected. p Values are for the treatment effect (Pearson's correlation coefficient).

Horizontal distribution of swimming and benthic chironomid larvae showed some patterns in Lake Katanuma (Fig. 8). During the stratification period (10 July and 7 August), swimming larval densities in the littoral zone (stations A and B) tended to be lower than those at deeper stations (stations C, D, E, and F). During the circulation period (2 and 30 October), densities of swimming larvae tended to increase with increasing depth. On 12 June and 5 September, shortly after the circulation period started, the density of swimming larvae at station A (the shallowest station) was higher than that at the other stations. Benthic chironomid larvae were mainly distributed above the thermocline (at stations A and B) during the stratification period. However during the circulation period, benthic larvae were found at all depths.

Discussion

The swimming larvae of *C. acerbiphilus* collected by net tended to be mainly early instars, especially 1st instars, although all four instars were represented (Table 1). First-instar larvae were never found in benthic samples collected by grabs. Some other chironomids (e.g., *Chironomus gregarius*, *Chironomus tentans*, *Tanytarsus dissimilis*) are

planktonic in the 1st instar (Oliver, 1971; Davies, 1976a), and this may be true of *C. acerbiphilus* in Lake Katanuma.

The swimming larvae collected by sediment trap were mainly 3rd and 4th instars. Some researchers have collected swimming chironomid larvae with similar traps. Hirabayashi et al. (1996) collected only late 4th instars of *Phaenopsectra kizakiensis* (Tokunaga) in Lake Kizaki. Davies (1976b) collected mainly older chironomid larvae (e.g., *Chironomus anthracinus*, *Cryptochironomus pararostratus*) in Loch Leven, although all larval stages were represented.

First-instar larvae are hardly ever collected by sediment traps, probably because they swim differently than 3rd- and 4th-instar larvae. The older larvae may be able to swim more actively, resulting in their being trapped more easily.

Egg masses of *C. acerbiphilus* were observed only on hard substrata such as stones and logs in the shallows of the lake, whereas swimming larvae were distributed across much of the lake. First-instar chironomid larvae (*Nilodorum brevibucca*) disperse more uniformly and rapidly than later stages (McLachlan, 1969). In Lake Katanuma, 1st-instar *C. acerbiphilus* larvae might disperse rapidly throughout the lake irrespective of swimming ability. This instar may function as a dispersal phase.

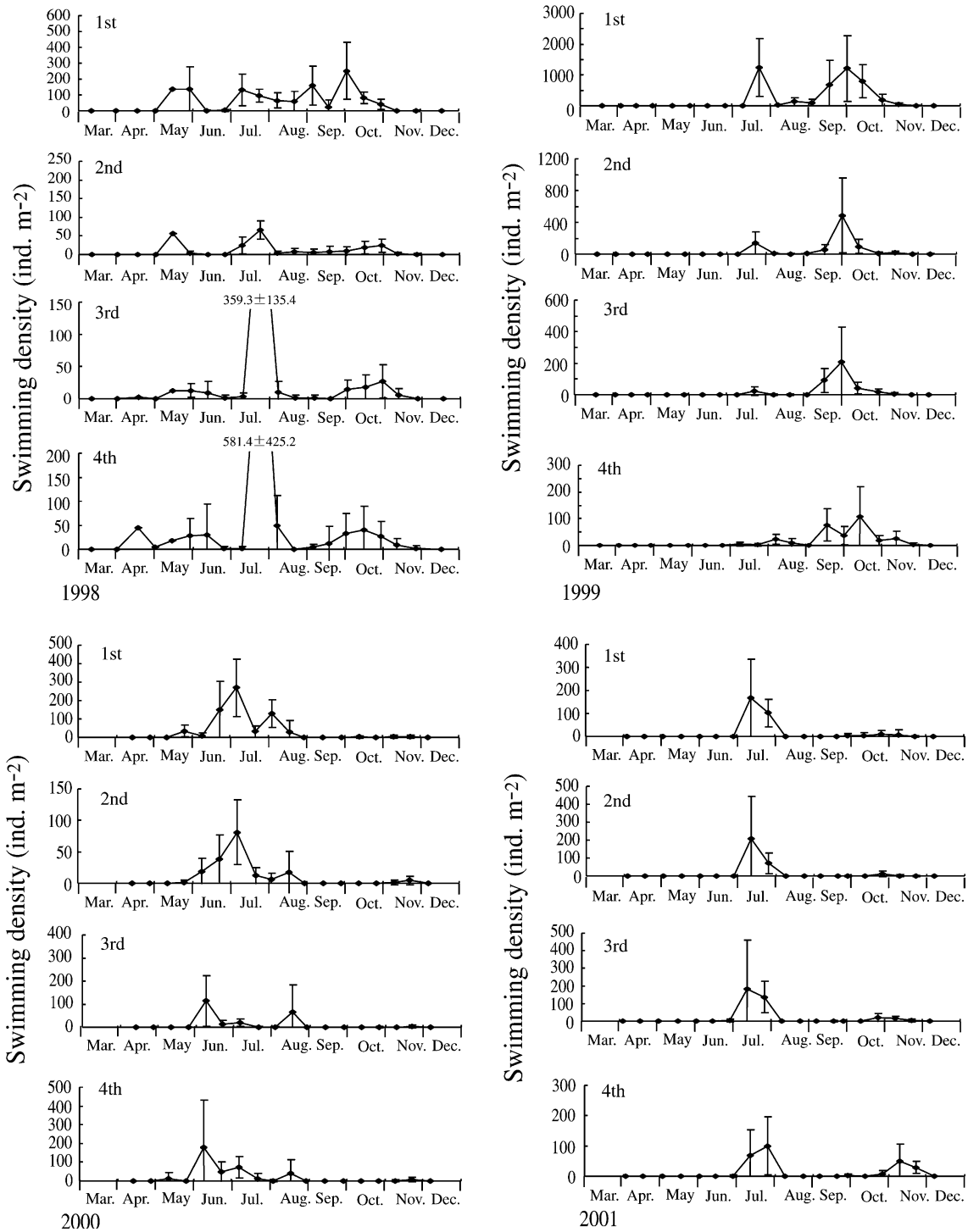


Figure 6. Seasonal changes in mean density of swimming larvae per instar collected by nets. Vertical bars show ± 1 S.D.

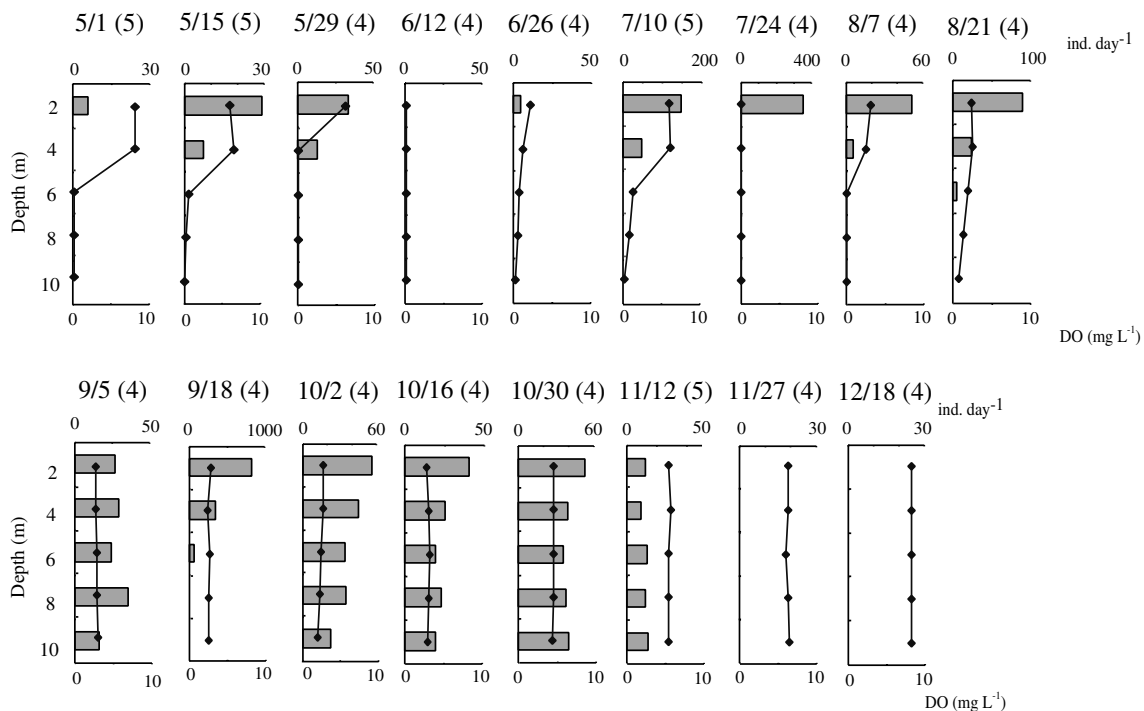


Figure 7. The mean number of swimming larvae collected with traps set at different depths in 1998. The date when traps were set are shown above each panel and the numerals in parentheses show the term (days) traps were set. Solid diamonds show the concentration of dissolved oxygen (DO) on the day traps were set.

C. acerbiphilus larvae in Lake Katanuma seem to have higher tendency of showing swimming behaviour than other chironomid species that live in lentic waters. Yamagishi & Fukuhara (1971) reported that only 63 *Chironomus plumosus* larvae were collected by parallel tow of fish larvae nets from the south edge to the center of Lake Suwa (with an area of 14.45 km²). Davies (1976b) set traps (funnels with a diameter of 20.3 cm) in Loch Leven and collected a maximum of only about 10 chironomid larvae per day. Hirabayashi et al. (1996) set sediment traps (funnels with a diameter of 15 cm) in Lake Kizaki and collected a maximum of only 57 *Phaenopsectra kizakiensis* larvae over 7 days.

In Lake Katanuma, the maximum number of *C. acerbiphilus* larvae collected by nets (vertical tow from bottom to surface) was 287 on 1 October 1999 at station E (when the anomalous 24 July 1998 is not considered). The maximum collected by sediment trap (funnels with a diameter of 20 cm) was 3804 at 0.5 m depth over 4 days (22 to 26 June 2000). Predation is known to one of the reason that restrict swimming behaviour

(Yamagishi & Fukuhara, 1971; Mousavi et al., 2002). In Lake Katanuma, a fishless lake, maybe no predation was one of the reasons of high density swimming.

Physico-chemical factors have a major role in determining the distributions of aquatic organisms. Changes in water chemistry (e.g., decreased dissolved oxygen concentrations, increased metal and insecticide concentrations) are known to affect the behaviour of chironomid larvae, including their swimming behaviour (Gerhardt & Janssen, 1995). According to Hirabayashi et al. (1996), decreased dissolved oxygen concentration in bottom water causes migration into the water of *Phaenopsectra kizakiensis* in Lake Kizaki. Similarly Kornijow (1997) reported that migration of *Chironomus* larvae from bottom sediments is usually stimulated by oxygen depletion in near-bottom water.

Our results of vertical distributions of benthic larvae and swimming larvae collected traps indicate that *C. acerbiphilus* larvae avoid conditions of anoxia and the presence of hydrogen sulfide (Figs. 7

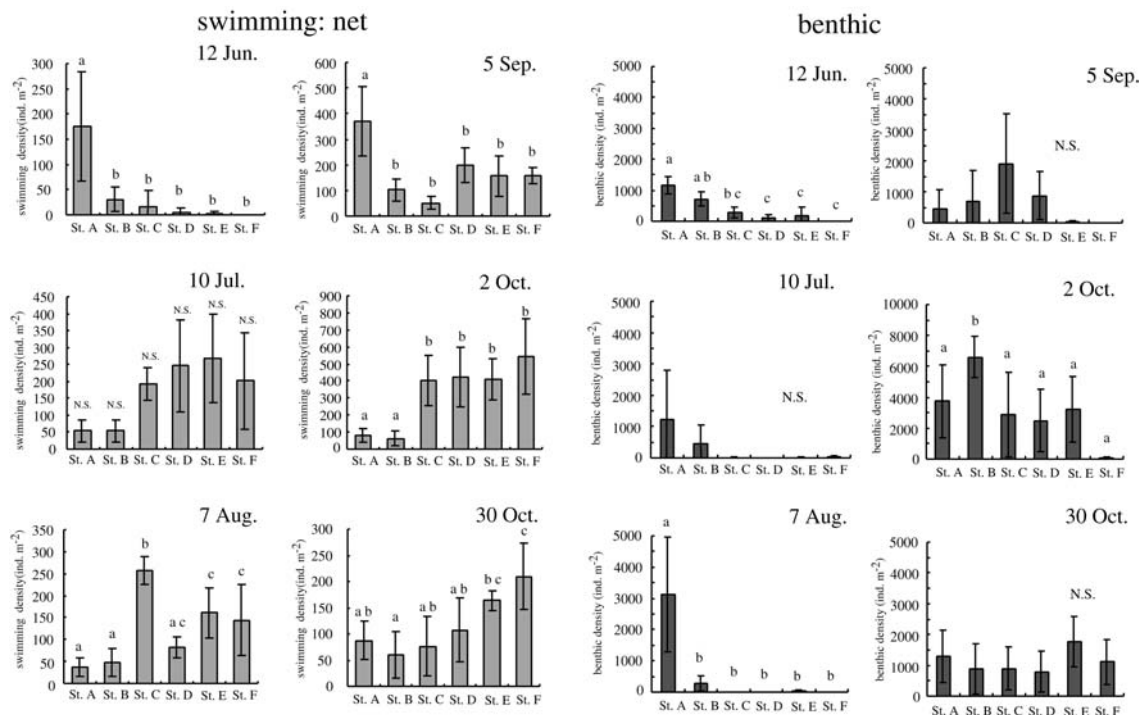


Figure 8. The density of swimming larvae collected by net per unit area (left figure) and the density of benthic larvae (right figure) collected from stations A, B, C, D, E, and F (at 1, 2, 4, 6, 10, and 15 m depths) in 1998. Vertical bars show ± 1 S.D. Different letters indicate significant differences between stations (Bonferroni's multiple comparison, $p < 0.05$). N.S. indicates no significant differences.

and 8). In Lake Katanuma, the whole water column became anoxic during holomixis and on the day holomixis started, we observed disastrous swimming behaviour. Large numbers of swimming larvae were collected in the uppermost water layer despite almost no dissolved oxygen there (Figs. 4, 6, and 7). Almost all benthic chironomid larvae swam out of the sediment to the water surface; the density of swimming larvae in surface water was sometimes so high that the water looked red (Fig. 9a).

Just after the start of each circulation period, swimming larvae were concentrated near the shore (Fig. 8). Dissolved oxygen concentration recovered earlier in the littoral zone than in the pelagic zone because of wave action and shallow water near the shore. We detected slight dissolved oxygen ($2\text{--}3 \text{ mg l}^{-1}$) at the shore when no oxygen at all was detected in the deepest water. *C. acerbiphus* larvae might migrate to the littoral zone to avoid anoxia.

Most *C. acerbiphus* larvae were stranded at the edge of the lake when holomixis occurred. After a few days, numerous dead larvae had accumulated at

the shore (Fig. 9b). As a result, the density of benthic *C. acerbiphus* larvae in Lake Katanuma decreased drastically right after holomixis (Fig. 4). The recovery of benthic larval density seemed to depend on the duration of oxygen depletion. In both 2000 and 2001, hydrogen sulfide gradually accumulated in the hypolimnion during the stratification period (from April to August), because no short-term holomixis occurred (Shikano et al., 2004). Anoxic conditions throughout the water column then persisted for longer than usual (about 2 weeks). In these years, *C. acerbiphus* larvae were scarce for about 2 months after the autumn turnover began.

Horizontal distribution of swimming chironomid larvae showed some patterns in Lake Katanuma. During the circulation period, densities of swimming larvae per unit area tended to increase with increasing depth of station or the volume of oxygen-rich water filtered by the nets (Fig. 7), since the swimming larvae were generally distributed only in oxygen-rich water, at similar densities per unit volume.

Seasonal appearance of *C. acerbiphus* may be affected by water temperature. In Lake Katanuma,

no swimming larvae were collected from December to April when the water temperature was low (Fig. 4), even though benthic larvae (almost all 3rd and 4th instars) inhabited the sediment. In addition, the density of swimming larvae decreased in November whereas that of benthic larvae remained high. Low temperature appears to restrict swimming behaviour.

Other factors may induce the swimming behaviour of *C. acerbiphilus* in Lake Katanuma, because swimming was observed in all instars (except during the period of low water temperature from December to April). The effect of over-crowding in benthic populations may explain the observed swimming behaviour.

In lotic aquatic ecosystems, some aquatic insects have been reported to drift in a density-dependent fashion (Dimond, 1967; Lehmkühl &

Anderson, 1972; Walton et al, 1977; Walton, 1980). When the carrying capacity of a stream bottom has not yet been reached, density and production of benthos may increase without competition; as the population density approaches the carrying capacity, increased competition results in increased drift as a means of population control (Waters, 1966, 1972). In lentic water, overcrowded conditions might also induce swimming behaviour as ways of dispersing to new, vacant habitats.

For 3rd- and 4th-instar larvae, large numbers of swimming larvae tended to be observed when benthic larvae were at high densities (Figs. 4 and 6). This finding suggests that seasonal variations in older swimming larvae also reflect the densities of benthic ones. The relationships between swimming and benthic larval densities showed a significant linear regression during the stratification period

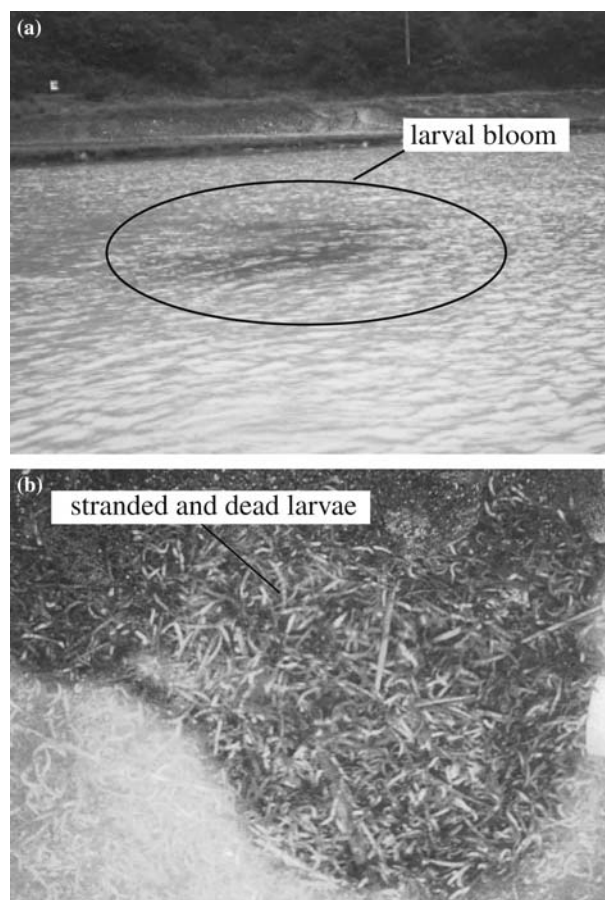


Figure 9. Chironomid larvae during the short-term holomixis on 24 July 1998. (a) The surface of Lake Katanuma is red because of a high density of swimming *C. acerbiphilus* larvae. (b) Dead larvae on the shore after the holomixis.

(Fig. 5). However, even though over-crowding was expected to increase density exponentially (Müller, 1954; Waters, 1966).

As a whole, our results suggested that higher densities of benthic larvae induced higher rates of swimming behaviour. But *C. acerbiphilus* larvae in Lake Katanuma might not be affected in a density-dependent fashion, since the regression between the swimming and benthic larval densities was linear. This regression suggests that a fixed percentage of benthic larvae seemed to swim irrespective of the benthic larval density.

Acknowledgements

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References

- Berg, C. O., 1950. Biology of certain Chironomidae reared from *Potamogeton*. Ecological Monographs 20: 83–101.
- Davies, B. R., 1976a. The dispersal of Chironomidae larvae: A review. Journal of the Entomological Society of Southern Africa 39: 39–62.
- Davies, B. R., 1976b. A trap for capturing planktonic chironomid larvae. Freshwater Biology 6: 373–380.
- Dimond, J. B., 1967. Evidence that drift of stream benthos is density related. Ecology 48: 855–857.
- Doi, H., E. Kikuchi & S. Shikano, 2001. Carbon and nitrogen stable isotope ratios analysis of food sources for *Chironomus acerbiphilus* larvae (Diptera Chironomidae) in strongly acidic Lake Katanuma. Radioisotope 50: 601–611.
- Fujimatsu, K., 1938. On the aquatic organisms found in Lake Katanuma, a very strong acid water lake in Japan. Ecological Review 4: 131–140. In Japanese and English summary.
- Garhardt, A. & L. Janssens, 1995. Behavioural, developmental and morphological responses of *Chironomus* gr. *thummi* larvae (Diptera, Nematocera) to aquatic pollution. Journal of Aquatic Ecosystem Health 4: 205–214.
- Hirabayashi, K., T. Ichimura & H. Hayashi, 1996. Studies on swimming behaviour of *Phaenopsecta kizakiensis* larvae (Diptera Chironomidae) in lake Kizaki, Japan. Japanese Journal of Limnology 57: 99–106.
- Kornijow, R., 1997. The impact of predation by perch on the size-structure of *Chironomus* larvae – the role of vertical distribution of prey in the bottom sediments, and habitat complexity. Hydrobiologia 342–343: 207–213.
- Lehmkuhl, D. M. & N. H. Anderson, 1972. Microdistribution and density as factors affecting the downstream drift of mayflies. Ecology 53: 661–667.
- McLachlan, A. J., 1969. Substrate preferences and invasion behaviour exhibited by larvae of *Nilodorum brevibucca* Freeman (Chironomidae) under experimental conditions. Hydrobiologia 33: 237–249.
- Mousavi, S. K., S. Sandring & P. Amundsen, 2002. Diversity of chironomid assemblages in contrasting subarctic lakes – impact of fish predation and lake size. Archiv für Hydrobiologie 154: 461–484.
- Moon, H. P., 1940. An investigation of the movements of freshwater invertebrate faunas. Journal of Animal Ecology 9: 76–83.
- Müller, K., 1954. Investigations on the organic drift in North Swedish streams. Report of the Institute of Freshwater Research, Drottningholm 35: 133–148.
- Oliver, D. R., 1971. Life history of the Chironomidae. Annual Review of Entomology 16: 211–230.
- Satake, K., 1975. Water temperature in Lake Katanuma. Japanese Journal of Limnology 36: 1–5. In Japanese with English summary.
- Sato, G., 1995. A formation mechanism of water temperature and water quality in the Lake Katanuma in the Narugo volcano. Journal of Japanese Society of Water Environment 18: 829–836. In Japanese with English summary.
- Shikano, S., E. Kikuchi, S. Takagi & H. Doi, 2004. Volcanic heat flux and short-term holomixis during the summer stratification period in a crater lake. Limnology and Oceanography 49: 2287–2292.
- Walton, O. E. Jr, 1980. Invertebrate drift from predator–prey associations. Ecology 61: 1486–1497.
- Walton, O. E. Jr., S. R. Reice & R. W. Andrews, 1977. The effects of density, sediment particle size and velocity on drift of *Acroneuria abnormis*. Oikos 28: 291–298.
- Waters, T. F., 1966. Production rate, population density, and drift of a stream invertebrate. Ecology 47: 595–604.
- Waters, T. F., 1972. The drift of stream insects. Annual Review of Entomology 17: 253–272.
- Yamagishi, H. & H. Fukuhara, 1971. Note on the swimming behaviour of *Chironomus plumosus* larvae in Lake Suwa. Japanese Journal of Ecology 20: 256–257. In Japanese with English summary.
- Yamamoto, M., 1986. Study of the Japanese *Chironomus* inhabiting high acidic water (Diptera, Chironomidae). Kontyu 54: 324–332.
- Yoshimura, S., 1934. The strongest acid Lake Katanuma at Narugo Onsen. Kagaku 4: 498–499. In Japanese.