

Body size of *Holopedium gibberum* under the influence of fish predation in small subarctic lakes

Konstantin Popadin

Introduction

Predation is an important factor, influencing the life history, morphology and behavior of zooplankton species. However, body size is the trait that is under highest selective pressure (BROOKS & DODSON 1965). The basic assumption of many models predicting zooplankton community structure is the relationship between body size and vulnerability of the species to different predators (DODSON 1974a, LYNCH 1979). Visual-feeding predators (fish) select large prey and the tactile-feeding predators (i.e. predaceous copepods) select small prey (DODSON 1974b).

Various constraints and limits, either morphological or physiological, on the potential response to different selection pressures exist within different phylogenetic groups (STEARNS 1977). Hence, to avoid this additional 'noise' it is necessary to compare different populations of one species that are exposed to different selection pressures (LYNCH 1980).

Populations of the cladoceran *Holopedium gibberum* were studied in three freshwater lakes in the neighborhood Biological Station of the Moscow State University. The lakes are very different with respect to predator pressure, so an attempt was made to study the adaptive response of *Holopedium* faced with different selective pressures.

Lake sites and background

The study included three lakes near the Biological Station of the Moscow State University at the shore of Kandalaksha Bay of the White Sea (66° N). Verkhneye and Vodoprovodnoye Lakes are small (1 and 0.6 ha, respectively) and are within approximately 300 m of each other. The third – Lake Nilma – is 5 km from the others and is larger (15 ha). All of the lakes are shallow (2–3 m); therefore, temperature stratification is absent. These lakes are very different in terms of predator pressure (Table 1).

There is only one predator – the planktivorous nine-spined stickleback (*Pungitius pungitius*) – in Verkhneye Lake. Up until June 1997, there had been no predators in Vodoprovodnoye Lake, with the exception of the small populations of invertebrate predators *Chaoborus* sp. and *Polyphemus pediculus*. In 1997, nine-spined sticklebacks invaded the lake (from Verkhneye Lake, probably) and caused the complete elimination of large-bodied zooplankton species (BIZINA 2000).

Nilma Lake is unique because of its great variety of vertebrate and invertebrate predators. It is the only lake among those investigated that contains consumers of the third level – northern pike (*Esox lucius*), perch (*Perca fluviatilis*), brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*).

Table 1. Predator species in the investigated lakes.

Predators	Lake Verkhneye	Lake Vodoprovodnoye		Lake Nilma
		Before 1997	After 1997	
Vertebrate predators	<i>Pungitius pungitius</i>	–	<i>Pungitius pungitius</i>	<i>Salmo trutta</i> , <i>S. salar</i> , <i>Coregonus lavaretus</i> , <i>C. albula</i> , <i>Esox lucius</i> , <i>Perca fluviatilis</i> , <i>Gasterosteus aculeatus</i>
Invertebrate predators	–	<i>Chaoborus</i> sp., <i>Polyphemus pediculus</i>	–	<i>Leptodora kindtii</i> , <i>Bythotrephes longimanus</i> , <i>Polyphemus pediculus</i>

Materials and methods

Zooplankton samples were collected with a Juday net (67- μ m mesh net). In the Verkhneye and Vodoprovodnoye Lakes, samples were collected every 3 days from the beginning of June until the middle of August 2000. Taking into account the probable irregular distribution of the zooplankton, the samples were taken at five sampling points in the pelagic part of the lake and then combined into one integral sample. The integral samples were used to estimate the abundance of *H. gibberum* and other zooplankton species (crustaceans and rotifers). Nilma Lake was sampled only twice, and the dynamic parameters of the local *H. gibberum* population were not measured.

In all samples, the numbers of *H. gibberum* were counted. Males were not found in all three populations throughout the study period, although females with resting eggs were found in the Verkhneye and Nilma Lakes at the beginning of August. For all individuals found in the sample, body length (from the compound eye to the posterior tip of the carapace) and body height (from the ventral to the dorsal edge on the carapace at the middle of the body) were measured, and the size and type (parthenogenetical or resting) of the brood determined (if present).

Population dynamics (GHILAROV 1987)

The instantaneous rate of population increase (r) was calculated for each interval of time as:

$$r = \{\ln(N) - \ln(N_0)\}/(t - t_0)$$

where N and N_0 represent population abundance in time t and t_0 , and $t - t_0$ is the time interval between two consequent samplings.

Birth rate (b) was estimated as:

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

where E being overall number of the species eggs in the sample, N overall number of individuals of the species in the sample, and D duration of the development of eggs, which is estimated as:

$$\ln D = 2.3279 + 1.2472 \ln t - 0.5647 (\ln t)^2$$

where t is temperature (t °C).

Death rate (d) was estimated as the difference between the birth rate and the instantaneous rate of increase:

$$d = b - r$$

and fecundity F_a as:

$$F_a = E_0/N_a$$

i.e. the number of eggs per adult female (N_a , the number of adult females).

Body size

The size at maturity was determined as the minimal size of a female carrying eggs in brood at a given date. All smaller organisms were considered as juvenile, while those larger were considered as adults. The data are presented in Table 2. To compare the patterns of body growth in the population studied, the Coefficient of Functional (geometric mean) Regression (CFR) between length and height of the carapace was used (SOKAL & ROHLF 1997). The multiple regression with clutch size as the second variable was used to determine the influence of fecundity on the body shape.

Results

Seasonal changes in population abundance

In Vodoprovodnoye Lake, the density of the *H. gibberum* population constantly decreased after the hatching from resting eggs in spring and reached zero level in the middle of July (Fig. 1). Neither males nor resting eggs were found. A similar pattern was observed during the 4 years (1997–2000) after the stickleback invasion (BIZINA 2000).

The average value of birth rate in this lake was 0.06 ± 0.04 day⁻¹ while the death rate was 18 ± 0.19 day⁻¹ throughout the whole period. The fraction of the adult individuals during the entire season was low (32%).

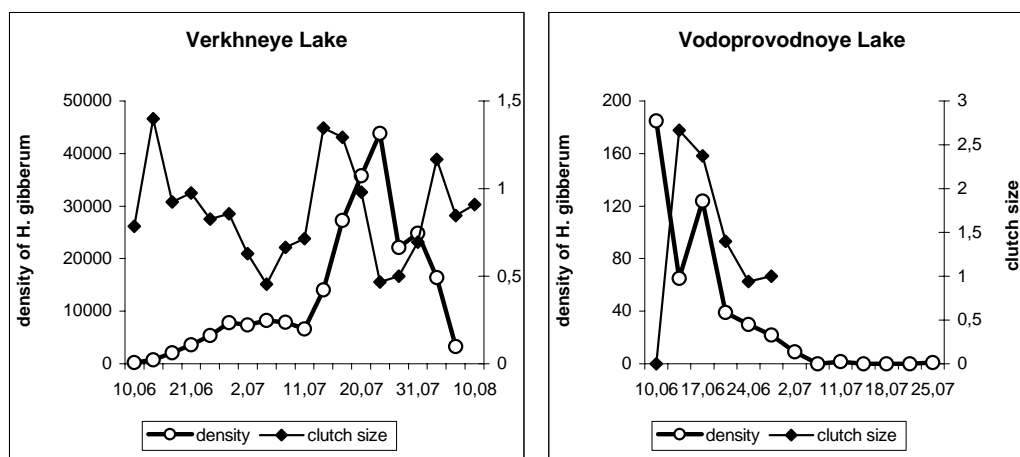
In Verkhneye Lake, the density of the population of *H. gibberum* grew slowly and gradually in June and at the beginning of July, and abruptly reached its peak at the end of July (Fig. 1). The fraction of adult individuals decreased by half (from 60% to 31%) during the peak of abundance (from July 15 until August 4). Average birth rate was 0.09 ± 0.015 day⁻¹ before July 15, and after that was 0.16 ± 0.04 day⁻¹. The death rate had also increased by the end of July (from 0.02 ± 0.14 day⁻¹ in the first half of the summer to 0.11 ± 0.14 day⁻¹ in the second half).

Body size

The populations differed significantly in size at

Table 2. Size at maturity and maximal adult size in three populations of *H. gibberum*.

Parameters		Lake Verkhneye	Lake Vodoprovodnoye	Lake Nilma
Size at maturity (μm)	Body length	375	375	600
	Body height	300	500	950
Maximal size (μm)	Body length	575	700	1500
	Body height	700	800	2750

Fig. 1. Density and seasonal changes in clutch size (eggs per adult female) of *H. gibberum* in Verkhneye and Vodoprovodnoye Lakes in 2000 (from June 10 until August 10).

maturity (Table 2). Between-sample variation in size at maturity was very low in all populations.

It is interesting to compare the present data with those obtained in previous years (BIZINA 1998). For example, in 1996, body length at maturity in Verkhneye Lake was 550 μm (375 μm in 2000) and in Vodoprovodnoye Lake it was 750 μm (375 μm in 2000). Therefore, an abrupt decrease in the size at maturity is evident in both populations over the 5 years. Although lengths at maturity of *H. gibberum* from Lakes Verkhneye and Vodoprovodnoye are equal (375

μm), they differ significantly in carapace height at maturity (300 and 500 μm , respectively).

The comparison of the CFR between the length and height of the juvenile and adult individuals is given in Table 3. The juveniles and adults from one population have similarly shaped growth curves. Changes in the proportions of the body are not discernible after maturation.

The CFR is very different between populations. The value of this coefficient is close to 1 in Lakes Verkhneye and Vodoprovodnoye, while in Nilma Lake it is close to 0.5. It means

Table 3. Relation between the length and height of the carapace in juveniles and adults of *H. gibberum* in three populations.

		Verkhneye	Vodoprovodnoye	Nilma
CFR	Juvenile	0.91	0.79	0.58
	Adult	0.77	0.80	0.49

that the growth pattern is almost isometric in the first two lakes, while in Nilma Lake the height of the carapace increases twice as fast as its length in this population.

CFRs do not change distinctly if the clutch size is added as an additional variable in regression analysis (Table 4). Therefore, the fecundity does not strongly affect the growth and body shape of *H. gibberum*.

Table 4. Multiple correlation between the length, height and clutch size ($P < 0.0001$ for all cases).

	Verkhneye	Vodoprovodnoye	Nilma
Standard error	0.03	0.10	0.04
CFR	0.83	0.88	0.51

Discussion

Population dynamics

Evidently the cause of the drastic decrease of *H. gibberum* population density in Vodoprovodnoye is the predation of the nine-spined stickleback, which invaded the lake 4 years ago. A similar decline of the population density was observed in 1997, when the stickleback appeared for the first time (BIZINA 1998, 2000). A decline in the abundance of *H. gibberum* occurred at the same time as in the previous 3 years. The clutch size and fraction of adults decreased in parallel to changes in population abundance. Since the birth-rate was high during the decrease in population abundance, it is assumed that this decrease was caused by fish predation.

During 4 consecutive years, the population crashed completely before any resting eggs had been produced (1997–2000). Therefore, it is presumed that the long-term bank of diapausing eggs provides the spring renewal of the population. This example supports the important role of the resting eggs bank in the persistence of zooplankton populations during long, unfavorable periods (HAIRSTON et al. 1988, HAIRSTON 1996, CACERES 1998).

In this case, the long-term bank of resting eggs can be considered as insurance against the frequent change of dominating predators (vertebrate and invertebrate). According to the

switch between vertebrate and invertebrate predator pressure, the trend of body size selection changes drastically. Before 1997, only invertebrate predators that eliminated smaller size classes were present in Vodoprovodnoye Lake. The selection favored the increase in body size. In 1997 the invading fish not only shifted the evolution trend of size of *H. gibberum* (by elimination of small-sized individuals) but also eliminated the population of invertebrate predators (*Chaoborus* sp.).

Hatching from the resting eggs also plays an important role in the *H. gibberum* population in Verkhneye Lake, as could be concluded from the dynamic characteristics of this population. The period of sharp increase of the population (from the middle of July until the beginning of August) was observed, although a very slight increase in clutch size was acknowledged also (from 0.82 ± 0.18 to 0.92 ± 0.34). The almost doubling of birth rate (from 0.09 ± 0.015 to $0.16 \pm 0.04 \text{ day}^{-1}$) was compensated by a rise in the death rate (from 0.02 ± 0.14 to $0.11 \pm 0.14 \text{ day}^{-1}$). The recruitment of individuals from the bottom sediments is also evident from the double reduction of the number of adults during the peak (from 60% to 31%).

It is suggested that the July–August peak of abundance of the population from Verkhneye is explained mainly by the mass hatching of resting eggs. The phenomenon of the prolonged hatching is known for some other cladoceran species (DE STASIO 1990, GALIMOV et al. in preparation).

Body size

The interpopulation differences in size (particularly the size at maturity) could be explained by the species composition of the predators in these lakes.

The smallest form inhabits Verkhneye Lake. Only one predator of this lake (*Pungitius pungitius*) selects prey based on small body size. The rate of individual growth quickly levels off after maturity in this population (BIZINA 1998).

A middle-sized form of *H. gibberum* inhabited Vodoprovodnoye Lake in the past. The experiments on growth rate of *H. gibberum* (BIZINA 1998) show that this form had a larger

size at maturity and grew faster after maturity (two to three times, in comparison with the Verkhneye Lake population). This pattern of curve growth is more advantageous under invertebrate predator pressure.

The reduction of the size at maturity cannot be explained as an evolutionary response to the invasion of fish, because the population had no opportunity to produce diapausing eggs in these years (1997–2000). It is assumed that heritable intrapopulation variation in sizes at maturity exists among clones hatching from the egg bank in Vodoprovodnoye Lake. The range of sizes at maturity among different clones is then modified by the clonal selection caused by predators. The small-sized clones are eliminated under the pressure of invertebrate predators, and vice versa.

The other potential explanation is the possible existence of genetic correlations between the duration of diapause and the size at maturity. If the long period of dormancy correlates with the smaller size at maturity, average body size would decrease after several years of hatching.

In Nilma Lake, the large body size could be explained by the existence of the consumers of the third level (*Salmo salar*, *S. trutta*, *Esox lucius*, *Perca fluviatilis*). According to the Fretwell–Oksanen hypothesis (OKSANEN et al. 1981, FRETWELL 1987), if the third level is present in the community, predators of the second level do not control the level of herbivores. Thus, the size structure of the *H. gibberum* population in Nilma Lake provides 'microevolutionary' evidence for this hypothesis. Individuals from Nilma Lake are considerably larger than in the two other lakes.

TESSIER (1986) described similar interpopulation differences in the life-history traits of *H. gibberum* in Pennsylvanian lakes. In a lake where large individuals represent the *Holopedium* population, the major vertebrate predator is the young-of-the-year yellow perch (*Perca flavescens*), which is incapable of catching the large adult *H. gibberum*, hence mimicking the effect of invertebrate predation. A similar explanation can be applied to the selection of large *H. gibberum* in Nilma Lake also (juveniles of *Coregonus lavaretus* and *Perca fluviatilis*, juvenile and

adult *Coregonus albula* are able to establish a similar effect).

Considerable differences between the populations under study might be accounted for by the differences in predation patterns, and also by different resource availability in the lakes. These populations may represent the different life history strategies (ROMANOVSKY 1984). Microevolutionary adaptations may derive from different level oscillations of resources (K-species – not changing resources; r-species – changing resources). In the case of fluctuating resources (r-species), differing adaptations aid survival during the unfavorable periods. The various types of the latter strategy (r-species) are most probably present in the lakes studied herein.

Acknowledgements

I thank A. M. GHILAROV, Y. E. ROMANOVSKY, and YAN GALIMOV for commenting on this manuscript. The work was supported by grants 98-04-49140 and 01-04-48384 from the Russian Foundation for Basic Research.

References

- BIZINA, E. V., 1998: PhD Thesis. – Department of General Ecology of M. V. Lomonosov Moscow State University. Moscow (in Russian).
- BIZINA, E. V., 2000: Predators, resources and trophic cascades in the regulation of plankton communities in freshwater oligotrophic lakes. – *Zh. Obshch. Biol.* 61: 601–615 (in Russian).
- BROOKS, J. L. & DODSON, S. I., 1965: Predation, body size and the composition of plankton. – *Science* 150: 28–35.
- CACERES, C. E., 1998: Interspecific variation in the abundance, production, and emergence of *Daphnia* diapausing eggs. – *Ecology* 79: 1699–1710.
- DE STASIO, B. T., 1990: The role of dormancy and emergence patterns in the dynamics of freshwater zooplankton community. – *Limnol. Oceanogr.* 35: 1079–1090.
- DODSON, S. I., 1974a: Zooplankton competition and predation: An experimental test of the size-efficiency hypothesis. – *Ecology* 55: 605–613.
- DODSON, S. I., 1974b: Adaptive change in plankton morphology in response to size-selective predation: A new hypothesis of cyclomorphisms. – *Limnol. Oceanogr.* 19: 721–729.
- FRETWELL, S. D., 1987: Food-chain dynamics: the central theory of ecology? – *Oikos* 50: 291–301.
- GHILAROV, A. M., 1987: Population dynamics of freshwater planktonic crustaceans. – *Nauka*. – Moscow: 188 pp. (in Russian).

- HAIRSTON, N. G., 1996: Zooplankton egg banks as biotic reservoirs in changing environments. – *Limnol. Oceanogr.* 41: 1087–1092.
- HAIRSTON, N. G. & DE STASIO, B. T., 1988: Rate of evolution slowed by a dormant propagule pool. – *Nature* 336: 339–242.
- HEBERT, P. D. N. & FINSTON, T. L., 1997: Taxon diversity in the genus *Holopedium* (Crustacea: Cladocera) from the lakes of eastern North America. – *Can. J. Fish. Aquat. Sci.* 54: 1928–1936.
- LYNCH, M., 1979: Predation, competition, and zooplankton community structure: an experimental study. – *Limnol. Oceanogr.* 24: 253–272.
- LYNCH, M., 1980: The evolution of cladoceran life histories. – *Q. Rev. Biol.* 55: 23–41.
- OKSANEN, L., FRETWELL, S. D., ARRUDA, J. & NIEMELA, P., 1981: Exploitation ecosystems in gradients of primary productivity. – *Am. Nat.* 118: 240–261.
- ROMANOVSKY, Y. E., 1984: Individual growth rate as a measure of competitive advantages in cladoceran crustaceans. – *Int. Rev. Gesamten Hydrobiol.* 69: 613–632.
- SOKAL, R. R. & ROHLF, F. G., 1997: *Biometry: the Principles and Practice of Statistics in Biological Research*. – W. H. Freeman and Company. USA: 887 pp.
- STEARNS, S. C., 1977: The evolution of life-history traits: a critique of the theory and a review of the data. – *Annu. Rev. Ecol. Syst.* 8: 145–171.
- TESSIER, A. J., 1986: Life history and body size evolution in *Holopedium gibberum* Zaddach (Crustacea, Cladocera). – *Freshwater Biol.* 16: 279–286.

Author's address:

K. POPADIN, c/o Prof. Alexey Ghilarov, Dept. of General Ecology, Biol. Fac. of M. V. Lomonosov, Moscow State University, 119899 Moscow, Russia.