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Gjøkvatn revisited: repeated visual observations of plankton swarms in a subarctic forest lake

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ABSTRACT

Distinct swarms of *Bosmina longispina* (Leydig, 1860) (Crustacea: Cladocera) were visually observed and described in Gjøkvatn, a Norwegian forest lake at 69°N, in 1969 and again in 1996 and 2021. The repeated observations after many years show that *Bosmina* swarms occur regularly in the lake. The swarming is likely to be an anti-predation behaviour against the predatory cladoceran *Polyphemus pediculus* (Linnaeus, 1761).

Key Words: anti-predation behaviour, *Bosmina*, Crustacea, *Polyphemus*,

Dense swarms of zooplankton occur both at sea and in lakes, on small and large scales, and for abiotic and biotic reasons, as thoroughly reviewed by Ambler (2002). Persistent aggregations on small scales, centimetres to meters, have been reported for many taxa, most of them crustaceans. Microcrustacean plankton communities in the sea are dominated by copepods. Lake communities are different because high diversities of cladocerans are found along with copepods and because rapid asexual propagation by parthenogenesis gives high densities of many of them, especially species of Daphniidae and Bosminidae. These abundant, slow-moving, and small animals are attractive prey for fish but also for invertebrate predators, including the large cladocerans *Bythothrephes longimanus* (Leydig, 1860) and *Polyphemus pediculus* (Linnaeus, 1761) (Flössner, 2000; Dumont & Negrea, 2002). It is commonly found that the prey species protect themselves from predation by swarming (Jakobsen *et al.*, 1994; Pijanowska, 1994; Kvam & Kleiven, 1995; Jensen *et al.*, 1999; Castro *et al.*, 2007; Raveh *et al.*, 2018). The basic assumption is that the high prey densities in swarms result in a confusion effect that decreases the predator's feeding rate (Milinski, 1984; Pijanowska & Kowalczewski, 1997; Ambler, 2002; Jeschke & Tollrian, 2005).

Plankton swarms in lakes are studied with various methods (Jakobsen & Johnsen, 1988; Ambler, 2002) but are rarely observed by eye because waves often impair vision and because pelagic copepods and cladocerans are small, transparent, and often show little colour contrast against the water. Visual observations allow descriptions of swarm properties that are difficult to achieve by ordinary sampling, such as their shape, size, consistency, and exact position in the water. When seen, complete swarms can be caught, and the number of individuals estimated.

Gjøkvatn is a 25-ha dimictic, sub-arctic forest lake located at 69° N and 96 m a.s.l. in northeastern Norway. The 14 km^2 catchment drains peat bogs and pine woods and the 4 km outlet stream enters the Pasvik River system on the border between Russia and Norway. The lake has a 14 m deep main basin and two shallow bays on the east side. The littoral zone is stony, with little vegetation, the water is clear with a yellow brown humous colour and surface temperatures in July are 15−17 ° C. Epilimnion was 4−6 m deep in 1969 (Klemetsen, 1973). The pelagic community consisted of *Daphnia galeata* Sars, 1863, *D. longiremis* Sars, 1861, *Bosmina longispina* (Leydig, 1860), *Holopedium gibberum* Zaddach, 1855, and *Bythotrephes longimanus* in addition to copepods (Klemetsen, 1973). *Bosmina longispina* shows very low densities in the pelagic zone. The fish species are perch *Perca fluviatilis* Linnaeus, 1758 and pike *Esox lucius* Linnaeus, 1758. Stomach analyses have demonstrated that perch is a plankton predator with a strongly size-selective diet in Gjøkvatn (Klemetsen, 1973). The large-size *Bythotrephes longimanus* and *D. galeata* were almost always exclusively taken, whereas the smaller-size species, including *B. longispina*, were largely ignored. This shows that fish predation on *Bosmina* is not important in the lake.

Cloud-like plankton swarms with definite borders were observed along the shore of the southeastern bay of Gjøkvatn in late June 1969 (Klemetsen, 1970). There was good light and no waves, and the swarms were clearly visible because of a colour contrast between the grey-yellowish tinge of the individuals and the humous-brownish colour of the water. The swarms were elongated vertically, 10–50 cm high and mostly 3–5 cm wide. Three complete swarms of different sizes were caught intact and preserved for identification and counting (Klemetsen, 1970). The

sampling was done from a boat with a 100 μ mesh, 25 cm in diameter plankton net. Apart from very few individuals of *P. pediculus* and *D. galeata*, only *Bosmina longispina* (identified by Klemetsen (1970) as *Bosmina obtusirostris* Sars, 1862, a junior synonym of *B. longispina*; see Bledzki & Rybak, 2016) was present in the samples. By subsampling, the total numbers of *Bosmina* were estimated to be 62,300, 37,700, and 3,050 in the three swarms, respectively, demonstrating that dense, monospecific swarms occurred as distinct units in the littoral zone of the lake. It was not known, however, if the swarming was a regular phenomenon, which could be tested by repeated observations. Gjøkvatn was revisited two times, in late July 1996 and 2021, after 27 and 52 years.

On both revisits, and with good conditions for observation, the same kind of cloud-like swarms as in 1969 were clearly and easily seen along the shore of the same bay as before. The swarms occurred in the top 70–80 cm surface layer and 2 – 40 m from the shore in 1969. Their positions in the water were similar in the two later years. In 2021, 11 swarms along a 100 m shore stretch had distances between them of 0.5, 1, 1, 3, 5, 2, 0.5, 5, 5, and 1 m, in that order, as measured by eye and by pacing. In all three years, the shape of the swarms was elongated vertically and often spindle-like and slightly curved, but also fan-shaped and sometimes with protrusions on the side or top. Several swarms were observed closely for 5–10 min on all occasions. They always moved very little and kept their size and shape remarkably constant except for some slow movements at the margins.

By comparing five vertical net samples taken closely along swarms and from 70 cm depth with five random samples from the same depth, but away from the swarms in 1969, it was found that the numbers of the cladoceran *Polyphemus pediculus* were clearly higher close to the swarms than elsewhere. This led Klemetsen (1970) to suggest that the *Bosmina* swarming in Gjøkvatn was an anti-predation behaviour against *Polyphemus*. Jakobsen & Johnsen (1988) also advanced the view that swarming behaviour in *Bosmina* and other cladocerans is typically a predator-avoidance mechanism. Much experimental research, mostly with sticklebacks *Gasterosteus aculeatus* Linnaeus, 1758, but also with invertebrate predators has later supported this hypothesis (see review by Ambler, 2002). In a survey of more than 2,000 lakes, Walseng *et al.* (2006) found that *Polyphemus pediculus* had a much higher occurrence in the littoral than in the pelagic zones. This was confirmed from Gjøkvatn, as no *Polyphemus* were found in vertical net hauls in the pelagic zone (Klemetsen, 1973), but common in the littoral (Klemetsen, 1970). This large cladoceran is generally described as a predator (Dumont & Negrea, 2002; Bledzki & Rybak, 2016) that takes small cladocerans, especially *Bosmina* (Flössner, 2000). Its presence in the littoral zone but not farther out increased the predation risk for *Bosmina* in this habitat. Swarming can result for abiotic and biotic reasons (Ambler, 2002) but in lacustrine cladocerans it is mostly found to be an anti-predation behaviour and a major driving force against predation pressure from fish and invertebrates (Castro *et al.*, 2007). The results and observations from Gjøkvatn support that it is against *Polyphemus* in this lake because predation from perch was unimportant (Klemetsen, 1973).

The random revisits to Gjøkvatn during many years indicate that *Bosmina* swarming is a regular phenomenon in the lake. *Bosmina longispina* and *Polyphemus pediculus* are common species in northeastern Norway (Walseng, 2018). Anti-predation swarms like those in Gjøkvatn may therefore occur in other forest lakes in this sub-arctic region.

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