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Active and colorful life under lake ice

Winter in boreal ecosystems is characterized by freezing temperatures and often a thick snow cover leading to the most challenging season for plant and animal survival. Organisms that cope with such extreme environmental conditions must rely on a wide range of adaptations to stay alive. Because migration and hibernation are efficient but energetically very costly strategies, many organisms stay active in their habitats throughout the winter, dealing with cold conditions and a lack of resources by a variety of other adaptations. To survive winter, the accumulation of energy reserves is a common strategy used by many animal species. This accumulation of energy takes place either by saving and gathering food that will be ingested during the winter or by accumulating body fats before winter.

Lakes undergo major environmental changes when ice and snow block most solar radiation from reaching the water column (Schneider et al. 2016). As phytoplankton abundance declines in the low light environment of winter, active aquatic consumers must use accumulated energy reserves or find alternative heterotrophic sources of energy to survive. However, most aquatic organisms have been rarely studied in the winter so we do not know the extent of these survival strategies.

The biological research station of Lake Simoncouche situated in Quebec (Canada) is an ideal location from which to survey a natural lake ecosystem at a high temporal frequency, including through the winter months (Schneider et al. 2016, Grosbois et al. 2017). Over the last years, we have regularly sampled this lake during winter and were surprised to observe that many species of zooplankton remained active. Moreover, this zooplankton community retained a high total biomass, including the annual biomass maximum, in winter (Fig. 1), which means that the under-ice community represents an important share of the biomass present in the lake all year-round. These observations challenge the widespread view of dormant aquatic life in winter (Marchand 2014). Zooplankton under the ice were previously assumed to pass the winter either in diapause with dormancy or in active diapause without dormancy. Diapausing individuals with dormancy remain completely inert, their guts do not contain food, and they disappear to the profundal zone or bottom sediments of the lake. Active diapause is characterized by a different physiological state including arrested development, lack of significant gut contents and the presence of large, orange lipid droplets in the body cavity (Dahms 1995). Individuals in active diapause can be found in the pelagic or profundal zones and they are characterized by sluggish movements.

However, this pattern was not the case for two particularly active and vigorously swimming copepod species: *Leptodiaptomus minutus* (63% of the winter biomass) and *Cyclops scutifer* (22% of the winter biomass). A video of the active winter zooplankton community is available in the supplementary material (Video S1). Both active species were first noticed because they were very colorful (Fig. 2). The colors come from carotenoid pigments identified as antioxidant agents used in photoprotection against solar ultraviolet (UV) radiation (Kobayashi and Sakamoto 1999). However, UV radiation is rarely harmful in winter when snow- and ice-cover reflect and scatter insolation. Therefore, these pigments are not required for photoprotection in winter (Schneider et al. 2016). Despite this, pigment analyses

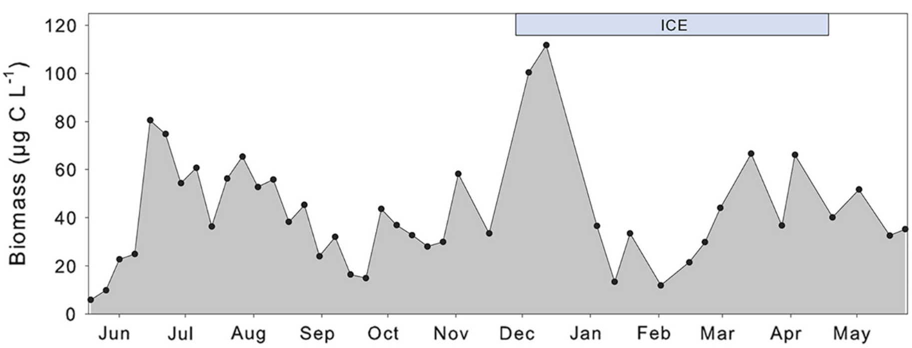

Fig. 1. Zooplankton biomass over an annual cycle. All individual stages (nauplii, copepodites, juveniles, adults) and species (copepods and cladocerans) have been counted and measured under an inverted microscope. Lengths were converted to biomass using length-biomass equations.

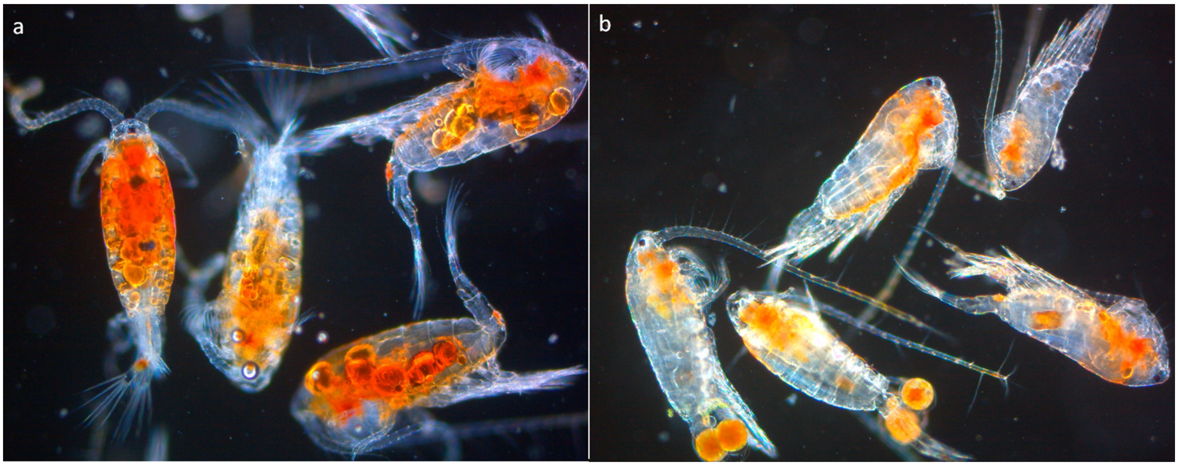

FIG. 2. Copepods (*Leptodiaptomus minutus*) from Lake Simoncouche, (a) under the ice in winter (27 January 2017) and (b) in summer (18 September 2017). Photos were obtained from an inverted microscope with phase-contrast (Photo: Guillaume Grosbois).

using high-performance liquid chromatography demonstrated that mid-winter was the period when *L. minutus* was the most colorful (Schneider et al. 2016).

So, why were these organisms bright red in the dark of winter? One clue is that the pigments were chemically associated with fatty acids, the major constituent of lipids. In winter, these fat reserves were easily detectable in zooplankton as large droplets of lipids (Fig. 2). The antioxidant properties of the pigments are likely essential in preventing the peroxidation of stored lipids in the zooplankton (Schneider et al. 2016). Copepod colors in winter might thereby preserve the highly valuable fatty acid molecules from oxidative stress (Valko et al. 2006). Other taxa such as *Daphnia* spp., *Bosmina* spp. and *Mesocyclops edax*, known to spend the winter season in dormancy as resting eggs or copepodite stages, were much less colorful (see Video S1 in the supporting information).

Pigmentation makes zooplankton more visible to fish and copepods can reduce their pigment concentrations in response to molecular cues liberated by predatory fishes (Hylander et al. 2012). However, as the relatively dark environment under the ice is disadvantageous to visual predators, zooplankton may remain colorful in the darkness and benefit from the physiological fatty acid protection provided by the pigments without being exposed to fish predation. The occasional sunlight that may pass through the ice and the snow cover is of low intensity and likely has only a minor effect on predation success, although not much is known about how fish react to changes in light intensity through winter.

From the consumer's point of view, a high biomass of active, fat, and colorful zooplankton would be an excellent food resource during the winter. However, when these zooplankton can finally be seen—as winter ends, light penetration increases through the melting snow and ice—the copepods reduce their pigmentation by investing the pigments and fatty acids in reproduction and eggs (Schneider et al. 2017). Thus, the large-sized adults become less visible to any visual predators. Copepod larvae, the nauplii, bright red due to an abundance of maternal fats and associated pigments, are too small to be threatened by fish predation. Lipid accumulation for winter is a life strategy widely used in polar and boreal marine ecosystems while in tropical seas, zooplankton have only small lipid reserves (Lee et al. 2006). Our observations (Fig. 2) show that this strategy also occurs in freshwater systems. To stay active and survive the winter, *L. minutus* and *C. scutifer* need to accumulate lipids that can be used when the availability of other food resources in the water column is low (Grosbois et al. 2017). The use of energetic reserves may provide a selective advantage to these overwintering species compared to winter-dormant organisms, allowing a high standing stock of active zooplankton in winter to be ready to benefit from the spring resources when they become available (Mariash et al. 2017). This can occur weeks before temperatures rise and the dormant zooplankton hatch or become active (Schneider et al. 2017).

Our observations have raised many scientific questions and hypotheses: How widespread are actively overwintering zooplankton in lakes? How do different lipids sustain activity during the winter? How does the nutritional quality of winter and summer zooplankton differ? What is the ecological significance of the active and colorful zooplankton community in the lake food web? Lake ecologists are just beginning to study life under the ice in detail, responding to an urgent need for research focused on under-ice ecosystem dynamics (Hampton et al. 2017). As ice-cover duration is predicted to decrease over the coming decades (Magee and Wu 2017), it is necessary to understand the importance of this winter accumulation of fatty acids by copepods for their life cycle and the higher trophic levels. Highly energetic fatty acids in prey are vital for the development of higher consumers including fish (Paulsen et al. 2014). As winter processes determine how the life cycle of aquatic organisms develops during the "growth" season, increasing our knowledge of the natural history of active winter organisms will help us to understand the dynamics of ecosystems over the entire annual cycle and uncover the still largely unknown consequences of the currently changing winter conditions.

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