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Are warm temperatures the key factor to prevent winter swarms of *Hemimysis anomala* in peri-alpine lakes?

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Abstract – The invasive bloody red mysid, *Hemimysis anomala*, has recently colonised peri-alpine lakes in Western Europe. During the last decade, scuba divers have regularly reported observations of substantial winter swarms of this animal in Lakes Bourget (France) and Geneva (Switzerland-France). During the last four years, we have regularly dived and observed such phenomena in a variety of habitats, revealing thousands to millions of individuals during the period between December and March, with maximal densities occurring in the water column and small open wrecks in January or February. Surprisingly, however, no swarm was observed during the winters of 2022–2023. This led to the hypothesis that temperature could be the main direct or indirect factor responsible for this lower abundance, resulting in the absence of significant gatherings. Some possible explanations are discussed.

Keywords: Lake Geneva / temperature / winter / invasive alien species / *Hemimysis anomala*

1 Introduction

The bloody-red mysid (*Hemimysis anomala*, Sars, 1907) is an invasive crustacean of the family Mysidae that is native to the Ponto-Caspian region (Chandra *et al.*, 2008). It has recently settled in some peri-alpine lakes (Frossard and Fontvieille, 2018). The spread of the animal was mainly made possible through Europe via ballast water from commercial vessels, but also likely through other secondary dispersal vectors, such as pleasure boats or birds (Wittmann, 2007; Kota and Kota, 2010). *H. anomala* was first detected in 2003 in the Rhône River (Daufresne *et al.*, 2007), which is known as a major fluvial vector that supports the geographic expansion of a variety of invasive alien species, along with the Rhine River (Dumont and Muller, 2010). It is likely that the settlement of the mysid in Lake Geneva was favoured by this hydrographic feature, and divers noticed the first episodic appearances of this species in Lake Geneva in 2007.

In Lakes Bourget (France) and Geneva (Swiss France), swarms have been regularly observed in the littoral zone in the last decade, with thousands to millions of individuals located in near-surface waters (<20 m) in winter. Such winter aggregations have also been reported elsewhere (Borcherding *et al.*, 2006; Dumont and Muller, 2010; Ricciardi *et al.*, 2012). To increase our knowledge on this recently settled animal, we investigated the quantitative significance, behaviour, and population dynamics of *H. anomala* using a variety of

methods, such as scuba diving (including both scientists and recreational divers in a participative science project; see <https://youtu.be/ASdvzyUiJKI>), eDNA approaches, and the deployment of high-frequency measuring devices (acoustic and visible/IR video cameras). Such efforts to observe, film, and sample *H. anomala* underwater have allowed us to obtain some interesting results (*e.g.* Frossard *et al.*, in revision; Rogissart *et al.*, submitted).

Typically, we observed that large and significant swarms develop in littoral zones in winter (from the end of December to the end of March). At this time, the temperature is low (<8–9 °C), and potential predators, including fish such as the European perch (*Perca fluviatilis*), leave the surface layers for deeper waters. Light was shown to be a key factor that determines the behavioural rhythms of the animal, particularly during the transitions between day and night. Specifically, animals move towards the pelagic water column more rapidly just after dusk and return just before dawn to places where they can be protected from predation and hide to maximise their chances of survival (*e.g.* cavities, wrecks, and pipes).

We also identified a diverse set of prey throughout the year ranging from autotrophic protists to zooplankton. This supports the seasonality of the diet of *H. anomala*, which has larger trophic niche widths and, to a smaller extent, richer diets in spring and summer compared to autumn and winter. It also seems that *H. anomala* can be preferential prey for perch since we noticed that the collapse of swarms is concomitant with the perch's return to surface layers at the beginning of spring, and we could find up to 84 mysids in the stomach of a

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13.5-cm 21.2-g specimen. Together, these results shed light on the fact that assessments of ecological impacts of the bloody-red mysid should account for the temporal variations of its biotic interactions with the native biodiversity, which should ideally be captured at a relatively high time-scale frequency.

Divers, including myself, have observed large swarms of the animal during winter for at least the past four years, but very surprisingly, no swarm was detected during winter of 2022–2023 in places where gatherings had been observed previously. This short note discusses some potential hypotheses based on the assumption that temperature is a significant factor that regulates the population dynamics of *H. anomala*. Although the focus is on Lake Geneva, it is noteworthy that similar observations were also made in the neighbouring Lake Bourget based on feedback obtained from recreational divers.

2 Materials and methods

Lake Geneva is a deep peri-alpine lake and the largest natural lake in Western Europe. It is located between Switzerland and France (Lat= 46°27'N, Long= 06°32'E). It is a warm, monomictic lake situated at an altitude of 372 m and characterized by a surface of 582 km², an average depth of 153 m (maximum depth = 309 m), and a total water volume of ~89 km³. This lake has been ecologically monitored since the middle of the past century through the action of the International Commission for the Protection of Waters of Lake Geneva (CIPEL; for more details, see <https://www.cipel.org/en/>; Jacquet *et al.*, 2014; Rimet *et al.*, 2020).

In this study, two sites were surveyed: one located at Thonon-les-Bains (Saint –Disdille, Lat= 46°24'05"N – Long= 6°30'07"E) and another at Amphion-les-Bain (near la plage du Miroir, Lat= 46°23'51"N – Long= 6°32'10"E). These are both situated in the southern French part of the lake at a distance of about 10 km from each other. The first site consists of a variety of habitats with small wrecks (former pleasure or fishing boats) at different depths (*e.g.* at 14, 18, 20, and 27 m). Nearby, the animals have been observed to form significant aggregations in winter inside wrecks or in the surrounding water column. The second site also offers a variety of habitats and was chosen because of the presence of an open pipe measuring 2.5 m long with a diameter of about 0.9 m. It is located at 45 m from shore at a depth of 4.5 m. Here, a swarm was present from January to March during the last four years.

At both sites, from winter 2019/2020 to winter 2022/2023 (December to March), more than 150 dives were done by either scientific divers or recreational practitioners. A little more than half were done as part of this study, approximately once a week in the period of 2022/2023. From the fall of 2019, temperature was measured using continuous measuring loggers (TG-4100 Tinytag Aquatic 2 sensors; Agro Ressource, Orange, France). Two loggers were placed, respectively, at 4 and 12 m near the Thonon-les-Bains (Lat: 46.37 Long: 6.453) study site. The loggers measured temperature every hour, generating between 672 and 744 data each month. Loggers were removed from the lake and checked every 6 months at the laboratory for potential recalibration (note that loggers recalibration was not necessary during the study period). For each depth, the pair of loggers

gave very similar data, providing confidence in the data obtained.

The focus was on autumn and winter months (from October to March), corresponding to the period of interest for the development and observations of the swarms (a few months before and during the phenomenon).

Statistical analyses were performed using Systat (version 10).

3 Results and discussion

During several visits, swarms were observed in the different places we are used to visit through diving and reflect the mass grouping observed each year in winter for at least the past four years but 2022–2023 (Fig. 1). Autumn 2022 was very warm, and cold winter only arrived after 15 January 2023, which suggested that temperature could be responsible for the absence of the swarms. An extra element supporting the idea to investigate the role of temperature was the presence of perch, which were still present at the end of February inside the deepest wrecks (at 27 m) on both sites (Thonon and Amphion). They were never observed there in past years. Indeed, it has been well known for quite a long time that this fish leaves the littoral zones and the upper water layers for more pelagic and deeper zones at the end of fall. They only come back to the littoral zone around April to spawn as a response to both light (photoperiod) and temperature (>11°C) (Ferguson, 1958; Forney, 1971; Imbrock *et al.*, 1996; Gillet and Dubois, 2003; Guillard *et al.*, 2006).

The analysis of the water temperature supported the existence of a significantly warmer fall period in 2022 than previous years. Figures 2 and S1 summarize the evolution of the mean temperature from October to March for the different periods of 2019–2022 to 2022–2023. Clearly, the period of October 2022 to January 2023 was significantly warmer than the same periods during previous years (ANOVA, $p < 0.01$), while the difference decreased and became negligible in February. The difference was particularly marked in November 2022 compared to previous years, with mean temperature higher than 2.4 to 3.1°C at 4 m and 1.7 to 2.3°C at 12 m (Figs. 2C, 2D). Such differences were comparatively low for the other months, although still significant (+0.8 to +2.0°C (mean values) for October (Figs. 2A, 2B), +0.8 to +1.6°C for December (Figs. 2E, 2F) and +0.5 to +1.3°C for January (Figs. 2G, 2H)).

After 15 January 2023, for two to three consecutive weeks, a wave of cold temperature associated with a strong northern wind (locally called “*la bise*”) dramatically decreased both air and water temperatures such that the difference between our four years monthly temperatures rapidly became insignificant (Fig. 2I–L). Sunny and relatively warm conditions occurred again during two weeks in the middle part of February, followed again by very cold conditions. However, in February and March, water temperatures were very similar to previous years with an average difference of +0.04°C (from –0.32 to +0.26°C).

It is proposed that the relatively high temperature recorded in fall and early winter is the main factor explaining the absence of swarms, which could directly or indirectly prevent

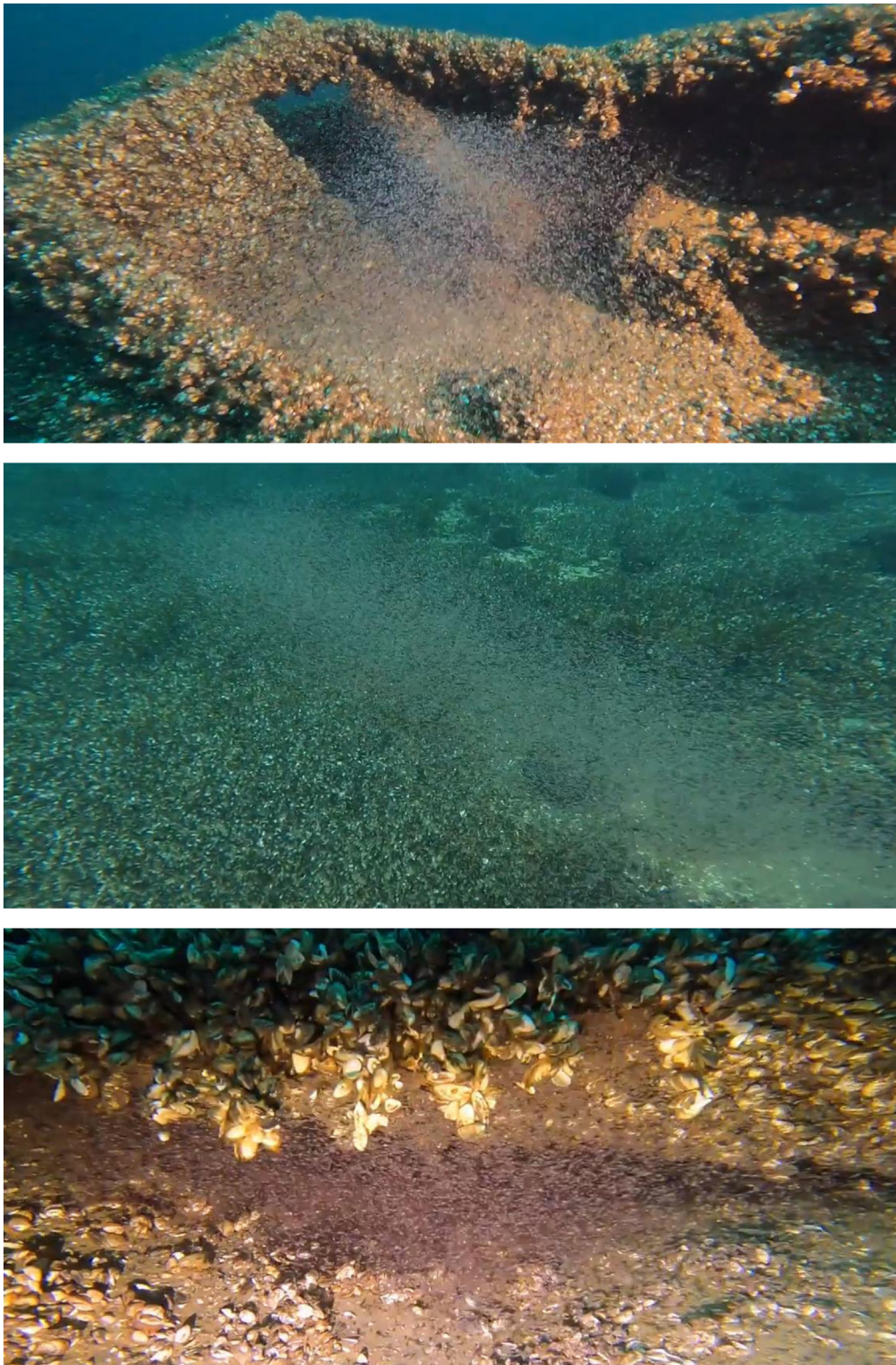


Fig. 1. Typical gatherings observed in the different sites of Lake Geneva before fall/winter 2022–2023: near and inside a wreck, in the water column and near the bottom, in a cavity, and in a pipe. These pictures were extracted from videos that show the quantitative importance of the mysids in typical winter swarms (<https://www.youtube.com/watch?v=EuhiGWoyttMandt=11s>; <https://www.youtube.com/watch?v=KBvkgpm4i5kandt=208s>).

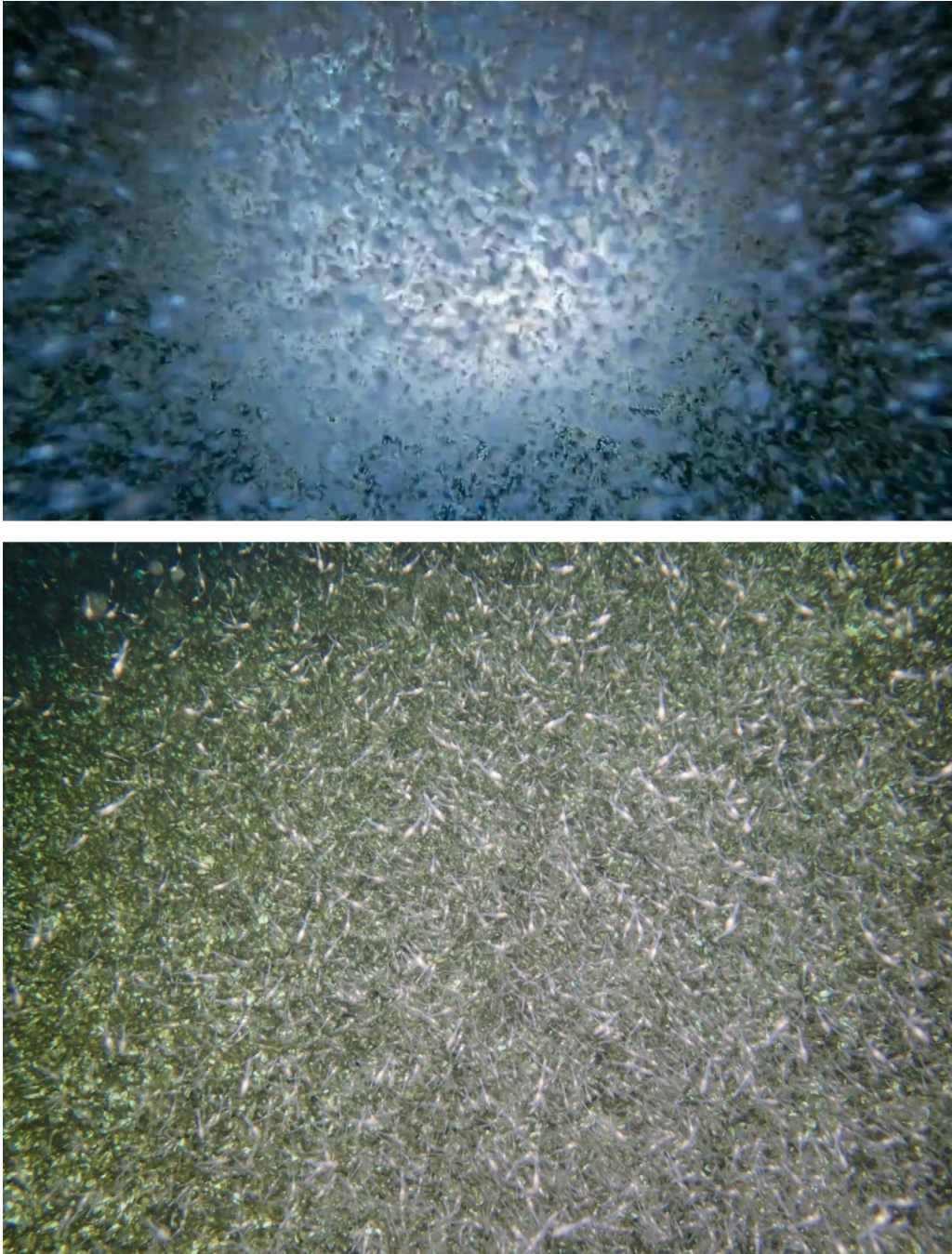


Fig. 1. (Continued).

the mysid's development that had usually been observed until now. Firstly, it was assumed that temperature could act directly on the physiology and reproductive capacities of the animals. It has already been reported that mating begins when the water temperatures reach 8–9 °C (Pothoven *et al.*, 2007). There seems to be no mention in the literature about the need for a very low temperature for aggregation (Borcherding *et al.*, 2006; Dumont and Muller, 2010; Ricciardi *et al.*, 2012). It is even often considered that growth is higher with the increase of temperature. However, as pointed out by Dumont and

Muller (2010), *H. anomala* is negatively phototactic and subject to predation by fish. Thus, winter has been proposed as the ideal season for gathering since this period is characterized by short days, low light levels, and the fasting of many fish due to low temperatures.

Dumont and Muller (2010) also reported large mysid gatherings beginning in mid-December when the water reaches 7 °C, followed by dispersal to isolated colonies at the beginning of April, when the water reaches 8–9 °C. Such a development was also observed during several consecutive

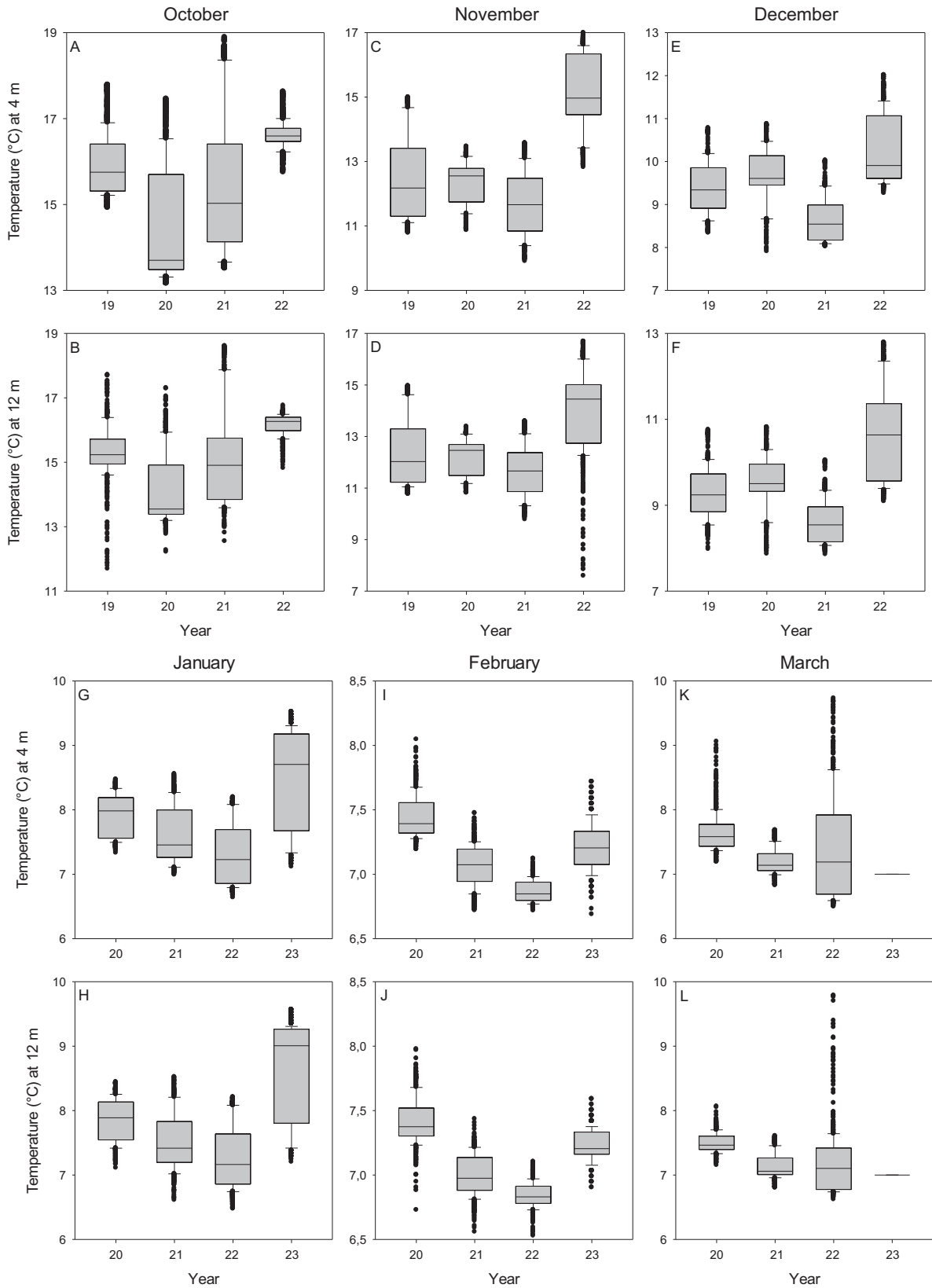


Fig. 2. Box plot representation of the evolution of temperature data considered at 4 and 12-m depths in Lake Geneva. (i) Autumn months: October (A,B), November (C,D) and December (E,F) between 2019 and 2022. (ii) Winter months: January (G,H), February (I,J) and March (K,L) between 2020 and 2023.

winters with the observation of females carrying eggs in March, which supports that the gathering has reproductive goals. The massing of many individuals allows genetic mixing that cannot occur during the rest of the year, when *H. anomala* lives and reproduces in small colonies dispersed in various shelters. Secondly, temperature is likely an important variable explaining the presence of perch, which could prevent and control the onset of the mass development through direct predation on *H. anomala*. Indeed, the mysids were observed as likely being a favourite prey for this fish, and significant trophic interactions exist between these two species (Rogissart *et al.*, unpublished data).

Another and non-exclusive hypothesis of the indirect effect of temperature involves another recently settled invasive species, the quagga mussel (*Dreissena rostriformis bugensis*). Warmer temperatures in fall and early winter could have enhanced the mussel's activity, which in turn could have significantly reduced plankton resources for *H. anomala*. The quagga mussel has colonized the entire lake, and its abundance and biomass are substantial. The bivalves are everywhere where the mysids are (Fig. S1), and it is tempting to infer that the main resource for *H. anomala* (phyto or zooplankton) is significantly and negatively impacted by the mussel's very significant filtering activity (Box 1). This hypothesis deserves to be carefully tested and verified, but there is no doubt that water transparency has increased during recent years at the same time as the mussel invasion in Lake Geneva (Karatajev and Burlakova, 2022), and the chlorophyll *a* concentration has decreased dramatically, especially in 2022/2023 (Fig. S2).

Box 1

With the massive implantation of quagga mussels, another invasive alien species in Lake Geneva also originating from the Ponto-Caspian area, a significant volume of water is filtered by these organisms. A known direct consequence is the production of faeces and pseudo-faeces (undigested filtered parts), which reflect a transfer of energy (organic matter) from the seston (from the water column) to the benthos (MacIsaac, 1996; Mayer *et al.*, 2014). The densities of plankton suspended in the water column decrease, including phytoplankton via direct consumption by mussels and (micro)zooplankton in response to lower levels of phytoplankton on which to graze (Kissman *et al.*, 2020). This drop in the concentration of that plankton that were previously present in Lake Geneva has clearly been perceptible on the littoral zones all around the lake in recent years. Waters have become extremely clear, and light penetrates much deeper into the lake, which also seems to have clearly favoured the development of macrophytes, which are now more abundant and distributed more deeply than before (Jacquet *et al.*, 2017). This process is referred to as "benthification" (Mayer *et al.*, 2014), which involves habitat modification that has significant consequences on benthic invertebrate and fish populations, but this aspect has not been investigated yet for Lake Geneva (Haltiner *et al.*, 2022).

While no swarm was detected in winter 2022/2023, a few individuals were still observed in a variety of natural cavities (approximately 10 to 30 individuals in a very limited volume of <math><1-2\text{ dm}^3</math>). These "hotspots" of mysids are very interesting since *H. anomala* is associated with the signal crayfish (*Pacifastacus leniusculus*) in most cases. Although it is probably not a rule (*e.g.* http://riedbleu.free.fr/films_Hemimysis.html), it is noteworthy that divers have rarely observed *H. anomala* in cavities where the crayfish is absent. This may suggest a mutualistic relationship between the two animals, where the bloody red mysid benefits from important protection by the larger crustacean. In turn, it is tempting to propose that faeces or the mysids themselves could provide a source of food to the crayfish. However, this assumption should be verified (Fig. S3). This could be a way of maintaining the mysid populations before they can aggregate *de novo*.

4 Conclusion

Temperature is known to be a very important factor linked to animal behaviour, physiology, and biotic interactions, among others. In this study, this variable was proposed to be a determinant of the presence/absence of *H. anomala* swarms and gatherings in Lake Geneva, as well as elsewhere, such as in Lake Bourget, where such an observation was also anecdotally reported by recreational divers. Temperature is suggested to be responsible for such observations through direct (reproductive capacities) and indirect (biotic interactions) effects that likely influence the development of mysid swarms. Although it is too early to make any definitive conclusion, if our hypothesis turns out to be correct, one can wonder about implications of future water temperature increase due to climate change (Desgué-Itier *et al.*, 2023) on the potential of this species to maintain viable populations in these lakes.

Results obtained during this study were made possible thanks to an important set of *in situ* observations made by both scientific and recreational scuba divers. Without this observation tool, which is undoubtedly complementary to other materials and methods, we would likely have missed what has happened under the surface of Lake Geneva.

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Supplementary Material

The Supplementary Material is available at <https://www.kmae.org/10.1051/kmae/2023008/olm>.

Fig. S1: Evolution and comparison of mean temperatures from October to March from 2019–2020 to 2022–2023 in Lake Geneva. This representation provides another view highlighting how much the period of interest in 2022–2023 differs from the others.

Fig. S2: Evolution and comparison of mean values of chlorophyll a concentrations from October to March for 2019–2020 and 2022–2023 in Lake Geneva. Data are from CIPEL (Rimet et al., 2020).

Fig. S3: Pictures detailing a few animals in a pelagic swarm or when associated in cavities with the signal crayfish *Pacifastacus leniusculus* and the quagga mussel *Dreissena rostriformis bugensis* (courtesy of Marc Vassart).

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