






# Multiple drivers shape winter swarms of the bloody-red shrimp *Hemimysis anomala*

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**Abstract** – The bloody-red shrimp *Hemimysis anomala*, a Ponto-Caspian mysid, has invaded many large lakes in Europe and North America. It exhibits a pronounced seasonal behaviour, forming massive winter swarms (WS) whose dynamics are likely driven by different processes implying reproduction capacities, responses to resource availability and/or predation pressure. We hypothesize that these different processes may not be mutually exclusive but could rather be successively involved in explaining the formation and disappearance of WS. We also expected that water temperature may be a major indirect driver of WS dynamics by indirectly controlling the above processes. To test these hypotheses, we used a combination of high-frequency video monitoring (through acoustic and visible-infrared cameras), direct diving observations, and diet analyses to track the dynamics of a WS of *H. anomala* in Lake Geneva at different time-scales. Our results reveal adult-juvenile successions during swarm formation while swarm ending was associated to the presence of only juveniles suggesting an effective implication of reproduction for WS formation and possibly its collapse. Temperature had a negative indirect effect on *H. anomala* abundance during the WS collapse and was only partly mediated by the littoral returns of perch (*Perca fluviatilis*) for which active predation was clearly identified from videos.

**Keywords:** Lake / invasive species / mysids / temperature / reproduction / predation

## 1 Introduction

Massive aggregation is a widespread phenomenon among species worldwide that can be caused by diverse drivers related to facilitation of mate encounters for reproduction (Domeier and Colin, 1997; Wilcove and Wikelski, 2008; Erisman *et al.*, 2012), supply of local resources (Genin, 2004), anti-predation strategies (Clark and Mangel, 1986; Lindén, 2007; Menezes, 2021) or the search for suitable habitat refugia (Hunt *et al.*, 2019). The actual mechanism behind the aggregation of individuals can hence be questionable for particular species especially for those whose ecology remains poorly known, which is typically true for exotic species within newly invaded ecosystems. Indeed, when exotic species colonize new environments, they encounter new environmental conditions as well as novel ecological interactions with the native fauna (Sih *et al.*, 2010; Saul *et al.*, 2013). Together, these factors or processes can drive rapid behavioral adaptations that diverge from those

observed in their native ranges, forming the basis of their ecological impacts on recipient ecosystems (Wright *et al.*, 2010; Ruland and Jeschke, 2020). For instance, previously undocumented massive aggregations of wels catfish (*Silurus glanis*) have been recorded in the Rhône River (France), and although the underlying mechanism remains to be elucidated, they can represent important biogeochemical hotspots (Boulêtreau *et al.*, 2011), as also observed for aggregations of invasive loricariid catfishes (Capps and Flecker, 2013). Furthermore, these aggregations can also drive significant ecological and socio-economic impacts, as shown by the invasive ctenophore *Mnemiopsis leidyi*, which has been associated with zooplankton collapse and fishery declines (Marambio *et al.*, 2013; Roohi *et al.*, 2024; Piccardi *et al.*, 2025).

The mysid *Hemimysis anomala*, commonly known as the bloody-red shrimp, is a small crustacean of the order Mysida (family Mysidae). It is characterized by rapid growth and high fecundity, producing multiple generations per year with approximately 20–50 embryos per female (Borza, 2014). The species also exhibits broad physiological tolerance across

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a wide range of environmental conditions, including temperature (2–28 °C), salinity (0–18 ‰), and conductivity (98–29, 200  $\mu\text{S cm}^{-1}$ ; Wittmann, 2007), but see Rogissart *et al.* (2025) for a recent review. This mysid is a generalist feeder consuming both zooplankton and phytoplankton but also detrital resources (Ketelaars *et al.*, 1999; Borchering *et al.*, 2007; Evans *et al.*, 2018; Frossard *et al.*, 2024). Native to the Ponto-Caspian region, it has invaded many large lakes in Europe and North America and has often been reported to form massive winter swarms (WS) in open water, at shallow depths (<20 m) in littoral habitats. These WS can reach up to 20 m in length and 5 m height, and be composed of thousands to millions of individuals (Golaz and Väinölä, 2013; Jacquet, 2023; Rogissart *et al.*, 2024, 2025). These aggregations generally disappear rapidly from the water column within a few days during the winter-to-spring transition (Wachala *et al.*, 2025). This raises questions regarding the factors or processes driving the temporal dynamics of these WS. Several biological and environmental drivers have been hypothesized to contribute to both formation and disappearance of WS, including reproductive processes (Ketelaars *et al.*, 1999; Dumont and Muller, 2010), resource availability (Frossard *et al.*, 2024; Wachala *et al.*, 2025), predation pressure (Lantry *et al.*, 2012; Gallagher *et al.*, 2015), and temperature-mediated effects acting indirectly on these processes (Pothoven *et al.*, 2007; Jacquet, 2023; Rogissart *et al.*, 2025). Firstly, WS formation is expected to support a reproductive function since such aggregations generally include ovigerous females (Dumont and Muller, 2010; Frossard and Fontvieille, 2018; Jacquet, 2023). Alternatively, *H. anomala* WS may also represent a feeding-related behavior, potentially enhancing foraging efficiency or reducing energetic costs associated with resource acquisition, consistent with a trophic function (Ritz *et al.*, 2001; Wachala *et al.*, 2025). Indeed, differences in diet compositions between individuals sampled in pelagic swarms and those collected from benthic habitats further support a link between swarming behavior and resource acquisition (Wachala *et al.*, 2025). Regarding WS disappearance, its suddenness could suggest an on-off mechanism. This could be related to the end of reproductive events associated with a synchronic collective release of young juveniles followed by adult dispersal and / or individual mortality following reproduction (Mauchline, 1980; Ketelaars *et al.*, 1999). Indeed, in the nearby Lake Bourget, a marked transition from adult-dominated to juvenile-dominated populations was observed prior to WS disappearance in early spring (Frossard and Fontvieille, 2018). An alternative hypothesis explaining the termination of WS could involve temperature rising affecting resource availability (Ketelaars *et al.*, 1999). Indeed, in Lake Geneva, WS collapse typically occurs with increasing littoral water temperature during winter-to-spring transition from March to April (Jacquet, 2023), a period that is also characterized by a marked rise in phytoplankton biomass (CIPEL, 2023). This can enable *H. anomala* to access a wider range of trophic resources as compared to those available in winter times (Frossard *et al.* 2024), possibly implying a change in trophic strategies where aggregation is no more efficient (Wachala *et al.*, 2025). At the same time, the warming of littoral temperature fosters fish activity and *H. anomala* individuals swimming in open water may be particularly vulnerable to predation in this context. In large peri-alpine

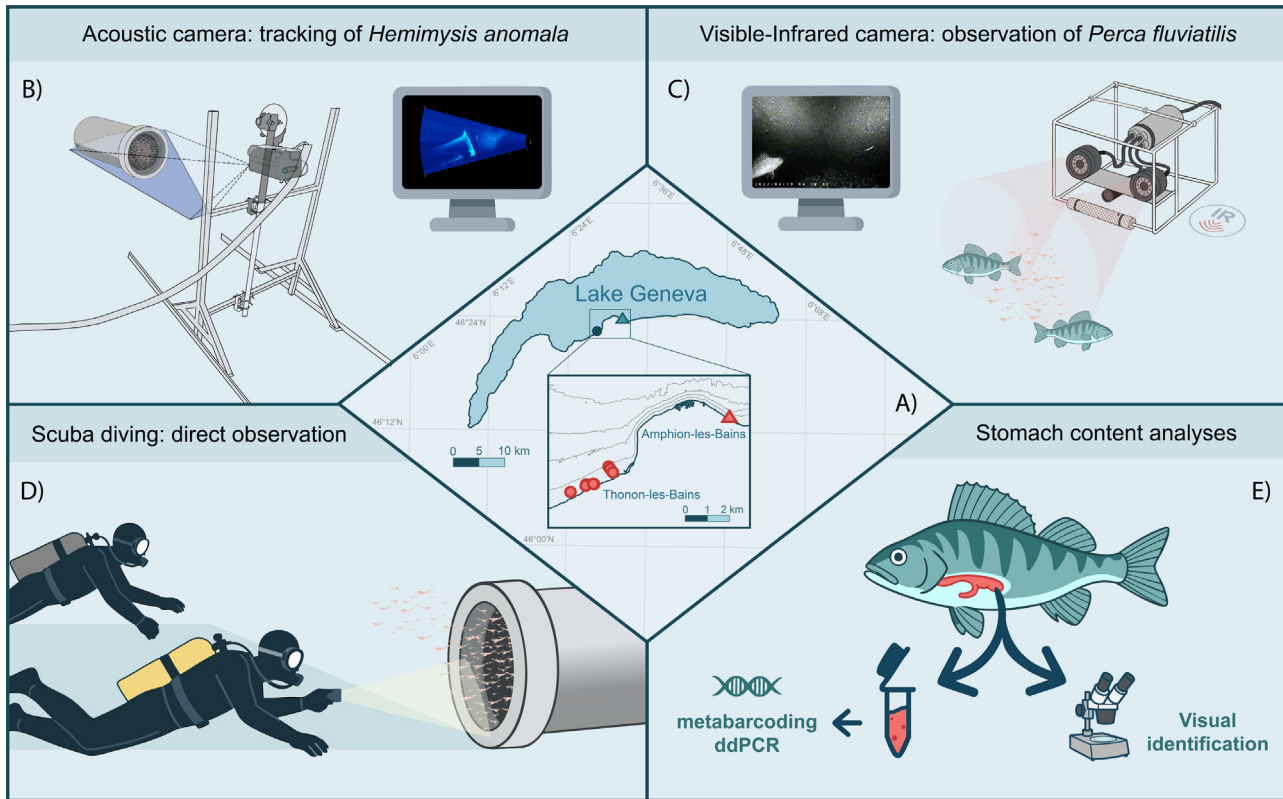
lakes, the European perch (*Perca fluviatilis*) dominates fish communities (Anneville *et al.*, 2017) and represents a strong candidate for *H. anomala* predation (Borchering *et al.*, 2007; Gallagher *et al.*, 2015). Yet, other fish species can also consume *H. anomala* such as pumpkinseed (*Lepomis gibbosus*) or burbot, *Lota lota*, but their densities are minor relative to perch and their predation pressure is then expected to be minor. European perch exhibits seasonal migrations, overwintering in deep offshore waters (water depth >20 m up to 60 m depth) and returns towards littoral habitats in early spring when temperatures are rising (Thorpe, 1977; Imbrock *et al.*, 1996; Guillard *et al.*, 2006). Hence, the perch return to the littoral zone may typically coincide with the disappearance of *H. anomala* WS. In this sense, temperature rising during the winter-to-spring transition could be a major indirect driver of WS dynamics by conditioning its termination mediated by both an increase in resource availability and predation pressure.

In this study, we mobilized a wide array of monitoring approaches to track, at complementary temporal scales, the dynamics of an *H. anomala* WS and its potential drivers in Lake Geneva. At the seasonal scale, we characterized the development stages present in *H. anomala* WS to evaluate whether it could be linked to a reproductive process. The implication of predation on WS dynamics was assessed using two complementary ways. First, we investigated perch stomach contents using both visual and molecular approaches across multiple depths, covering a temporal sequence from late winter to early autumn (February–October) over several sampling years. Secondly, high-frequency acoustic and visible-infrared cameras were deployed to focus on the sudden WS disappearance during a winter-to-spring transition (February–April 2022). During this period, we quantified short-term fluctuations in swarm density and tracked concurrent changes in water temperature and perch presence in the littoral zone of Lake Geneva. This multi-scale integrative approach design allowed us to test how the dynamics of *H. anomala* WS could be mediated by a set of successive processes implying reproductive opportunity, predation avoidance and resource availability together indirectly mediated by seasonal variations of water temperature.

## 2 Materials and methods

### 2.1 Study and sampling area

Lake Geneva is the largest peri-alpine lake located between France and Switzerland (46°27'N, 06°32'E), covering a surface area of 582 km<sup>2</sup>, with a maximum depth of 309 m (mean depth: 157 m) and an elevation of 372 m above sea level (Fig. 1A). During the last decades, this ecosystem allowed the settlement of a variety of exotic species, amongst which the bloody-red shrimp (Golaz and Väinölä, 2013; Lods-Crozet, 2020). The survey of *H. anomala* WS was conducted at Amphion-les-Bains on the French shore of the lake (46°23'51"N, 6°32'10"E; Fig. 1A) at 45 meters from the shoreline and at a depth of 4 meters where animal aggregation has been observed by divers each winter since 2019 in a concrete pipe of known volume (Rogissart *et al.*, 2024). This survey included video recordings from two types of cameras (acoustic for WS and visible-infrared for perch detection;



**Fig. 1.** Schematic overview of the methodological framework used to track the dynamics of *Hemimysis anomala* winter swarms in Lake Geneva. The central panel (A) shows the study area near Amphion-les-Bains and Thonon-les-Bains. Triangle indicates the site of instrument deployment (acoustic and infrared cameras), while red points indicate perch stomach sampling sites (littoral and deeper offshore locations). The study combined four complementary approaches: (B) high-frequency acoustic camera to quantify mysid swarm dynamics; (C) visible-infrared video recordings to monitor perch (*Perca fluviatilis*) presence with direct observation of predation events; (D) direct underwater observations of mysid swarms by scientific and recreational divers; and (E) analysis of perch stomach contents using environmental DNA approaches (metabarcoding, ddPCR) and visual identification.

Figs. 1B and 1C) and diving observations from both recreational and scientific divers (Fig. 1D).

## 2.2 Seasonal survey of *Hemimysis anomala*

The seasonal survey of *H. anomala* WS was conducted through direct underwater observations by scientific and volunteer divers (citizen science) at the concrete pipe site in Amphion-les-Bains between October 2021 and April 2022. In total, 47 dives were performed, corresponding to 23 h 32 min of underwater observation. Dives were conducted during daytime, primarily in the morning (09:00–10:30), with a limited number of dives in the early afternoon (14:00–15:30;  $n = 5$ ). This timing ensured that *H. anomala* winter swarms had retreated into their shelters, facilitating accurate counts and life-stage assessments. During each dive, divers visually estimated the density of *H. anomala* within a 1.4 m<sup>3</sup> reference cylinder (concrete pipe) using the standardised underwater protocol described in Rogissart *et al.* (2025; Appendix 1), in which abundance classes (ind. m<sup>-3</sup>) and life-stage proportions (juveniles, adults) are recorded on a waterproof submersible plate. This approach provided estimates of density and life

stage composition throughout the seasonal cycle, from initial swarm formation to its complete disappearance. The estimated number of individuals present during each dive was obtained by multiplying density by the pipe volume (1.4 m<sup>3</sup>), and juvenile-adult counts were derived from the observed life-stage proportions. Monthly juvenile and adult proportions were weighted by this estimated number of individuals inside the pipe.

## 2.3 Monitoring the winter swarm collapse

The Adaptive Resolution Imaging Sonar (ARIS) Explorer 3000 (Sound Metrics Corporation, Washington, USA) was used to monitor *H. anomala* WS over successive periods between February 20th and March 30th, 2022. A total of nine monitoring sessions, each spanning two consecutive days, were equally spaced throughout this period to capture swarm dynamics during the disappearance phase. These sessions encompassed the onset of perch arrival in the littoral zone. After aligning data from overlapping sessions, daily *H. anomala* detections were summed and log-transformed, resulting in eight daily values used for analysis of WS

abundance in relation to perch detections obtained from the infrared camera. Each deployment covered the night-time period from 5:00 pm to 9:00 am, providing continuous observations as a proxy for WS abundance. Operating at high frequencies, the ARIS produces video-like acoustic images by capturing reflected signals from objects with densities different from the surrounding medium. The sonar was set to 3 MHz to achieve maximum resolution (2.9 mm) within a detection range of 1.1 to 6 meters. The first meter was excluded from analysis due to strong echoes that caused signal distortion. Data were continuously recorded in 10-minute intervals using ARIScope software (v. 2.7.3) and subsequently aggregated to daily sums to match the time resolution of perch abundance and water temperature data. Hourly water temperature data (0–4 m depth) were obtained from the Alplakes platform (Baracchini *et al.*, 2020; Wüest *et al.*, 2021). The study site corresponds to a grid cell of the hydrodynamic model encompassing Amphion-les-Bains.

A detailed description of the setup and methodology is provided in Rogissart *et al.* (2024).

## 2.4 Monitoring fish presence and predation events

To investigate the impact of fish density on *H. anomala*, an infrared (IR) camera (Abyse 650P, LCTECH, France) was deployed at the same location as the acoustic camera. The IR camera was mounted on a metallic frame and equipped with two infrared LED projectors to enhance night visibility. The camera operated between March 15 and March 30, 2022, recording six-hour periods each night (5:00–11:00 pm and 4:00–10:00 am), with 15-minute file intervals. The camera's effective detection range extended to approximately 2 m at night under infrared illumination and up to about 6 m during daylight conditions, providing clear visibility of the concrete pipe and the adjacent bottom area. A total of 156.7 hours of video footage (Tab. S1) was analyzed, which was processed at  $\times 4$  speed using VLC Media Player (v. 3.0.18, VideoLAN Organization). For each video, all fish visible within the camera's field of view were manually recorded by noting the video file name, date, time of observation, and the number of individuals present. Perch (*P. fluviatilis*) largely dominated the assemblage, whereas other species were only occasionally observed and are not known as potential predators of *H. anomala* (e.g., *Esox lucius*). The video file name, date, and the time of each perch sighting were logged and stored in a CSV file for further analysis. Unlike the acoustic camera, the visible-infrared camera enabled the direct visualization of perch predation events on *H. anomala* during both daytime and nighttime observations (Movies S1–S3). Video data from two recording sessions (15 and 18 March) and from two consecutive days (24–25 March) were lost due to equipment malfunction (Tab. S1). Daily perch detections were aggregated and standardized as counts per hour of observation effort, to correct for variation in sampling duration (two days with 6 h and 6.7 h compared to the usual 12 h). Perch detections were used as a proxy of predation pressure, encompassing both consumptive interactions and non-consumptive effects mediated by predator cues (e.g., visual or chemical signals) that can trigger behavioural responses in *H. anomala*.

## 2.5 Diet analyses of perch

To identify whether perch consumed *H. anomala* across sites and sampling periods, we analyzed perch stomach contents using complementary visual and molecular approaches. Perch stomachs were collected at depths ranging from 5 to 45 m in the vicinity of Thonon-les-Bains (Figs. 1A and 1E), where both scientific surveys and fishery-based sampling were conducted during winter 2021–2022 and summer 2022. We also sought to assess whether predation persisted after swarm disappearance, which would indicate dispersion of individuals rather than mortality. To this end, we compiled stomach samples collected across multiple periods and depth, from littoral sites (5–10 m) to offshore sites down to 45 m.

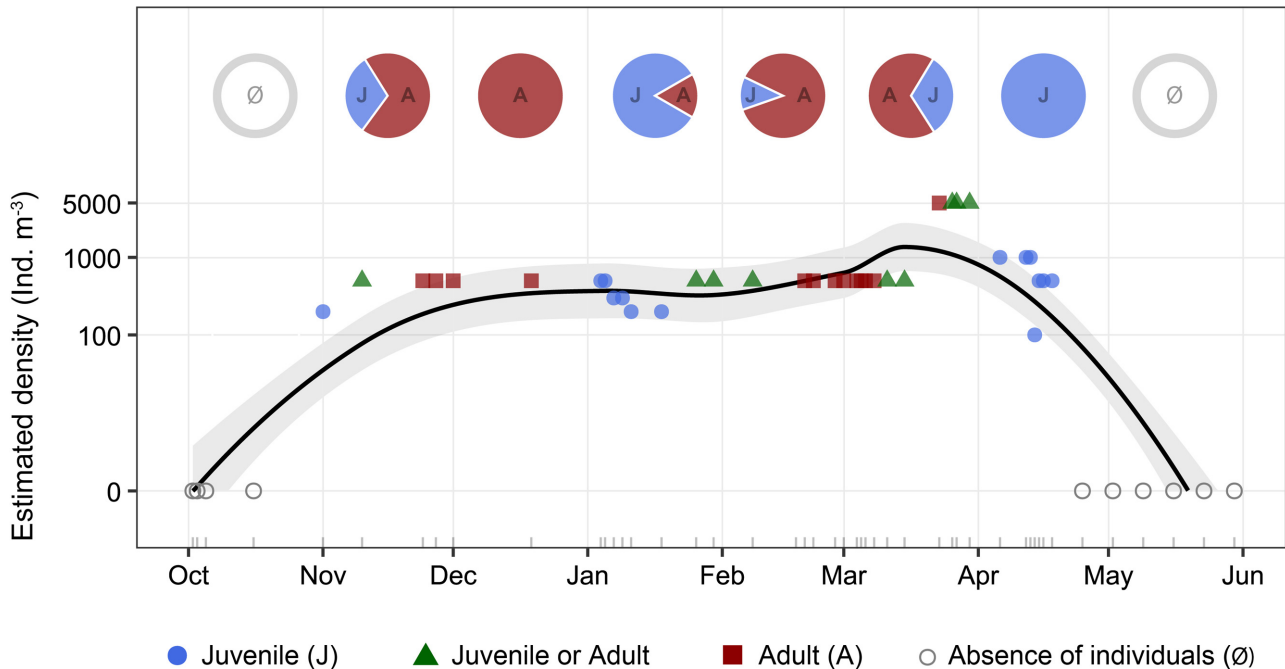
A total of 187 perch were collected during scientific survey campaigns (2018 and 2022) and from professional fishers in the Thonon-les-Bains area of Lake Geneva (2022–2023). Fish were retrieved early in the morning following night fishing, using gillnets of various mesh sizes ranging from 12.5 to 29 mm (Tab. S2). For each sampling campaign, the number of perch analyzed, gillnet mesh size, depth range, and mean total lengths (TL) were recorded (Tab. S2). This sampling design yielded individuals with mean TL ranging from approximately 116 to 168 mm. Stomachs were excised from captured fish and preserved in 70% ethanol (Hyslop, 1980). Stomachs with no visible content ( $n = 15$ ) were excluded from further analyses. Stomach contents were inspected under a stereomicroscope (Olympus SZ-CTV) equipped with a camera (AxioCam MRc) to identify prey based on morphological remains (Hyslop, 1980).

To complement visual identification, 16 additional perch obtained from a professional fisher in the Thonon-les-Bains area across eight sampling dates between February and April 2023 were analyzed using molecular tools (Figs. 1A and 1E). Metabarcoding was used to characterize the overall prey composition within stomach contents, while droplet digital PCR (ddPCR) provided a highly specific quantification of *H. anomala* DNA. Sampling and extraction procedures followed standard eDNA protocols for stomach content analysis. Detailed laboratory procedures for DNA extraction, amplification, sequencing, and ddPCR are described in Appendix S1.

## 2.6 Data analysis

Due to the limited sample size, to assess causal pathways between water temperature, perch detections and *H. anomala* swarm abundance, we applied a simple mediation analysis using the classic three-equation approach (Baron and Kenny, 1986; Preacher and Hayes, 2008). Each path was estimated using linear models, allowing us to test both direct and indirect effects of water temperature on *H. anomala* WS abundance, mediated through perch detections. The significance and 95% confidence interval (CI) of the indirect effect were assessed using non-parametric bootstrap resampling with 10,000 iterations (Preacher and Hayes, 2008).

To handle missing data in the time series, we used two generalized additive models (GAMs, quasi-Poisson distribution, log link) for imputation purposes with a smooth term for day index. Two missing days (24–25 March) and two partially



**Fig. 2.** Seasonal dynamics of *Hemimysis anomala* estimated density (ind. m<sup>-3</sup>) from winter 2021 to summer 2022, based on diving observations of the swarm located in the reference concrete pipe (1.4 m<sup>3</sup>). Points represent individual observations, distinguished by life stage (blue circles = Juvenile, green triangles = Juvenile or Adult, red squares = Adult) and by absence of individuals (open grey circles, *i.e.*, no mysids detected). The black line and grey shaded area show a loess smoother with its 95% confidence interval. The y-axis is shown on a logarithmic scale. Inset pie charts above each month summarize the proportion of juveniles (J) and adults (A) (weighted by total individuals observed across dives).

sampled days (15, 18 March) were completed by predicting the number of perch detections for the missing hours to reach 12 h. In addition, daily *H. anomala* WS abundance was imputed for days lacking complete acoustic coverage within the perch monitoring period (see Fig. 3).

Statistical analyses were performed using R (v. 4.3.2; R Core Team 2024). GAMs were fitted using the *mgcv* package (Wood, 2017), and results were visualized using the *ggplot2* package (Wickham, 2011).

### 3 Results

#### 3.1 Seasonal dynamics of winter swarm

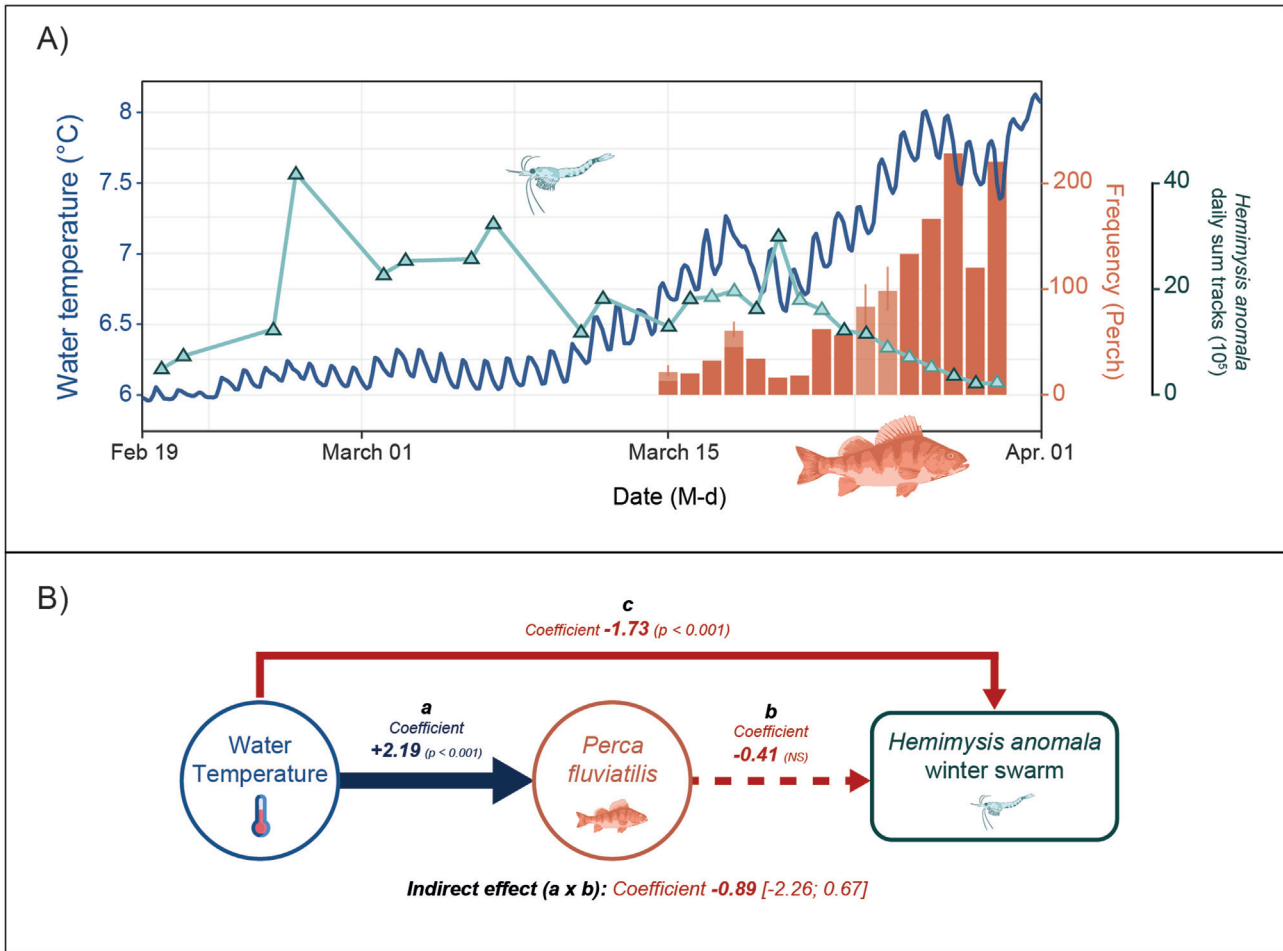
Diving observations revealed marked seasonal changes in the estimated density of *H. anomala* swarms (Fig. 2). No individuals were detected in early autumn, but swarm density increased progressively from late autumn, peaked during winter until early spring, and declined rapidly thereafter. No swarms were observed from mid spring onward, corresponding to zero-density observations (open grey circles in Fig. 2). Both adults and juveniles were found within the WS, indicating that these aggregations encompassed multiple life stages rather than a single cohort. Throughout the winter, their relative occurrence alternated, with adults predominating from December to March and juveniles being observed both in mid-winter (January) and during the late phase of the WS. By late March, adults were no longer observed, while juveniles persisted until spring. Peak winter densities exceeded 10<sup>3</sup> ind. m<sup>-3</sup> (max. observed = app. 5,000 individuals), consistent with dense winter aggregations described in Lake Geneva.

#### 3.2 Disappearance of winter swarm

During the infrared camera monitoring period (15–30 March), mean littoral water temperature increased from 6.7 to 7.8 °C, while the daily abundance of *H. anomala* swarms declined markedly (from 1.3 × 10<sup>6</sup> to 2.1 × 10<sup>5</sup>; Fig. 2). Subsequent dive surveys conducted after the monitoring period revealed a complete absence of *H. anomala* swarms from 25 April onward, when mean water temperature reached approximately 10 °C (9.96 °C). The mediation analyses showed that temperature was significantly associated with both perch detections and WS abundance. Specifically, water temperature had a significant positive effect on perch detections ( $a = 2.19 \pm 0.23$ ,  $p < 0.001$ ; Fig. 3B) and a significant negative total effect on winter swarm abundance ( $c = -1.73 \pm 0.30$ ,  $p < 0.001$ ). The relationship between perch detection and *H. anomala* WS abundance was negative but non-significant ( $b = -0.41 \pm 0.35$ ,  $p = 0.26$ ). Nevertheless, temperature also exerted an indirect negative effect on WS abundance through perch detections ( $ab = -0.89$  [95% CI -2.26; 0.67]). This indirect pathway accounted for approximately 52% of the total temperature effect (Tab. S3).

#### 3.3 Stomach content analyses (visual and molecular)

Among the 187 perch stomachs analyzed, *Hemimysis anomala* was only detected in individuals captured at shallower depths (5–12 m) during summer (July–September; Fig. 4). No occurrences of *H. anomala* in perch collected



**Fig. 3.** Temperature, detection of *Perca fluviatilis* and *Hemimysis anomala* winter swarm in Lake Geneva. A) Water temperature (blue line), daily sum tracks of *H. anomala* recorded by the high-frequency acoustic camera (green triangles) and daily *P. fluviatilis* detections from infrared video monitoring (orange bars, March 15–30, 2022). Counts for March 15 and 18 (completed) and March 24 and 25 (no direct observations) were predicted from a GAM (95% confidence intervals, CI95). Abundance values of *H. anomala* for days lacking complete acoustic coverage were similarly predicted with associated CI95. B) Mediation model depicting the direct and indirect effects of water temperature on daily perch detection, and *H. anomala* swarm abundance. Path coefficients were estimated from linear regressions; the indirect effect ( $a \times b$ ) was computed by bootstrap (10,000 iterations). Solid arrows indicate significant effects ( $p < 0.05$ ), dashed arrows non-significant effects ( $p > 0.05$ ). Arrow colour denotes the direction of effect (blue = positive, red = negative).

deeper than 20 m earlier in the season (February–June) could be identified. However, during the second part of March when the visible-infrared camera was deployed, perch predation events on *H. anomala* swarms could be actually recorded by visible-infrared camera, both during day and at night times (Movies S1–S3), providing visual confirmation of active trophic interactions during the WS collapse.

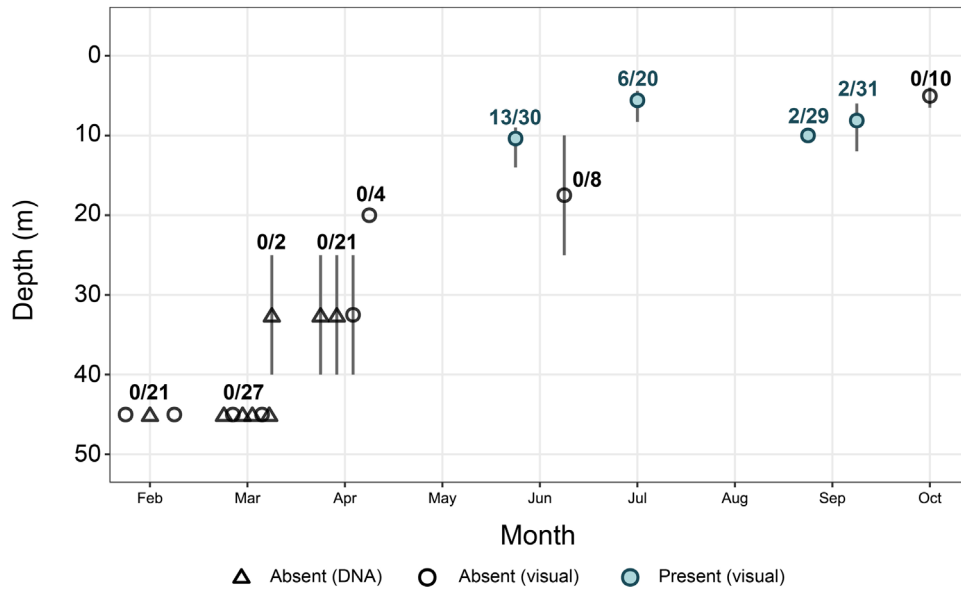
Complementary, metabarcoding of 16 perch stomachs revealed a diverse set of prey taxa, including the pelagic cladoceran (*Daphnia galeata*, *Bythotrephes longimanus*) and benthic macroinvertebrate (*Dikerogammarus villosus*) and fish (*Rutilus rutilus*, *Coregonus sp.*, *Tinca tinca*) (Fig. S1). However, no reads were assigned to *H. anomala* in the stomach contents of these 16 individuals. Consistently, species-specific ddPCR assays confirmed the absence of *H. anomala* DNA, supporting the metabarcoding results while validating detection sensitivity (Fig. S2).

## 4 Discussion

By integrating automated monitoring devices, direct diving observations and stomach content analyses, our results support the role of multiple drivers in the formation and disappearance of *H. anomala* winter swarms. Swarm formation seemed consistent with a reproductive function, whereas swarm disappearance coincided with seasonal warming that could act as an indirect environmental driver of perch activity and resource availability.

### 4.1 Reproduction implication in WS dynamics

Our study provides evidence of active reproduction during the WS period. Both adults and juveniles were present during the WS formation with alternating dominance where adults prevailed from December to March, while juveniles were



**Fig. 4.** Depth distribution of perch stomachs analyzed for the presence of *Hemimysis anomala* (all campaigns pooled). Each point represents a sampling campaign and its associated depth, with vertical bars showing the depth range of gillnets tracking perch bathymetric distribution. Symbols indicate the detection of *H. anomala* in perch stomach contents (blue filled circles: present, white open circles: absent by visual inspection, open triangles: absent by DNA analysis). Numbers above points indicate the number of stomachs where *H. anomala* was present, relative to the total stomachs examined.

observed both in mid-winter and during the final phase of the WS. There could hence be multiple reproductive events during the WS period. Such dense aggregations confer reproductive advantages, notably by increasing mate encounter rates and facilitating successful pairing (Clutter, 1969; Ritz *et al.*, 2011; Sinclair and Arnott, 2016). Interestingly, the disappearance of adults by late March was concomitant with a sharp increase in juveniles suggesting that the termination of WS could be associated with the end of a major reproductive event. This pattern aligns with observations in other peri-alpine lakes, where gravid females dominate winter aggregations, and juveniles appear during early spring when WS disappears (Dumont and Muller, 2010; Frossard and Fontvieille, 2018).

While these elements clearly demonstrate that reproduction is closely associated with WS, they do not by themselves establish reproduction as the primary driver of swarm formation. Instead, they indicate that reproductive processes likely contribute to the seasonal timing and internal structure of WS, alongside other mechanisms such as predation pressure and changes in resource availability. In line with the recent findings of Wachala *et al.* (2025), no mass mortality was observed following the WS disappearance in diving observations. Adult individuals could hence be expected to disperse into other habitats after their massive aggregation phase. If reproduction could be an important process behind WS formation and maintenance, the processes implied in adult dispersal leading to WS disappearance may hence be related to other factors than a reproductive constraint.

#### 4.2 Predation as driver of WS disappearance

The negative effect of perch on WS density was identified by our mediation model, although its effect was limited. Complementarily, perch predation was directly confirmed by

visible-infrared recordings, where perch attack and consumption of *H. anomala* were observed several times during the WS collapse. These results are consistent with observations from other invaded systems, where perch rapidly incorporate *H. anomala* into their diet with up to hundreds of mysids ingested per individual (Lantry *et al.*, 2012; Gallagher *et al.*, 2015). The consumption of *H. anomala* by perch is likely fostered by its high lipid content and nutritional value (Borcherding *et al.*, 2007) making it an energetically attractive prey for perch especially by the end of the overwintering period. Additionally, non-consumptive effects mediated by perch cues such as chemical signals or visual presence, are also likely to affect *H. anomala* behaviour (Boscarino *et al.*, 2020) and contribute to WS collapse. Indeed, *H. anomala* possesses a strong behavioural plasticity (Van Gool and Ringelberg, 2002; Boscarino *et al.*, 2020; Rogissart *et al.*, 2025) that can facilitate changes in collective behaviour (swarm formation) and habitat use (dispersion in safer habitats) in the presence of predators. The WS disappearance hence coincided with the return of overwintering perch within the lake littoral habitats that could represent a non-negligible predation pressure possibly constraining *H. anomala* to adjust its behaviour by shifting from a massive swarm to a dispersed use of safer habitats.

At a larger time scale, the seasonal survey of perch diets highlighted that perch predation on *H. anomala* was spatially restricted to the lake littoral with positive detections in stomach contents limited to shallow waters (5–12 m) while it was absent from perch diets caught in deeper waters (>20 m). In the littoral habitats, the predation seemed to operate whenever perch were present with positive presence in perch stomach from mid-May to Mid-September. This result indicates that predation pressure on *H. anomala* could be temporally restricted to spring to summer time when perch are present in surface waters of the littoral zone. The effect of predation

pressure of perch on the termination of the WS could thus represent the onset of post-winter trophic interactions between these two species that will last until the following autumn, when perch will travel back to deeper waters to overwinter. Moreover, perch predation during summer times, where no massive aggregation occurs, may suggest that perch could efficiently exploit smaller aggregates of *H. anomala* in the littoral.

### 4.3 Temperature as an indirect forcing of WS dynamics

During the winter-to-spring transition, the disappearance of *H. anomala* WS coincided with a marked increase in water temperature, together with a concomitant increase in perch detections, and complete absence of swarms at water temperatures around 10 °C. Mediation analyses revealed that temperature was significantly associated with both perch presence and WS abundance, highlighting the integrative role of temperature in the processes driving swarm disappearance. More specifically, increasing temperature was associated with a higher detection of perch, while the relationship between perch detections and WS abundance was negative but non-significant. These results indicate that if perch predation may contribute to WS disappearance additional temperature-related processes were involved.

The effect of perch predation can be interpreted as an indirect effect of temperature, as perch phenology and specifically its migration from deep to shallow waters is temperature-dependent (Thorpe, 1977; Imbrock *et al.*, 1996; Guillard *et al.*, 2006).

Complementary diving observations indicated that winter swarms (WS) comprised both adults and juveniles. Adults progressively disappeared toward the end of the swarm period, whereas juveniles were still observed shortly before complete swarm disappearance. The strong statistical association between water warming and WS decline, together with the presence of juveniles, suggests that temperature may also influence the timing of reproduction, representing an additional indirect effect of temperature on WS dynamics. This interpretation is supported by the strong thermal sensitivity of mysid reproductive cycles (Ketelaars *et al.*, 1999; Pothoven *et al.*, 2007).

Finally, rising temperature by the end of winter also increase resource availability that can encourage individuals to disperse (Clobert *et al.*, 2009; Kreuzinger-Janik *et al.*, 2022; Wachala *et al.*, 2025). In Lake Geneva, spring warming is accompanied by a marked increase in phytoplankton biomass and by a two- to three-fold rise in zooplankton abundance (CIPEL, 2023). Taken together, these results suggest that temperature could hence possibly serve as an environmental cue marking the end of the reproductive period and triggering the dispersal of adults due to predation pressure and new resource availability.

The dominant control of temperature on WS was recently reported by Jacquet (2023) during the winter 2022 where no WS was observed concomitantly to a very warm autumn/winter time. In the context of global warming, the formation of these massive WS in lakes may become increasingly sporadic, or they may even disappear entirely. This would be a major effect of climate change on the phenology of this species.

## 5 Limits and perspectives

Despite these clear temporal associations, the limited sample size prevented a robust assessment of the relative contributions of temperature and perch predation. Our observations were limited to one single winter-spring season and a limited number of sites. Moreover, we did not have direct mortality estimates and we could not clearly disentangle a disaggregation from a true decline in population. Indeed both high mortality (Ketelaars *et al.*, 1999; Pothoven *et al.*, 2007) and individual survival (Wachala *et al.*, 2025) have been reported following reproduction. Future endeavors could replicate this integrative approach in different sites and years to evaluate the spatial and temporal variability of *H. anomala* population dynamics. Integrating experimental approaches involving predators, prey, and environmental variables would allow better quantification of the causal pathways linking abiotic forcing, predation pressure, and swarm dynamics. Such integrative monitoring efforts, combining direct observations, citizen-science contributions, acoustic camera and molecular tools, have recently been recommended as the only effective way to capture the full dynamics of *H. anomala* populations across heterogeneous habitats (Sepulveda *et al.*, 2020; Rogissart *et al.*, 2025). This work will be essential for predicting the eventual ecological consequences of invasive mysids in freshwater ecosystems.

## 6 Conclusions

The diverse methodological approaches employed in this study across multiple timescales allowed us to demonstrate that the formation and disappearance of *H. anomala* winter swarms (WS) in Lake Geneva are governed by several interacting processes. The presence of multiple life stages within WS, along with the persistence of juveniles during the final phase of the swarms, supports the hypothesis of a reproductive role for winter swarms. Rising water temperatures during the winter-to-spring transition emerge as a major indirect driver, likely influencing both increased predation pressure and resource availability. These findings highlight the importance of integrative monitoring approaches to disentangle the contributions of such interacting drivers to the seasonal phenology of invasive mysids. In particular, combining high-frequency observations with longer-term surveys is essential to capture the full spectrum of behavioral and demographic processes underlying WS formation and disappearance across years and sites. Future studies should investigate whether warming-driven shifts in swarm phenology alter predator-prey overlap and, beyond predation, whether dense swarms act as transient hotspots that reshape resource availability and indirect interactions within invaded food webs.

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## Conflicts of interest

One of the authors serves as the Editor-in-Chief of the journal. To ensure the impartiality of the editorial process, the management of this article was conducted entirely by Young-Seuk Park, guest associate editor.

## Author contribution statement

Hervé Rogissart: Conceptualization, Methodology, Visualization, Formal analysis, Data curation, Writing – original draft, Writing – review & editing. Victor Frossard: Conceptualization, Methodology, Writing – review & editing. Jean Guillard: Conceptualization, Writing – review & editing. Marine Vautier: Methodology (ddPCR), Formal analysis (ddPCR), Writing – review & editing. Valérie Hamelet: Methodology (stomach content), Formal analysis (stomach content), Writing – review & editing. Cécile Chardon: Methodology (ddPCR), Formal analysis (ddPCR), Writing – review & editing. Stéphane Jacquet: Project leader, Funding acquisition, Conceptualization, Methodology, Writing – review & editing; installed underwater cameras, conducted direct observations through diving, invited recreational divers to participate in the survey.

## Supplementary material

**Table S1.** Sampling effort for visible-infrared camera observations of perch detections (number of individuals, n) in March 2022. For each sampling date, observation time slots and total daily duration (hours) are indicated. All times are given in local time (CET).

**Table S2.** Summary of perch sampling campaigns in Lake Geneva. For each campaign, the sampling type (scientific survey or professional fishers), mesh size of gillnets, depth range, number of analyzed perch and mean total length  $\pm$  standard deviation (sd).

**Table S3.** Summary of linear model (LMs) used to estimate the direct and indirect path coefficients (a, b, c) in the mediation analysis between water temperature, perch detections and *Hemimysis anomala* winter swarm abundance in Lake Geneva. Estimates ( $\beta$ ), standard errors (SE), t-values, adjusted R<sup>2</sup>, and p-values are reported.

**Figure S1.** Main prey taxa detected in perch (*Perca fluviatilis*) stomachs using three metabarcoding markers, including MiFish-U (fish-specific 12S rRNA), COI\_MG2 (targeting arthropods and other metazoans) and Leray-XT (broad-spectrum COI for invertebrates). Bars show the total number of reads per taxon, partitioned by marker. Only relevant prey taxa were retained (non-prey taxa such as parasites, environmental contaminants or bacteria were excluded). No reads were assigned to *Hemimysis anomala*.

**Figure S2.** Droplet digital PCR (ddPCR) quantification of DNA from perch (*Perca fluviatilis*) and *Hemimysis anomala*. Left panel: stomach content samples analysed by molecular methods (CARA\_1-CARA\_16). Right panel: positive controls (*H. anomala* dilution series at 1000, 200, 8 and 1.6 pg; perch; perch and *H. anomala*) and negative controls (extraction control, T\_ext; no-template control, NTC).

**Supplementary Movies S1-S3.** Underwater infrared recordings documenting predation of perch (*Perca fluviatilis*) on *Hemimysis anomala* in Lake Geneva. These sequences illustrate direct predation events observed during late winter. Available at: <https://figshare.com/s/cc03cf128e9ea7c1fb28>

**Movie S1.** Predation event recorded on 18 March 2022 at 04:29.

**Movie S2.** Predation event recorded on 18 March 2022 at 04:30.

**Movie S3.** Predation event recorded on 22 March 2022 at 05:58.

**Appendix S1.** Detailed molecular protocols for perch stomach content analysis.

The Supplementary Material is available at <https://www.limnology-journal.org/10.1051/limn/2026001/olm>.

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