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Research paper

Annual endogenous cycle and thermal drivers of cocoon hatching in the earthworm *Amynthas tokioensis*

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Abstract

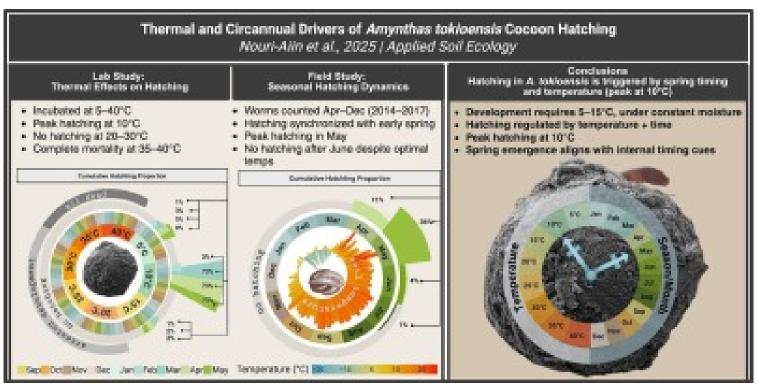
The earthworm *Amynthas tokioensis* (Megascolecidae), an introduced species in North America, has drawn attention for its geographic spread and potential soil impacts. This study examined the influence of temperature and endogenous rhythms on hatching from cocoons (oothecae), where eggs develop, using controlled-environment experiments and long-term field observations.

In a laboratory experiment over nine months, development to hatching-ready embryos occurred at 5–15 °C, but hatching was most successful at 10 °C (73 %). At higher temperatures, development was arrested (20–30 °C) or embryos died (≥35 °C), indicating a nonlinear effect of temperature on hatching. Although embryos developed early, hatching was delayed for six months until early spring, suggesting regulation by an endogenous cue rather than temperature alone.

Field data (Vermont, USA) from 2014 to 2017, where hatchling *A. tokioensis* were counted every two weeks, confirmed that hatching occurred only when soil temperatures were near 10 °C, with a flush in April/May. Although similar temperatures were observed later in the season, no hatching occurred beyond July.

Our results show that hatching is driven by temperature within a narrow range and by endogenous circannual rhythms to coincide with favorable spring conditions. This biological clock delays hatching to avoid low temperatures, while maximizing time for adult reproductive success. These findings improve our understanding of the thermal ecology and life history of *A. tokioensis*, highlighting its seasonal strategies. Future research should explore the molecular basis of circannual rhythms, their interactions with environmental factors, and their role in regulating population dynamics, including expansion and constraints on distribution.

Graphical abstract



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Introduction

Earthworms play a central role in shaping soil structure, chemistry, and biodiversity, with implications for both below- and above-ground ecosystem function (Singh et al., 2019). Darwin (1892) was perhaps the first to recognize the importance of earthworms, and now these annelids are viewed as ecosystem engineers and even keystone species within the complex soil community (Eisenhauer, 2010). While vital for soil health for many organisms and biodiversity, some earthworm species thrive in new environments and disrupt soil structure, ecosystem processes, and native communities (Chang et al., 2021).

Examples of introduced earthworm species are those in the pheretimoid group (Megascolecidae) native to East Asia (China, Hainan and Taiwan islands, Korea, and the Japanese archipelago) (Sato et al., 2023). Of ~700 known pheretimoid species, 90% fall under the genus *Amynthas* (now including *Metaphire*) (Sato et al., 2023). Three *Amynthas* species—*A. agrestis*, *A. tokioensis*, and *A. hilgendorfi*—have become widespread in the USA and southern Canada, earning the nickname "jumping worms" for their hyperactive behavior and high metabolic rate (Chang et al., 2021; Moore et al., 2022; Mathieu et al., 2024; Nouri-Aiin and Görres, 2024).

Amynthas earthworms have drawn attention for their ecological impacts and unusual reproductive biology. They spread via horticultural materials, especially through cocoons or oothecae—tiny, hard-to-detect egg cases that facilitate long-distance dispersal (Fig. 1) (Nouri-Aiin et al., 2022; Dávalos et al., 2025). While research has advanced our understanding of their taxonomy, distribution, genetics, dispersal, feeding behavior, and reproductive strategies (Hendrix and Bohlen, 2002; Uchida, 2004; Blakemore, 2009; Zhang et al., 2010; Schult et al., 2016; Keller and Schall, 2020; Nouri-Aiin et al., 2022; Sato et al., 2023; Schall et al., 2023), the biology of cocoons remains poorly understood—despite their central role in establishment and spread.

As annual species, *A. agrestis*, *A. tokioensis*, and *A. hilgendorfi* synchronize their life cycles with seasonal changes, producing cocoons in summer that overwinter and hatch in spring—surviving desiccation and freezing. This seasonal rhythm makes temperature a key driver of their development and survival. Like other temperate earthworms, *Amynthas* species are most active at 10–20°C, while their tropical relatives perform best at 20–30°C (Lee, 1985). In *A. agrestis*, hatching success peaks around 10°C, while viability declines above 40°C (Blackmon et al., 2019; Johnston and Herrick, 2019).

In both eastern North America and Japan, *Amynthas* hatching begins in April/May as temperatures rise above freezing. Juveniles grow rapidly, reaching adulthood by July, and largely perish after the first hard freeze in November (Uchida and Kaneko, 2004; Nouri-Aiin and Görres, 2019). Since adults do not survive beyond a single season, cocoons are critical for population persistence. Under unfavorable conditions like drought, development can pause, and cocoons remain viable for years—tolerating moisture loss up to 54% (Murchie, 1960; Gates, 1961). In *Amynthas* species cocoons may remain viable for years, forming a "cocoon bank" that buffers populations against harsh or unpredictable conditions—a bet-hedging strategy analogous to seed banks in plants (Lowe and Butt, 2014; Nouri-Aiin and Görres, 2019). In earthworms, reproductive success hinges on both cocoon production and hatching success, which are shaped by traits such as cocoon survival, structure, egg number, and tolerance to desiccation or freezing (Leirikh et al., 2004; Singh et al., 2019; Chaudhuri and Datta, 2020).

Hatching is likely regulated by developmental stage, soil moisture, temperature, and possibly an intrinsic circannual rhythm. Endogenous biological clocks like these are widespread across taxa, allowing organisms to align key life events—such as reproduction—with favorable environmental conditions (e.g., Buckley et al., 2017; Beer et al., 2019). This alignment reflects a broader "risk vs. opportunity" strategy, in which delayed or staggered emergence (e.g., bet-hedging) improves survival and long-term fitness under uncertain conditions (Warkentin, 2011).

Across earthworm species, cocoon production and hatching strategies vary dramatically—from prolific reproducers like *Perionyx excavatus* (1000+ cocoons/year) to low-output species like *Eutyphoeus gammiei* (1 cocoon/year) (Bhattacharjee and Chaudhuri, 2002). Hatching times also span weeks to years, shaped by environment and species. While some species produce cocoons with multiple viable eggs, most yield a single hatchling, and hatching timing is often finely tuned to climatic constraints (Lowe and Butt, 2014; Edwards et al., 2022).

Within this spectrum, *A. tokioensis* exemplifies a K-selected strategy: low fecundity (~10–50 cocoons per lifetime), slow development (~100-day maturation), and sensitivity to environmental conditions (Pianka, 1970; Nouri-Aiin and Görres, 2019). In New England, hatching can be delayed up to two years (Nouri-Aiin, 2022). Given their slow production rate (one cocoon every two days), hatching timing is critical—April hatchlings may yield up to 60 cocoons, while July hatchlings might produce as few as seven.

For *A. tokioensis*, precise hatching timing is essential to balance internal rhythms with environmental cues, especially temperature. Emerging too early risks cold-induced mortality, while late hatching shortens the reproductive window and limits cocoon output. As an epi-endogeic species confined to topsoil, *A. tokioensis* is especially vulnerable to freezing and desiccation compared to deeper-burrowing endogeic or anecic species.

Given that *A. tokioensis* thrives within an optimal temperature range of 10–20°C, we hypothesized that cocoons hatch early in spring to maximize the growing season and reproductive output. Earlier emergence may allow individuals to reach maturity sooner and produce more cocoons before senescence. We also considered that hatching may be shaped not only by temperature, but by endogenous seasonal timing—an internally regulated biological rhythm, evolved to anticipate and align key life cycle events—such as hatching—with predictable seasonal conditions, even in the absence of external environmental cues (Åkesson and Helm, 2020). This timing may reflect evolutionary adaptation to temperate climates, as *A. tokioensis* is native to Japan, where seasonal conditions closely resemble those in the northern USA and southern Canada. While our laboratory experiment was limited to the spring period, our four-year field study extended through summer and fall, enabling us to test this hypothesis across the full reproductive window.

To test this, we used two complementary approaches. First, a laboratory experiment evaluated the effects of temperature on embryonic development and hatching success, examined whether seasonal timing is regulated by an endogenous biological clock under constant conditions. Second, a four-year field study captured full-season dynamics, with year-round soil temperature monitoring and biweekly surveys of *Amynthas* life stages from spring through fall.

By integrating lab and field data, we characterize the hatching strategy of *A. tokioensis*, showing how temperature and seasonal timing regulate emergence. These insights are key to understanding population dynamics and managing this species in temperate ecosystems.

Section snippets

Cocoon collection and identification

To examine temperature and timing effects on hatching, we collected 1200 cocoons on August 25, 2023, from private land adjacent to a residential property in Burton, New Brunswick, Canada (45°86‘N and 66°40‘W, exact location withheld for privacy). The site was a lawned backyard with human-altered soils best classified as podzols, as anthropogenic soils. Soil textures ranged from sandy clay loam to clay loam, with some areas containing poorly drained silty clay (Bennett et al., 2024). Earthworm …

Embryonic viability

At the start of the laboratory study, nearly all embryos were at Stage 4, with only a small proportion undeveloped (Fig. 3). When incubated at 5–15 °C, embryos rapidly advanced to Stage 5 (ready to hatch) within a few weeks. At slightly higher temperatures (20–25 °C), development arrested at Stage 4, though embryos remained viable. Mortality increased at elevated temperatures: embryos died within 6–7 months at 30 °C and within weeks at 35–40 °C.

Kruskal–Wallis tests revealed significant …

Effect of temperature

The observed developmental arrest at moderate temperatures (20–25 °C) and high mortality at 30–40 °C suggest that *A. tokioensis* has a narrow thermal window for successful hatching. The ability of embryos to enter developmental arrest at 20–25 °C may serve as an adaptive mechanism, conserving energy and increasing resilience to short-term environmental stressors such as heat waves or drought. Although previous studies suggest that cocoons can survive for multiple years and that some arrested …

CRediT authorship contribution statement

Maryam Nouri-Aiin: Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Formal analysis, Data curation, Conceptualization. **Jos. J. Schall:** Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Ollie Leibovich:** Methodology, Data curation. **Erica Hoover:** Methodology, Data curation. **Kit Eller:** Methodology, Conceptualization. **Victor Izzo:** Writing – review & editing, Resources. **Josef Görres:** Writing – review & editing, Writing …

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. …

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