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REVIEW

Global change and premature hatching of aquatic embryos

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Abstract

Anthropogenically induced changes to the natural world are increasingly exposing organisms to stimuli and stress beyond that to which they are adapted. In aquatic systems, it is thought that certain life stages are more vulnerable than others, with embryos being flagged as highly susceptible to environmental stressors. Interestingly, evidence from across a wide range of taxa suggests that aquatic embryos can hatch prematurely, potentially as an adaptive response to external stressors, despite the potential for individual costs linked with underdeveloped behavioural and/or physiological functions. However, surprisingly little research has investigated the prevalence, causes and consequences of premature hatching, and no compilation of the literature exists. Here, we review what is known about premature hatching in aquatic embryos and discuss how this phenomenon is likely to become exacerbated with anthropogenically induced global change. Specifically, we (1) review the mechanisms of hatching, including triggers for premature hatching in experimental and natural systems; (2) discuss the potential implications of premature hatching at different levels of biological organisation from individuals to ecosystems; and (3) outline knowledge gaps and future research directions for understanding the drivers and consequences of premature hatching. We found evidence that aquatic embryos can hatch prematurely in response to a broad range of abiotic (i.e. temperature, oxygen, toxicants, light, pH,

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salinity) and biotic (i.e. predators, pathogens) stressors. We also provide empirical evidence that premature hatching appears to be a common response to rapid thermal ramping across fish species. We argue that premature hatching represents a fascinating yet untapped area of study, and the phenomenon may provide some additional resilience to aquatic communities in the face of ongoing global change.

KEYWORDS
climate change, ectotherm, embryonic development, environmental stressors, hatching mechanisms, hatching plasticity, precocious hatching

1 | INTRODUCTION

As anthropogenically induced changes to the natural world increase, organisms experience stimuli and stress beyond that to which they are adapted (IPBES, 2019). Extreme changes in climate, habitat loss and destruction, increased susceptibility to pathogens and invasive species, and emerging and legacy contaminants all threaten species viability (Díaz et al., 2019; IPBES, 2019). Within the life history of each species, there is an increasing recognition that certain life stages may be more vulnerable to stressors than others. Embryos have been proposed to be highly susceptible to environmental stressors, partly because of underdeveloped physiological systems, but also due to their immobility when faced with challenging environments (Dahlke et al., 2020; Doody, 2011; Du & Shine, 2022; Pottier et al., 2022). Indeed, hatching can only occur once certain developmental milestones are reached, rendering embryos susceptible to prevailing environmental conditions until hatching enables motility.

Despite widespread recognition that developmental constraints place a hard lower limit on when hatching can occur (i.e. sufficient development of the hatching mechanism), there is evidence for 'premature hatching' across taxa in response to acute perturbations (e.g. Doody, 2011; Warkentin, 2011a; Box 1; Box 2). In some instances, the phenomenon of premature hatching (i.e. hatching before the natural hatching time, when larvae may lack normally developed behavioural and/or physiological functions; Box 1) is likely to be adaptive if escaping the egg to avoid a stressor offers a higher survival probability than remaining in the egg in the presence of the stressor. On the other hand, premature hatching likely comes with individual costs, as egg emergence with underdeveloped behavioural and/or physiological functions can decrease the function and survival of the hatchling (Liang et al., 2017; Porter & Bailey, 2007; Wisenden et al., 2022), with potential flow-on effects at the population and community levels (Touchon et al., 2013; Figure 1).

Embryos in both terrestrial and aquatic systems may experience environmental conditions that cause premature hatching, offering a potential mechanism for embryos to respond to ongoing global change (Doody, 2011; Du & Shine, 2022). Yet, no study has explicitly explored its prevalence or consequences across taxa. Here, using a broad review of the literature (details in Supporting Information), we focus on aquatic embryos to synthesise what is known about premature hatching and discuss how this phenomenon is likely to become exacerbated with anthropogenically-induced global change. First, we review the mechanisms of hatching as well as the triggers that can prompt premature hatching in experimental and natural systems. Then, we discuss the potential implications of premature hatching at different levels of biological organisation from individuals to ecosystems. Finally, we outline knowledge gaps and future research directions aimed at understanding the drivers and consequences of premature hatching. We reveal that premature hatching represents an untapped area of study, but it is likely to provide some additional resilience to aquatic animals in response to ongoing global change.

2 | MECHANISMS OF HATCHING

Hatching of aquatic embryos is induced via several non-mutually exclusive mechanisms (e.g. Fritsch et al., 2020; Korwin-Kossakowski, 2012; Warkentin, 2011b).

Enzymatic digestion of the enveloping structures, followed by mechanical disruption that allows the larva to hatch from the egg, is common across a broad range of taxa including fish (Korwin-Kossakowski, 2012), amphibians (Nokhbatolfoghahai & Downie, 2007) and nemerteans (Davis, 1965). In teleost fish, upon reaching the appropriate developmental stage and following maturation of hatching glands, intrinsic or extrinsic factors trigger the release of protease enzymes (typically 'high' and 'low' choriolytic enzymes) that are packed in secretory granules within the hatching gland cells, leading to swelling and digestion of the inner layer of the egg envelope (Kawaguchi et al., 2010; Korwin-Kossakowski, 2012). Whether causal or correlational, most teleosts are thought to hatch when the oxygen requirements of the growing embryo exceed the oxygen supply through the egg surface (Czerkies et al., 2001). Embryonic movements typically increase prior to hatching, further increasing respiratory demand, and these movements eventually rupture the egg c emerge (Korwin-Kossakowski, 2012; Box 2).

Similarly in amphibians, the most common hatching mechanism is chemical, whereby hatching gland cells secrete proteolytic enzymes that facilitate hatching by weakening the enveloping structures (Nokhbatolfoghahai & Downie, 2007). Again, two different proteases appear to cooperatively hydrolyze the embryo envelope (Fan & Katagiri, 2001). For many amphibians, final emergence from

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BOX 1 (A) Glossary of terms and (B) hypothetical examples distinguishing between our definitions of precocious and premature hatching

A Glossary

Accelerated development: Compression of the developmental processes into a shorter time frame.

Developmental window: Time frame for a developmental process.

Environmentally cued hatching: Alteration of the time, age or developmental stage at hatching in response to environmental cues.

Full embryonic development: An embryo that has undergone the complete developmental process and reached a normal, species-specific stage of development prior to hatching. These embryos may be referred to as 'full-term' (e.g. Du & Shine, 2015; Gomez-Mestre et al., 2008).

Hatching: The process by which the developing animal emerges from the egg and fully enters the external environment.

Hatching competence: The ability of an embryo to hatch successfully. Embryos that have reached hatching competence can hatch fairly quickly in the presence of a trigger.

Hatching plasticity: Variation in the timing of hatching, developmental stage at hatching, or body size at hatching.

Natural hatching time: The time window when hatching of animals that have reached full embryonic development naturally occurs without an external stressor. Also referred to as 'spontaneous hatching timing' (e.g. Gomez-Mestre et al., 2008) or 'normal hatching time' (e.g. Helvik & Walther, 1992). The natural hatching time can be influenced by environmental factors like temperature and oxygen.

Precocious hatching: While the terms 'precocious' and 'premature' are sometimes used interchangeably in the literature, here we use 'precocious' to describe hatching of an individual that has undergone accelerated development, hatching sooner than is typical or expected, yet has reached a stage of development typically observed at the natural hatching time (i.e. full embryonic development).

Premature hatching: Hatching that occurs before the natural hatching time, prior to full embryonic development, as a result of exposure to a stressor (Figure 1). Prematurely hatched individuals are distinguished from precociously hatched individuals in that they hatch at an earlier stage of development and are expected to exhibit underdeveloped behavioural and/or physiological functions in comparison with individuals that are not triggered to hatch prematurely.

B Examples of precocious versus premature hatching

1. *Chronic temperature*: Chronically elevated temperature may cause accelerated development relative to a cooler temperature. If an individual hatches within the natural hatching time for this warmer temperature and has reached full embryonic development, then it is precocious relative to the cooler temperature group but not relative to other typical individuals at the warmer temperature. If an individual hatches earlier than the natural hatching time for this warmer temperature and it has completed full embryonic development, then it is precocious relative to typical individuals at the warmer temperature. If an individual hatches earlier than the natural hatching time for this warmer temperature and it has not completed full embryonic development, then it is premature.
2. *Chronic aquatic toxicants*: Chronic exposure to toxicants may not cause accelerated development but may result in embryos hatching earlier than the natural hatching time (e.g. due to deterioration of the egg capsule), with consequently incomplete embryonic development. This would be premature hatching.
3. *Acute hypoxia*: If embryos are incubated in normoxia, they will follow a developmental timeline that sees them hatch during the natural hatching time. If embryos are given a pulse of hypoxia before the natural hatching time that causes them to hatch before completing full embryonic development, this would represent premature hatching.

the egg capsule is then facilitated by mechanical mechanisms; for example, certain frogs use an 'egg tooth' to physically rupture their capsules (Nokhbatolfoghahai & Downie, 2007; Warkentin, 2011b). A similar hatching mechanism is thought to exist in nemerteans (e.g. the ribbon worm, *Carcinonemertes carcinophila*), whereby secretion of an enzyme softens the egg membrane and allows the ciliated larva to push its way out mechanically (Davis, 1965).

Parents may also participate in stimulating hatching of their embryos in species that display parental care (Blumer, 1982; Video S1). Reported mechanisms are often mechanical, for example, hatching in the barred-chin blenny (*Rhabdoblennius nitidus*) relies on vigorous paternal fanning to compensate for poor expression of choriolytic enzymes (Sano et al., 2019). Hatching assistance and regulation have also been described for egg-carrying crustaceans like crabs and lobsters, where abdomen pumping can be used to facilitate egg hatching (Fritsch et al., 2020).

Osmotic hatching mechanisms are common among crustaceans (Davis, 1965; Hall & MacDonald, 1975). Increasing osmotic pressure leads to swelling of the developing embryo, as well as the inner egg membrane, in most crustaceans, generating sufficient hydrostatic

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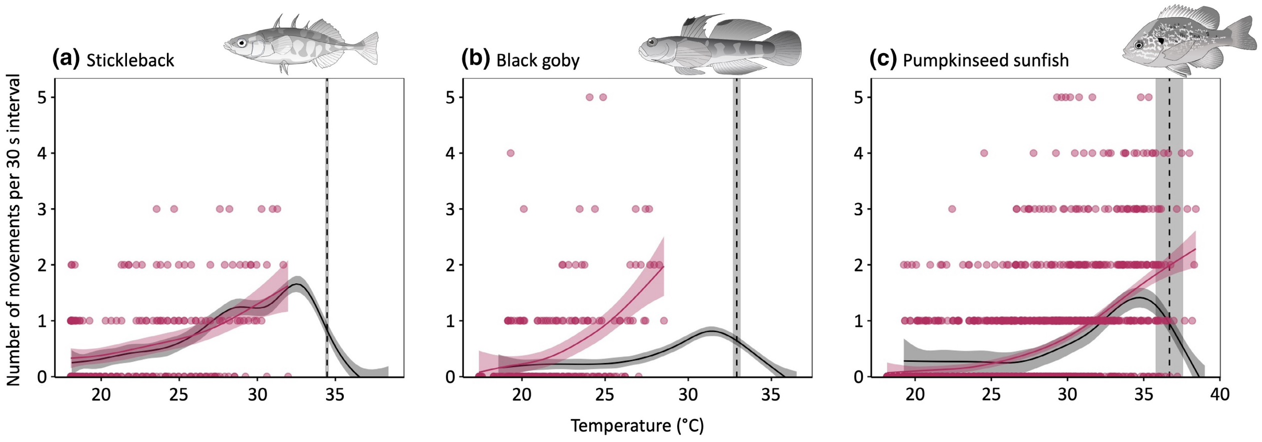
BOX 2 Experimental evidence for premature hatching as a response to thermal ramping

Experiments testing the critical thermal maximum (CT_{max}) in aquatic ectotherms typically involve acutely warming water in a test arena at a steady rate until the test subjects lose equilibrium (adults), are unresponsive (larvae), or cease movement (embryos) (Cowan et al., 2023). Here, we describe our observations of premature hatching during acute thermal ramping in embryos of three fish species: three-spined stickleback (*Gasterosteus aculeatus*) at 5–6 days post-fertilisation (dpf), black goby (*Gobius niger*) at 4–6 dpf and pumpkinseed sunfish (*Lepomis gibbosus*) at 0–2 dpf.

Full materials and methods concerning the temperature trials are provided in Cowan et al. (2023) and the Supporting Information. Briefly, embryos were placed into the test arena and exposed to a 0.3°C/min ramping protocol. The number of movements over 30 s intervals at the start of each minute (i.e. 30 s recording, 30 s not recording), as well as hatching time, were recorded every minute until group CT_{max} (loss of movement for all embryos in the trial) had been reached. Upon reaching group CT_{max}, all embryos were removed from the test arena and placed into recovery tanks. Post-test survival was monitored and all species showed high survival after 24 h (69%–84%).

During the thermal ramping trials, 23% of sticklebacks ($N = 11/48$), 9% of black gobies ($N = 10/112$) and 84% of pumpkinseed sunfish ($N = 36/43$) hatched prematurely. Hatching of unheated embryos in holding tanks occurred 12+ h later than embryos that were heated during CT_{max} trials.



Data from (a) 37 unhatched stickleback embryos, (b) 102 unhatched black goby embryos and (c) 7 unhatched pumpkinseed sunfish embryos were used to plot embryo activity curves (smoothed black GAM curve, fitted to the averaged movement of all unhatched embryos within a trial at each temperature point) and calculate the mean critical thermal maximum (CT_{max}) ± SE (vertical dashed lines and shaded bars) for all species (data from unhatched stickleback and black goby embryos are published in Cowan et al., 2023). CT_{max} was taken as the last movement of each individual embryo. Also presented (in red symbols) are data for embryos that hatched prematurely during the trial, and smoothed red GAM curves have been fitted to the movement of these individuals until the point of hatching ($N_{stickleback} = 11$; $N_{black\ goby} = 10$, $N_{pumpkinseed} = 36$).

pressure to rupture the chorion (Fritsch et al., 2020). Breaking of the inner membrane and escape from the egg may then be facilitated by enzymatic digestion or mechanical action of the hatchling or the mother (Fritsch et al., 2020).

The central and peripheral nervous systems have also been implicated in hatching of some teleost embryos including medaka (*Oryzias latipes*) and zebrafish (*Danio rerio*) (Schoots et al., 1983). The somatosensory system of unhatched (<3 days post-fertilisation) zebrafish embryos can already detect potentially threatening stimuli, including touch, noxious chemicals or temperature (Chen et al., 2016; Faucherre et al., 2013; Gau et al., 2013; Kucenas et al., 2006; Prober et al., 2008). Thanks to this role of detecting a wide variety of environmental stimuli, the somatosensory system could help regulate hatching. Furthermore, the somatosensory system projects sensory arborisations over the hatching gland in zebrafish (Metcalfe et al., 1990; Sagasti et al., 2005; Figure 2). At these arborisations, specialised ion channels and signalling molecules are localised (e.g. mechanosensory PIEZO and chemo- and thermosensory TRP ion channels) (Meltzer et al., 2021; Viana, 2011). It is likely that the somatosensory system communicates with the hatching gland this way to induce premature hatching when a threat is detected, but it is unknown how widespread this mechanism is.

Some components of the various hatching mechanisms may lend themselves to variations in timing more than others, and therefore can play a larger role in the premature hatching phenomenon. We discuss how these mechanisms may be triggered in the next section.

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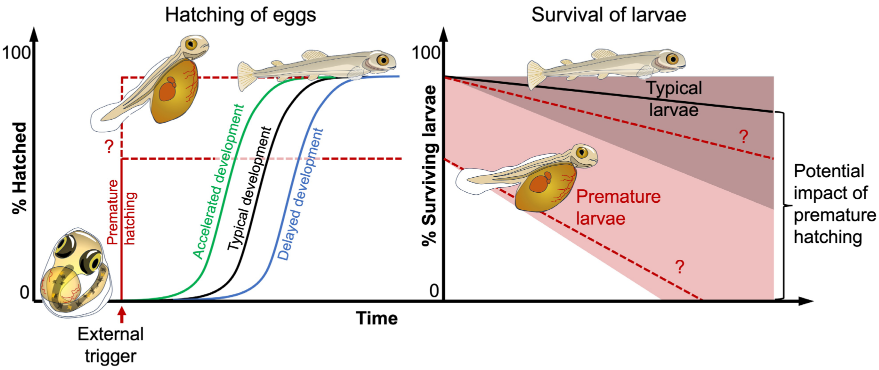

FIGURE 1 Putative impacts of premature hatching on hatching success and larval survival. Embryos of ectothermic animals typically hatch when fully developed for survival outside the egg capsule (typical development curve, black). In response to external environmental factors, such as temperature and oxygen levels, the speed of development and timing of hatching can be accelerated (green curve) and lead to precocious hatching relative to typical conditions, or delayed (blue curve) relative to typical conditions (see Box 1). Before full embryonic development is reached, eggs can prematurely hatch (red vertical line), caused by sudden external triggers such as heatwaves, altered water chemistry, or physical disturbance (Table 1). It is largely unknown how prevalent or successful this type of hatching is (red question marks, dashed red lines). Once hatched (right side of the figure), premature larvae may rapidly catch up in development with conspecifics that underwent full embryonic development, showing largely unaffected survival probability (shallow red dashed line). It is also possible that the post-hatch survival of prematurely hatched larvae is severely reduced compared with those that underwent full embryonic development (steep red dashed line). The impact of premature hatching on survival and the probability of future reproduction may depend on many factors, discussed in the main text.

3 | TRIGGERS OF PREMATURE HATCHING

Whether an environmental stressor induces an acute or chronic stress on a developing embryo depends on the duration of the environmental pulse and the typical embryonic development time. For example, a heatwave lasting 7 days would be experienced as an acute stress to embryos with long developmental times (e.g. salmonids), whereas the same heatwave may encompass the entire embryonic stage for species with a short developmental window (e.g. zebrafish). Thus, acute versus chronic stressors for embryos must be placed in the context of the developmental time of the species in question.

3.1 | Temperature

Many environments naturally experience daily and/or seasonal temperature fluctuations; however, rapid thermal changes beyond normal daily variation can impact ectotherm development and hatching phenology (Massey & Hutchings, 2021) (Table 1). Despite the harmful potential of acute warming on aquatic ecosystems (Ern et al., 2023; Wernberg et al., 2016), the effects of such temperature change on the hatching dynamics of aquatic embryos have hardly been explored (Massey & Hutchings, 2021). Prolonged heat stress can cause eggs to hatch prematurely. For example, increasing incubation temperature increased the rate of premature hatching in European squid (*Loligo vulgaris*) (Rosa et al., 2012). The percentage of embryos hatching at earlier developmental stages, with yolk sacs still attached to their bodies, was higher at 19°C (future summer temperature) compared to 13–17°C (present-day scenarios) (Rosa et al., 2012) (Table 1). Observations of premature hatching during thermal ramping in CT_{max} experiments on several species of fish embryos suggest that acute warming scenarios in nature could lead to widespread premature hatching and present major shifts in offspring phenology (Box 2). Indeed, the increased prevalence of local heatwaves is generating faster and more severe heating rates (Oliver et al., 2018), potentially triggering such premature hatching in nature.

3.2 | Oxygen

Shallow aquatic systems can experience fluctuations in dissolved oxygen (DO) levels—ranging from supersaturation (hyperoxia) to hypoxia—due to daily cycles in photosynthesis, respiration activity and temperature. An inadequate supply of oxygen to the developing embryo is thought to be one of the most important factors triggering chorionase secretion and hatching (Czerkies et al., 2001; Kamler, 2002). Thus, environmental factors limiting DO availability to the embryo have the potential to induce premature hatching. For example, premature hatching is observed following hypoxia exposure in whitefish (*Coregonus lavaretus*) (3.0 mg/L DO), vendace (*Coregonus albula*) (2.1 mg/L DO) (Czerkies et al., 2001), three-spined stickleback (*Gasterosteus aculeatus*) (~75% air saturation [AS]) (Fitzgerald et al., 2017) and tropical gar (*Atractosteus tropicus*) (~30% AS) (Martínez et al., 2021) (Table 1).

Importantly, because embryonic metabolic rate is temperature dependent (Hamor & Garside, 1976), increasing temperature can exacerbate the rate of hypoxia-induced premature hatching. In whitefish (*C. lavaretus*), elevated temperature amplified the response to hypoxia (0.2 mg/L DO for 60 min), with 43% premature hatching occurring at 8°C versus 95% premature hatching at 11°C (Czerkies et al., 2001). It is possible that any perturbation that increases the metabolic rate of a developing embryo will challenge the oxygen supply capacity across the egg membrane and influence hatching time.

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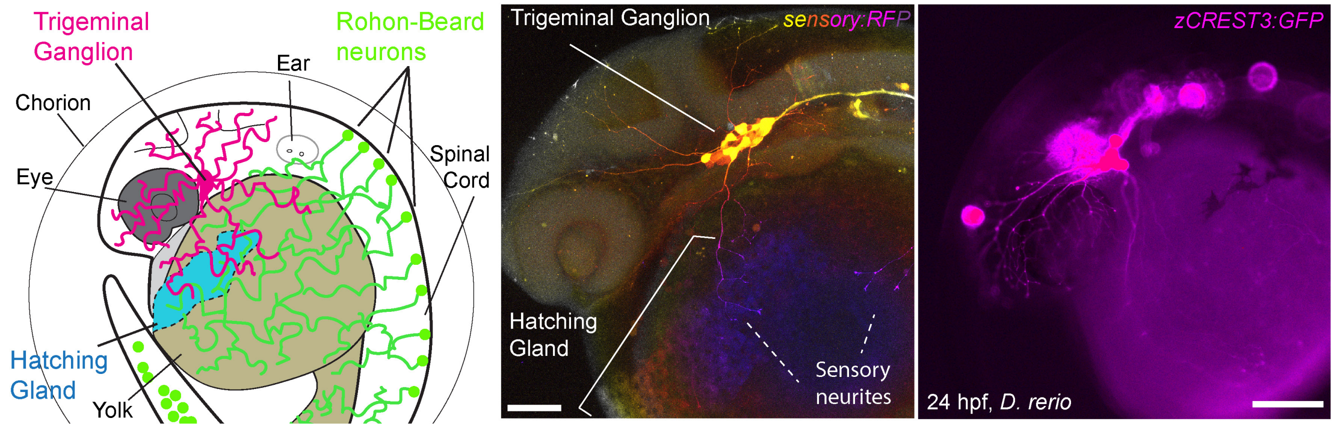

FIGURE 2 Innervation over the hatching gland of zebrafish (*Danio rerio*). Diagram (left) showing the innervation pattern of the somatosensory system of the head and trunk of embryonic zebrafish. Note the extensive arborisations of the Trigeminal Ganglion (magenta) and Rohon-Beard neurons (green) over the hatching gland. The two fluorescence microscopy photos show the innervation pattern over the hatching gland of two transgenic zebrafish at 24 hours post-fertilisation (hpf) with expression of red fluorescent protein (RFP) in sensory neurons (middle) or green fluorescent protein (GFP) in neural cells (right) near the head (images recoloured for optimal clarity). Scale bars equal 100 μm.

3.3 | pH and carbon dioxide

Aquatic systems can experience episodic, daily and seasonal fluctuations in pH as a result of variation in photosynthesis and respiration activity, precipitation, upwellings and interaction with surrounding (particularly carbonate) substrates (e.g. Reum et al., 2016). Additionally, increased atmospheric carbon dioxide (CO_2) leads to gradual acidification of water bodies as CO_2 dissolves and reacts with water molecules eventually forming bicarbonate (HCO_3^-) and free hydrogen ions (H^+) (Clark et al., 2024).

Exposure of embryos to extreme high or low pH is known to cause detrimental effects, including deformities, altered developmental rates, decreased hatching success and mortality, across a wide range of taxa (Carrick, 1979; Doyle & McMahon, 1995; Kamler, 2002; Schönbrunner & Eder, 2006). Variation in pH may also induce premature hatching. For example, rates of premature hatching in common cuttlefish (*Sepia officinalis*) at a high temperature of 22°C significantly increased from ~80% at pH 8.0 to 100% under a future acidification scenario of pH 7.5 (Rosa et al., 2013). Exposure to extreme alkaline conditions (pH 10) 3 weeks prior to the natural hatching time induced a small amount of premature hatching in Atlantic salmon (*Salmo salar*) under normoxia (Oppen-Berntsen et al., 1990). When extreme alkalinity was combined with hypoxia (oxygen partial pressure [pO_2] <5 mmHg), the prevalence of premature hatching at 3 weeks prior to the natural hatching time increased dramatically to 86%, suggesting some interaction between the two stressors (Oppen-Berntsen et al., 1990).

3.4 | Light

The influence of light conditions on hatching can be complex and factors such as light intensity and wavelength, and periods of darkness, are all important in the hatching response (e.g. Downing & Litvak, 2002; Villamizar et al., 2014). Premature hatching has been observed during exposure to constant light or high light intensity in fishes (rainbow trout [*Oncorhynchus mykiss*]; Bieniarz, 1973) and invertebrates (kisslip cuttlefish [*Sepia lycidas*]; Peng et al., 2019) (Table 1). Artificial light pollution, such as artificial light at night, has the potential to disrupt hatching timing in natural populations of aquatic embryos, depending on which light conditions serve as a cue for hatching for a particular species. Specifically, light pollution may promote premature hatching among species known to have light-induced hatching (e.g. fish such as medaka and zebrafish [Schoots et al., 1983] and branchiopod crustaceans such as Asian tadpole shrimp [*Triops granarius*] [Kashiyama et al., 2010]), whereas it could inhibit or prevent hatching in species with darkness-induced hatching (e.g. fish such as Atlantic halibut [*Hippoglossus hippoglossus*] [Helvik & Walther, 1992] and sergeant major [*Abudefduf saxatilis*] [McAlary & McFarland, 1993]).

3.5 | Salinity

Changes in salinity, which might occur due to factors including heavy rainfall, surface runoff, wastewater from oil and gas extraction and poor mixing in estuaries, can have far-reaching effects on normal embryonic development. Much of the research on salinity and hatching success in embryos has been done in the context of optimising conditions in aquaculture (e.g. Ban et al., 2022; Şen, 2005). In freshwater fishes, rearing embryos in brackish water can result in accelerated growth, and sometimes premature hatching (Albert et al., 2004). For example, in whitefish (*Coregonus lavaretus maraenoides*) embryos, the time for 50% of larvae to hatch decreased from 616 degree-days at 0.2 ppt to 239 degree-days at 6.2 ppt, with no other differences in the timing of morphological

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TABLE 1 Triggers of premature hatching in aquatic embryos.

Trigger	Direction of change	Natural/anthropogenic occurrences	Examples of altered hatching timing and premature hatching
Temperature	Up	Heatwaves in shallow waters, tide pools and nuclear effluent	Increasing incubation temperature increased the rate of premature hatching in European squid (*Loligo vulgaris*). The percentage of embryos hatching at earlier developmental stages, with yolk sacs still attached to their bodies, was higher at 19°C (future summer temperature) compared to 13–17°C (present-day scenarios) (Rosa et al., 2012) Higher temperatures caused stronger responses to hypoxia in whitefish (*Coregonus lavaretus*) (Czerkies et al., 2001) (see below) Preliminary data show that premature hatching of several fish species occurs during thermal ramping in critical thermal maximum (CT_{max}) experiments (Box 2)
	Down	Glacier melt, tidepool inundation, weather cold snaps	Temperature reductions are known to delay development rates and can decrease embryo survival and hatching rates (e.g., Wexler et al., 2011), but there is a lack of evidence for an association between temperature reduction and premature hatching
Oxygen	Up	Tidepool isolation during the day	Hyperoxia has been observed to affect time to hatching; for example, tropical gar (*Atractosteus tropicus*) exposed to hyperoxia (~117% air saturation [AS]) were observed to delay hatching (Martínez et al., 2021), but there is a lack of studies describing premature hatching in response to hyperoxia exposure
	Down	Proliferation of hypoxic zones	Hypoxia caused premature hatching in whitefish (*C. lavaretus*) (3.0 mg/L dissolved oxygen [DO]) and vendace (*Coregonus albula*) (2.1 mg/L DO) embryos. The sensitivity to hypoxia increased with development. When the first natural hatching occurred, critical DO for the hatching onset of vendace eggs had increased to 6.0 mg/L DO. Higher temperatures also caused a stronger response to hypoxia in whitefish (*C. lavaretus*): exposure to DO of 0.2 mg/L for 60 min resulted in 43% hatching at 8°C and 95% at 11°C (Czerkies et al., 2001) Premature hatching occurred following hypoxia (75 ± 0.5% AS) in three-spined stickleback (*Gasterosteus aculeatus*) (Fitzgerald et al., 2017) Hypoxia (~30% AS) caused premature hatching in tropical gar (Martínez et al., 2021) Rainbow trout (*Oncorhynchus mykiss*) hatching started 1 day earlier in hypoxic (5 mg/L DO) compared to normoxic (10 mg/L DO) and hyperoxic (15 mg/L DO) conditions (Ciuhandu et al., 2005) At 35 days post-fertilisation (dpf), Chinook salmon (*Oncorhynchus tshawytscha*) embryos exposed to hypoxia (2.5–5.0 mg/L) hatched prematurely compared to the control groups across all tested temperatures (12–17°C) (Martin et al., 2020). In the same study, delayed hatching up to 4 days was observed following hypoxia exposure (2.5–5.0 mg/L; 1 week) during early development (21 dpf) (Martin et al., 2020) Time to hatching decreased with decreasing oxygen from 6-9 days in 84% AS to 4–5 days in 6.5% AS in Southern leopard frog (*Rana sphenocephala*) and Pickerel frog (*Rana palustris*) (Mills & Barnhart, 1999) In laboratory experiments, quacking frog (*Crinia georgiana*) eggs incubated at a range of oxygen partial pressure (pO_2) from 5 to 25 kPa were observed to hatch sooner (10.8 days at 5 kPa vs 12.2 days at 25 kPa) and at an earlier stage of development with decreasing pO_2; however, further decreasing pO_2 (2 kPa) resulted in substantial developmental delays, morphological abnormalities and mortality (Seymour et al., 2000) Delayed hatching (i.e. no premature hatching) has also been observed following hypoxia exposure in three-spined stickleback (24.7% ± 0.9% AS) (Fitzgerald et al., 2017) and salmonids (DO concentration ~4–5 mg/L) (Côte et al., 2012)
pH	Up	Daily and seasonal cycles, runoff from certain substrates	Premature hatching is observed in Atlantic salmon (*Salmon salar*) under normoxic conditions at pH 10, however, under hypoxic conditions (pO_2 <5 mmHg) increasing pH (up to pH 9.5) is observed to exacerbate rates of premature hatching (Oppen-Berntsen et al., 1990)
	Down	Daily and seasonal cycles, pulses in runoff, ocean acidification	Significantly higher rates of premature hatching were observed in common carp (*Cyprinus carpio*) exposed to 0.8 mmol/L copper at pH 6.3 compared to pH 7.6 (Stouthart et al., 1996) At a high temperature of 22°C, rates of premature hatching in common cuttlefish (*Sepia officinalis*) significantly increased from ~80% at pH 8.0 to 100% at pH 7.5 (Rosa et al., 2013)

(Continues)

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TABLE 1 (Continued)

Trigger	Direction of change	Natural/anthropogenic occurrences	Examples of altered hatching timing and premature hatching
Light	Up	Artificial light at night (ALAN)	High light intensity (50.7 and 29.6 μmol/m^2/s) causes premature hatching in kisslip cuttlefish (*Sepia lycidas*) (Peng et al., 2019) Premature hatching, as well as increased deformities and mortality, is observed in rainbow trout (*Oncorhynchus mykiss*) incubated at constant light levels of 330–350 lux (Bieniarz, 1973)
Salinity	Up	Tidepool isolation during day, road salt exposure, mixture effluents from oil and gas wastewater	In chum salmon (*Oncorhynchus keta*), premature hatching and significantly increased mortality were observed in eggs that were fertilised and reared at 1.0 and 2.1 ppt compared to eggs fertilised and reared at <0.1 and 0.5 ppt (Ban et al., 2022) Zebrafish (*Danio rerio*) embryos reared at a salinity (5.0 ppt) just below the 24-h LC50 (lethal concentration for 50% mortality: 5.6 ppt) experienced lower survival than those reared at lower salinities (0.2 and 2 ppt), however, premature hatching (24 h earlier) was observed in surviving embryos (Ord, 2019). Exposure to salinity close to the upper tolerance limit (42 ppt) induced premature hatching in European squid (*L. vulgaris*) (Şen, 2005) Premature hatching was observed in bigfin reef squid (*Sepioteuthis lessoniana*) and Pharoah cuttlefish (*Sepia pharaonis*) exposed to high salinity (36 ppt) (optimal range is estimated to be 21.8–36.6 and 22.5–37.5 ppt, respectively) (Nabhitabhata et al., 2001) Elevated salinity led to premature hatching in whitefish (*C. lavaretus maraenoides*), whereby the time for 50% of larvae to hatch decreased from 616 degree-days at 0.2 ppt to 239 degree-days at 6.2 ppt, with no other differences in the timing of morphological development, however, the proportion of abnormal (e.g., body malformations, abnormal swimming patterns) eleuthroembryos increased rapidly beyond 2.5 ppt (Albert et al., 2004)
	Down	Heavy rainfall, glacier melt and stormwater run-off	Premature hatching was observed in bigfin reef squid (*S. lessoniana*) exposed to low salinity (16 and 20 ppt) (Nabhitabhata et al., 2001)
Toxicants	Up	Organic and inorganic chemicals: gas/oil spills, storm water outflows, industrial effluent, waste water run-off, mining and smelting, road runoff, pharmaceuticals	Trace metal contaminants consistently induce premature hatching; for example, silver (Davies, 1978) and cadmium (Lizardo-Daudt & Kennedy, 2008; Woodworth & Pascoe, 1982) in rainbow trout, silver in winter flounder (*Pseudopleuronectes americanus*) (Klein-Macphee et al., 1984), cadmium and mercury in Java medaka (*Oryzias javanicus*) (Ismail & Yusof, 2011), lead and cadmium in southern king crab (*Lithodes santolla*) (Amin et al., 1998) and zinc in fathead minnow (*Pimephales promelas*) (Brungs, 1969) In three-spined stickleback (*Gasterosteus aculeatus*), embryos exposed to copper and lowered air saturation showed only delayed hatching (Fitzgerald et al., 2017) Exposure to environmentally relevant concentrations (1 nM) of tributyltin induces premature hatching and reduces locomotor behaviours in hatched larvae of zebrafish (Liang et al., 2017) Perfluorooctane sulfonate (a PFOS) decreased average hatching time (from 21 to 14 days) and increased hatching rate (from 53% to 95%) of marine medaka (*Oryzias melastigma*) embryos (Wu et al., 2012) In zebrafish exposed to the polyaromatic hydrocarbon (PAH) benzo-[a]-pyrene, embryos hatched prematurely but with developmental deformities. Interestingly, this effect only occurred in the F1 generation, with F2/F3 generations failing to show the same effects (Corrales et al., 2014), indicating an organismal capacity to adapt to the effects of PAH exposure Imidacloprid (a neonicotinoid insecticide) induces premature hatching in fathead minnows, and this early hatching results in lower survival (Jeninga et al., 2023). Concerningly, the effects of imidacloprid occur at concentrations considered to be environmentally relevant Amoxicillin (an antibiotic) induced premature hatching in zebrafish (Oliveira et al., 2013) In the estuarine killifish (*Fundulus heteroclitus*), crude oil exposure induced premature hatching, particularly when combined with high temperature and salinity extremes (Lindén et al., 1979) In the Pacific herring (*Clupea pallasi*) premature hatching was observed when embryos were exposed to weathered crude oil and, in comparison to control fish, the prematurely hatched individuals had a higher incidence of yolk sac oedema and reduced jaw size and fin maturity (Carls et al., 1999) Premature hatching was observed in Pacific herring exposed to >0.24 mg/L crude oil in artificial seawater (Kocan et al., 1996)

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TABLE 1 (Continued)

Trigger	Direction of change	Natural/anthropogenic occurrences	Examples of altered hatching timing and premature hatching
Predator presence/ biological cues	Up	Predator presence	Green frog (*Rana clamitans*) embryos exposed to chemical cues from ovivorous leeches (*Nephelopsis obscura*) hatch at a smaller size and earlier developmental stage than non-exposed embryos, while chemical cues from a larval predator (dragonfly nymph, *Aeschna canadensis*) can delay hatching (Ireland et al., 2007) Embryos of the nudibranch (*Phestilla sibogae*) hatch up to 60% prematurely (before reaching a developmental stage of being competent to settle and metamorphose) when their gelatinous egg ribbons are physically damaged during predation by crabs (Strathmann et al., 2010) Fathead minnows exposed to chemical cues from virile crayfish (*Orconectes virilis*) that had foraged on minnow embryos hatched earlier and at a less developed stage compared to embryos exposed to a blank control (Kusch & Chivers, 2004) Zebrafish and American toad (*Bufo americanus*) showed accelerated hatching when exposed to chemical cues from crushed conspecific eggs, simulating predator action, resulting in poorer body condition and swim performance from larvae (Touchon et al., 2006; Wisenden et al., 2022) Waterborne chemical cues from adult conspecific snails accelerated hatching, but not developmental rate, in a marine snail (*Nucella lamellosa*) (Miner et al., 2010) Premature hatching was observed in market squid (*Doryteuthis opalescens*) following agitation by feeding activity of the bat star (*Patiria miniata*), and infestation with annelid worms (*Capitella ovincola*). The latter are suggested to feed on the matrix jelly and microorganisms of the capsule sheath and co-occurred with a decrease in sheath thickness and exposure of eggs (Zeidberg et al., 2004)
Pathogens	Up	Increasing pathogen prevalence	Mould infection induced premature hatching in spotted salamander (*Ambystoma maculatum*), wood frog (*Rana sylvatica*) and American toad (*Anaxyrus americanus*) (Gomez-Mestre et al., 2006; Touchon et al., 2006) Infection with *Pseudomonas fluorescens* induced hatching in brown trout (*Salmo trutta*) (Pompini et al., 2013)
Mechanical agitation and noise pollution	Up	Hurricanes/cyclones, more frequent and intense storms (wind), seismic surveys, mining, boating, stress-induced parental stimulation, predators attacking sibling eggs	The perceived threat of an approaching human observer led male two-spotted gobies (*Pomatoschistus flavescens*) to vigorously fan their eggs with their caudal fin, initiating hatching (Video S1) Mechanical disturbance during the last month of incubation induced premature hatching in spotted wolffish (*Anarhichas minor*) (Falk-Petersen et al., 1999)
Water level	Down	Damming, decrease in meltwater, drought	Earlier hatching is observed in several salmonids (arctic char [*Salvelinus alpinus*], brown trout, whitefish [*Coregonus* sp.]) when eggs are deposited closer to the water surface and are at risk of air exposure and desiccation, compared to those deeper in the water (Wedekind & Müller, 2005)

development; however, the proportion of abnormal eleuthroembryos increased rapidly beyond 2.5 ppt (Albert et al., 2004) (Table 1). Similarly, in zebrafish, exposure to salinity (5.0 ppt) just below the 24-h LC50 (lethal concentration for 50% mortality: 5.6 ppt) in both early and late stages of development caused premature hatching (Ord, 2019) and in chum salmon (*Oncorhynchus keta*), fertilisation and rearing of embryos at 1.0 and 2.1 ppt resulted in premature hatching and significantly increased mortality compared to embryos fertilised and reared at <0.1 and 0.5 ppt (Ban et al., 2022) (Table 1). Premature hatching has also been observed in cephalopod eggs exposed to non-optimal salinities. For instance, this is reported in European squid (*L. vulgaris*) exposed to salinity close to the upper tolerance limit (42 ppt) (Şen, 2005), and bigfin reef squid (*Sepioteuthis lessoniana*) and pharaoh cuttlefish (*Sepia pharaonis*) exposed to salinities outside of their optimal range (estimated to be 21.8–36.6 and 22.5–37.5 ppt, respectively) (Nabhitabhata et al., 2001) (Table 1).

3.6 | Toxicants

The environmental input of aquatic toxicants has increased exponentially in recent decades, to the extent that pollution in the aquatic environment is now considered one of the largest contributors to biodiversity loss (Sigmund et al., 2023). Critically, early life stages are generally more susceptible to toxicants than their freely moving adult counterparts. Premature hatching in aquatic embryos has been observed for several aquatic contaminants to date.

Trace metal contaminants consistently induce premature hatching; for example, silver (Davies, 1978) and cadmium (Lizardo-Daudt & Kennedy, 2008; Woodworth & Pascoe, 1982) in rainbow trout (*Oncorhynchus mykiss*), silver in winter flounder (*Pseudopleuronectes americanus*) (Klein-Macphee et al., 1984), cadmium and mercury in Java medaka (*Oryzias javanicus*) (Ismail & Yusof, 2011), lead and cadmium in southern king crab (*Lithodes santolla*) (Amin et al., 1998) and zinc in fathead minnow (*Pimephales promelas*) (Brungs, 1969)

(Table 1). At least in fish, these results may be attributed to metals inducing a hypoxia-like effect (Jezierska et al., 2009; Jezierska & Witeska, 2001) or softening the chorion and resulting in the egg breaking open (Alderdice et al., 1979; Benoit & Holcombe, 1978).

Organic contaminants are also known to impact fish hatching. One noted group are the per- and poly-fluoroalkyl substances, which are persistent within the environment and have been shown to induce premature hatching. For example, perfluorooctane sulfonate decreased average hatching time (from 21 to 14 days) and increased hatching rate (from 53% to 95%), as well as significantly decreasing survival rate within 1 week of hatching, in marine medaka (*Oryzias melastigma*) embryos (Wu et al., 2012) (Table 1). The mechanism underlying this effect is likely related to the upregulation of expression of the high and low choriolytic hatching enzymes. In addition, pesticide exposure can induce premature hatching in fish embryos. For example, neonicotinoid insecticides such as imidacloprid induce premature hatching in fathead minnows, resulting in lower survival (Jeninga et al., 2023). Importantly, the effects of imidacloprid occur at concentrations considered to be environmentally relevant. Antibiotics may also influence hatching timing, but in a chemical-dependent manner. While the antibiotic oxytetracycline delayed hatching in zebrafish, amoxicillin induced premature hatching (Oliveira et al., 2013) (Table 1). This likely indicates that the effects of this chemical class on fish embryo hatching are not mediated by their antibiotic properties, but rather through alternate chemical-specific mechanisms.

Finally, petroleum hydrocarbons can dysregulate hatching in fish. In the estuarine killifish (*Fundulus heteroclitus*), crude oil exposure can induce premature hatching, particularly when combined with high temperature and salinity extremes (Lindén et al., 1979) (Table 1). Additionally, premature hatching was observed in the Pacific herring (*Clupea pallasi*) when embryos were exposed to weathered crude oil and, in comparison to control fish, the prematurely hatched individuals had a higher incidence of yolk sac oedema and reduced jaw size and fin maturity (Carls et al., 1999) (Table 1).

3.7 | Predators

Different types of cues have been observed to induce premature hatching in response to predators across a range of taxa. Embryos of a nudibranch (*Phestilla sibogae*) hatch up to ~60% earlier when their gelatinous egg ribbons are physically damaged during predation by crabs, with prematurely hatched individuals lacking a propodium and the competence to settle and metamorphose relative to undisturbed late hatchlings (Strathmann et al., 2010) (Table 1). Similarly, premature hatching was observed in market squid (*Doryteuthis opalescens*) when the egg capsules were agitated by feeding activity of the bat star (*Patiria miniata*), or infested with annelid worms (*Capitella ovincola*) (Zeidberg et al., 2004) (Table 1). Chemical cues from predators or damaged conspecific eggs can also induce premature hatching. For example, fathead minnows exposed to chemical cues from virile crayfish (*Orconectes virilis*) fed with minnow eggs, combined with egg homogenate, were reported to hatch earlier and at a less developed stage compared to embryos that were exposed to a blank control (dechlorinated tap water) (Kusch & Chivers, 2004), and green frog (*Rana clamitans*) embryos exposed to chemical cues from ovivorous leeches (*Nephelopsis obscura*) hatch at a smaller size and earlier developmental stage than non-exposed conspecifics (Ireland et al., 2007) (Table 1). Likewise, both zebrafish and American toad (*Bufo americanus*) showed accelerated hatching when treated with chemical cues from crushed conspecific eggs, simulating predator action, resulting in poorer body condition and swimming performance of the larvae (Touchon et al., 2006; Wisenden et al., 2022) (Table 1).

The threat of predators may in some cases also be detected by the parents, who can initiate premature hatching of their offspring. For example, male two-spotted gobies (*Pomatoschistus flavescens*) can initiate hatching by vigorously fanning their eggs with their caudal fin. In the Video S1, this behaviour was apparently triggered in captivity by the perceived threat of an approaching human observer, but the mechanism has yet to be systematically studied or observed in nature in this species.

3.8 | Pathogens

Pathogens can also modify the timing of hatching. In amphibians, water mould can induce premature hatching in spotted salamander (*Ambystoma maculatum*), wood frog (*Rana sylvatica*) (Gomez-Mestre et al., 2006; Touchon et al., 2006) and American toad (Table 1). Similarly, premature hatching is observed in brown trout embryos (*Salmo trutta*) infected with the bacterium *Pseudomonas fluorescens* (Pompini et al., 2013) (Table 1). Such premature hatching could be an adaptive response by the embryo to avoid pathogen transmission from infected conspecifics but may also be precipitated by the pathogen itself physically damaging the egg capsule (Touchon et al., 2006). Synergistic effects between pathogens and other triggers, such as salinity, have also been documented. For example, increasing salinity favours the development of mould on wood frog embryos, leading to premature hatching (Coughlan et al., 2021).

4 | IMPLICATIONS IN A CHANGING WORLD

Many of the triggers of premature hatching outlined above and in Table 1 are likely to vary with ongoing global change. For example, aquatic systems are becoming warmer, more acidified and less oxygenated (e.g. Breitburg et al., 2018; Jane et al., 2021, 2023), aquatic toxicants and pathogens are increasing in prevalence (Byers, 2020; Marcogliese, 2008; Vezzulli et al., 2013), and global redistribution of species with climate change is going to lead to new species interactions (Pecl et al., 2017). Given the key role of oxygen in regulating the timing of hatching, described above (Czerkies et al., 2001), the ongoing deoxygenation of aquatic systems could prove widely detrimental to hatching phenology (Breitburg et al., 2018). In addition, there are

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BOX 3 Future research questions

Mechanistic:

- What physiological mechanisms and pathways are involved in premature hatching? How are these mechanisms affected by ontogeny and how are they influenced by external factors?
- The somatosensory system of embryos is molecularly complex and functional before hatching. Do all stimuli detected (e.g. temperature, mechanical, noxious chemicals) have the same valence towards premature hatching or are specific sensory pathways dominant?
- Do chronic and acute exposures to triggers differ in how they influence premature hatching? For example, will either a specific temperature threshold or degree-days cause premature hatching?
- Which biological, physical and/or chemical stressors have cumulative effects on the onset of premature hatching?

Ontogenetic:

- How plastic is premature hatching and what influences the plastic response? For example, if the rate of thermal ramping is slower, will premature hatching occur at a higher temperature?
- To what extent does parental (including behavioural) mediation influence hatching, and how is this mediation affected by global change?
- How does the relative access to energy reserves (e.g. size of yolk sac) impact the rate of development after a hatchling has emerged prematurely?

Adaptive:

- What is the slope of the survival curve (see Figure 1) for embryos hatched prematurely? Is natural survival consistently correlated with embryo maturation at hatching? Are organisms with short developmental periods differentially affected by premature hatching compared to those with longer developmental periods?
- Is there a fitness advantage to premature hatching, when a lower density of conspecifics decreases competition during early stages of development?
- Which traits are influenced by premature hatching and how do they contribute to survival and ultimately fitness? Which traits finish their development close to hatching? For example, will hatchlings emerging prematurely struggle with feeding and consequently grow slower?
- What is the phenotypic variation and scope for selection on premature hatching? For example, can there be evolutionary rescue from a factor causing increased premature hatching?

Phylogenetic:

- What are the phylogenetic links and constraints of the mechanisms of premature hatching, and how do they differ between clades?
- Are populations and/or species in certain regions more or less exposed and evolved to survive despite premature hatching?
- Are the embryos of species that lay large eggs more or less prone to premature hatching than those of species that lay small eggs?

Environmental and ecological consequences:

- What is the evidence for premature hatching occurring in nature, and can it influence species at a population level? For example, are particularly under-developed hatchlings more commonly observed after a heatwave?
- What are the projected frequencies and magnitudes of physical/chemical factors that trigger premature hatching, and how do they overlap with the phenology of spawning and embryonic development? For example, will species Y experience an increased frequency of premature hatching as factor X changes?
- What phenological matches exist in ecosystems where species are threatened by premature hatching events, and what will be the ecological cascades of these events? What differences exist in response to hatching triggers across species within the same aquatic ecosystem? Will their hatch times shift together, or will pulses arrive at different times and create trophic mismatch scenarios?
- Are there trophic-scale gains after premature hatching events, even if there are no species-level benefits; that is, are fatally underdeveloped hatchlings still quality food sources within a food web?
- Prematurely hatched individuals may not survive to reproductive maturity but still persist for a time in their conspecifics' habitat (e.g. Wu et al., 2012). These individuals, though perhaps less fit, can compete directly with conspecifics for resources, potentially imposing density-dependent costs that impact the local population (Touchon et al., 2013). In this way, does delayed mortality induced by premature hatching lead to stronger population-level impacts than immediate mortality?

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likely to be additive and synergistic effects between triggers. One potentially significant example of this is the interaction between low pH and heavy metals, as the solubility and bioavailability of heavy metals tends to increase at low pH (Saalidong et al., 2022). Indeed, significantly higher rates of premature hatching were observed in common carp (*Cyprinus carpio*) exposed to 0.8 mmol/L copper at pH 6.3 compared with pH 7.6 (Stouthart et al., 1996) (Table 1). There are also likely to be significant interactions between pathogens and temperature, as greater disease virulence at higher temperatures is well documented, and diseases of marine invertebrates are among those with the strongest links to climate change (Marcogliese, 2008). Understanding the effect of such interacting stressors on hatching should be a research priority. While the magnitude and breadth of change in many of the discussed triggers will only become clear as we see the rollout and relative success of management and mitigation actions, it is apparent that most parameters are moving in a direction that will increasingly trigger premature hatching of aquatic embryos.

The consequences of premature hatching appear to vary broadly between species and ecosystems, although few studies have tracked the long-term performance of prematurely hatched individuals. In some instances, premature hatching may have evolved as an adaptive response to environmental stressors (Warkentin, 2011a). Here, the adaptive value lies in the higher fitness of hatched individuals compared with those that stay in the egg and do not escape the stressor. For example, hatching in response to acute thermal ramping may be endogenously controlled and allow hatching-competent individuals to swim away, thus avoiding temperatures exceeding their thermal limits. For these adaptations to have evolved, prematurely hatched embryos should be able to avoid the lethal stressor upon hatching. In other cases, premature hatching may serve no adaptive benefit at all; for example, toxicants that dissolve the egg membrane may cause premature hatching without any endogenous control, likely resulting in rapid death.

Early hatching may allow individuals to prioritise short-term survival over continued development under stressful conditions. Even if it is not lethal to remain in the egg under stressful conditions to achieve full embryonic development, it may be more costly than emerging before this time. For example, early hatchlings of European squid have fewer abnormalities compared to late embryos when developing under temperature stress (Rosa et al., 2012, 2014). However, deformities and low growth performance, with likely downstream consequences for survival, also appear to be common costs of premature hatching (Mills & Barnhart, 1999; Nathanailides et al., 1995; Rosa et al., 2012). For example, early hatchlings of wood frog and American toad that were infected with mould were shorter and less developed (e.g. less developed gills, lacking muscular response) than control hatchlings that were not infected nor induced to hatch early, and early hatched wood frog were also significantly more vulnerable to predation (Gomez-Mestre et al., 2006). These consequences of premature hatching may prove increasingly lethal in a future world with a greater prevalence of pathogens, especially if prematurely hatched individuals have decreased ability to fight infections and consequently enhance the infection risk of the entire population.

5 | KNOWLEDGE GAPS AND FUTURE RESEARCH DIRECTIONS

The ability of embryos to exhibit hatching in response to a perceived threat is usually limited by two factors: (i) the ability to detect the stimulus and (ii) sufficient development of the hatching mechanism. Sensory systems are thought to develop and become functional in a specific sequence (tactile, vestibular, chemical, auditory, visual) across all vertebrates (Lickliter, 2011), and the sequence may be similar in invertebrates (e.g. Romagny et al., 2012). This sequential development increases the ability of the embryo to detect a wider range of stimuli with further development (Romagny et al., 2012). After developing the ability to detect the stimulus, embryos must have also reached hatching competence; that is, the hatching mechanism must be sufficiently developed. This field of research has received very little attention, and therefore, there are many unknowns regarding the mechanisms, fitness consequences and downstream population effects of premature hatching of aquatic embryos. To illuminate the extent of the challenge and offer directions for fruitful research in this field, we propose a number of research priorities in Box 3.

6 | CONCLUSIONS

Understanding the drivers, consequences and gaps in our knowledge of premature hatching in aquatic embryos is critical for conservation management in a time of global change. Despite the documented evidence of this phenomenon across a broad array of taxa and a wide range of biotic and abiotic triggers, surprisingly little research has focused on what premature hatching likely means for individuals, populations and communities in vulnerable ecosystems where conditions favouring hatching disruptions are likely to occur. As a result, we suggest that the study of premature hatching at both a mechanistic and ecological level represents an exciting and emerging research field with real-world consequences for aquatic ecosystem health and persistence at present and in response to an uncertain future. While we have focused on aquatic ecosystems, terrestrial embryos are also likely to be susceptible to premature hatching following similar perturbations (see Doody, 2011), the causes and consequences of which also merit further investigation. We urge researchers interested in global change, developmental biology, life-history strategies and organismal biology to tackle these challenging research questions from a variety of angles in order to better evaluate the role of premature hatching in ecosystems around the globe.

AUTHOR CONTRIBUTIONS

Zara-Louise Cowan: Conceptualization; data curation; formal analysis; investigation; project administration; visualization; writing – original draft; writing – review and editing. **Leon Green:** Conceptualization; data curation; investigation; writing – original draft; writing – review and editing. **Timothy D. Clark:** Conceptualization; investigation; writing – original draft; writing – review and editing. **Tamzin A. Blewett:** Conceptualization; investigation; writing – original draft;

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writing – review and editing. **Jeremy De Bonville:** Conceptualization; data curation; investigation; writing – original draft; writing – review and editing. **Thomas Gagnon:** Data curation. **Elizabeth Hoots:** Conceptualization; investigation; writing – original draft; writing – review and editing. **Luis Kuchenmüller:** Conceptualization; investigation; writing – original draft; writing – review and editing. **Robine H. J. Leeuwis:** Conceptualization; investigation; writing – original draft; writing – review and editing. **Joaquín Navajas Acedo:** Investigation; writing – original draft; writing – review and editing. **Lauren E. Rowsey:** Conceptualization; investigation; writing – original draft; writing – review and editing. **Hanna Scheuffele:** Conceptualization; investigation; writing – original draft; writing – review and editing. **Michael Richard Skeeles:** Conceptualization; investigation; writing – original draft; writing – review and editing. **Lorena Silva-Garay:** Conceptualization; investigation; writing – original draft; writing – review and editing. **Fredrik Jutfelt:** Conceptualization; funding acquisition; investigation; project administration; visualization; writing – original draft; writing – review and editing. **Sandra A. Binning:** Conceptualization; data curation; investigation; project administration; visualization; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data and script for this study are openly available in the figshare repository (https://doi.org/10.6084/m9.figshare.26763868.v1), following best practices (Roche et al., 2015), and were made available to editors and reviewers upon initial submission.

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