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REVIEW PAPER

Biological consequences of weak acidification caused by elevated carbon dioxide in freshwater ecosystems

Caleb T. Hasler · Jennifer D. Jeffrey · Eric V. C. Schneider · Kelly D. Hannan · John A. Tix · Cory D. Suski

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Abstract Weak acidification can occur in freshwater ecosystems when free carbon dioxide (CO_2) levels increase, which can happen for a variety of reasons. To define the state of knowledge for how weak acidification influences freshwater biota and ecosystems, a review of the primary literature was conducted. Despite few empirical studies focused on weak acidification in the primary literature (~100 studies), some themes have emerged from our literature review. Most studies focused on physiological responses at the organismal level, and fish were the most studied taxa. Animals exhibited reduced individual growth rates, and, in contrast, primary producers demonstrated increased individual and population growth rates. In animals, mortality, sub-lethal injuries, and changes to behaviours were also observed. Negative consequences to reproduction in macrophytes were found. Few studies have focused on population, community, or ecosystem levels, though broad scale studies suggest that weak acidification can limit species community diversity, specifically in invertebrates and fish. Moving forward, researchers need to continue to advance our understanding of the consequences of weak acidification for freshwater biota. Furthermore, priority should be placed on research that can evaluate the potential for weak acidification in freshwater to lead to changes in ecological regimes or economical outcomes, such as fisheries collapses.

Keywords Carbonic acid · Organismal response · Ecology · Freshwater biota

Introduction

Acidification of freshwater ecosystems has received considerable attention in the past due to human caused acid rain and acid mine drainage, and the ecological effects are complex (Schindler, 1988). Freshwater ecosystems exhibit a wide range of natural pH levels (<2–12). Some natural waters have pH values below 4.5, such as those water bodies in volcanic regions and bogs that are rich in dissolved organic matter. Other water bodies can have pH values as high as 9–12, which are common to endorheic regions where soda (Na_2CO_3) concentrations are high (Wetzel, 2001). Freshwater pH levels are typically driven by the production of protons (H^+) resulting from the

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C. T. Hasler · J. D. Jeffrey · E. V. C. Schneider · K. D. Hannan · J. A. Tix · C. D. Suski
Department of Natural Resources and Environmental Sciences, University of Illinois Urbana-Champaign, W-503 Turner Hall, 1102 South Goodwin Ave, Urbana, IL 61801, USA

C. T. Hasler (✉)
Department of Biology, The University of Winnipeg, 515 Portage Ave, Winnipeg, MB R38 2E9, Canada
e-mail: c.hasler@uwinnipeg.ca

hydrolysis of bicarbonate (HCO_3^-) and, by-and-large, most freshwater lakes have pH values that range from 6 to 8. The pH of a waterbody indicates the proportions of dissolved inorganic carbon (DIC) specimens (free carbon dioxide, CO_2; HCO_3; CO_3^{2-}) and is linked to the 'bicarbonate buffering system'. The pH of freshwater ecosystems can be further influenced by anthropogenic forces such as acid rain and acid mine drainage, which have the potential to change the proportion of DIC specimens (i.e., as pH decreases, the proportion of free CO_2 increases) (Patrick et al., 1981).

Acidification of freshwater can be classified as either strong or weak and refers to the tendency of an acid to lose a proton (H^+). Strong acids, such as nitric acid (HNO_3) and sulfuric acid (H_2SO_4), dissociate almost fully in freshwater, resulting in a substantial drop in environmental pH (i.e., multiple pH units). Most notably, strong acids that reach the atmosphere by air pollution and precipitate back to the Earth's surface are responsible for acid rain (Patrick et al., 1981). Acid rain has been extensively studied in freshwater ecosystems, especially in lakes and rivers where pH can fall below 4 (Schindler, 1988). Another type of strong acidification is due to acid mine drainage, which occurs when strong acids used in the metal or coal mining industry leak into water bodies. Contrastingly, weak acidification of freshwater can also occur by the addition of weak acids (e.g., carbonic acid [H_2CO_3] and acetic acid [CH_3COOH]) that only partially dissociate, and result in much smaller changes in environmental pH ($\sim$ one or two pH units). The following review will focus only on freshwater acidification induced by the addition of CO_2 and not on acidification caused by strong acids.

Recent studies have shown that some freshwater ecosystems are at risk of becoming weakly acidic due to elevated CO_2. Weak acidification from elevated CO_2 may occur for a variety reasons including increased atmospheric CO_2 (Phillips et al., 2015), high metabolism in lakes (Bogard & del Giorgio, 2016), invasive species (Lin & Guo, 2016), land-use changes (Jacinthe et al., 2004), and boosted terrestrial primary productivity and soil respiration because of global warming (Kling et al., 1992; Sobek et al., 2003; Arneth et al., 2010; Cory et al., 2014; Reich et al., 2014). Localized acidification may also occur in the future because elevated CO_2 has been proposed as a management tool to prevent the movement of invasive species (Noatch & Suski, 2012; Donaldson et al., 2016). The addition of CO_2 to freshwater, regardless of the source, alters the proportion of DIC specimens and results in the production of carbonic acid and the accumulation of H^+. When occurring in systems with a poor buffering capacity, CO_2 addition to freshwater may lead to weak acidification of the water body (Stets et al., 2017), particularly in headwater streams (Crawford et al. 2017). Of note, however, is the wide spatial and temporal variation in DIC, pH, and alkalinity of global freshwater ecosystems (Cole et al., 1994; Cole & Caraco, 2001; Butman & Raymond, 2011; Crawford et al., 2017). Due to this high level of spatial and temporal variation, the potential for freshwater ecosystems to become acidified by rising partial pressures of CO_2 (pCO_2) is likely site- and time-specific, and may also be influenced by several other factors including, substrate, the ratio of autotrophs to heterotrophs, precipitation, water sources, mixing patterns, and land-use (see Hasler et al., 2016a for summary). Overall, weak acidification of inland waters, by any of the various sources described above, is a potential novel stressor for freshwater ecosystems. Unlike strong acidification, weak acidification has rarely been the focus of freshwater ecological studies (Hasler et al., 2016a), and only recently has it been highlighted globally as a potential issue due to the growing concern over rising atmospheric CO_2 (e.g., Phillips et al. 2015) and other anthropogenic influenced changes (discussed above). It is possible that some fresh water bodies may be at risk due to increasing dissolved CO_2 levels, and this is concerning given the plight of ocean acidification being observed today.

The objective of this paper was to highlight potential biological consequences of weak acidification, caused by the addition of carbonic acid to freshwater ecosystems. Past reviews of acidification in freshwater ecosystems have largely focused on the consequences of large pH reductions due to anthropogenic impacts (e.g., Patrick et al., 1981; Schindler, 1988). The impacts of small reductions in pH have largely been ignored, though research in the past decade has observed serious consequences of ocean acidification on biota (Orr et al., 2005; Fabry et al., 2008; Ishimatsu et al., 2008; Clements & Hunt, 2015) and has shifted the focus of some freshwater biologists to study weak acidification in freshwater ecosystems (Hasler et al., 2016a). Based on our understanding of the potential for freshwater systems to become weakly acidified by anthropogenic factors (see above), in this review we have focused on studies where freshwater pH has been reduced by approximately two pH units and where pH values have not fallen below 5.5, which is typical for pH changes driven by carbonic acid (Hasler et al., 2016a). We have reviewed existing scientific studies for both proximate and ultimate consequences of weak acidification on freshwater biota through to ecosystems. Further, we have categorized impacts by the levels of biological organization (e.g., individuals, populations, communities) that were studied and the type of responses observed.

Literature review

The aim of the literature review was to identify any scientific study that observed biotic responses to weak acidification in freshwater caused by elevated CO_2 (i.e., carbonic acid). It was known a priori that there is a paucity of scientific research on weak acidification induced by elevated CO_2. Therefore, a literature review using some techniques typical of a systematic review was completed (Haddaway et al., 2015b). The search strategy used included a Boolean string in Thomson Reuters Web of Science ("freshwater" OR "lake" OR "river" OR "stream" OR "pond" OR "creek") AND ("carbonic acid" OR "low pH" OR "acidification") AND ("biota" OR "fish*" OR "zooplankton" OR "phytoplankton" OR "invertebrate" OR "macrophyte" OR "vegetation" OR "macro*"); a search of the terms ("weak acidification AND freshwater") and ("freshwater" and "carbon dioxide") in Google Scholar was also made and the first 80 pages reviewed for appropriate papers (Haddaway et al., 2015a). A review of primary literature known to the authors was also carried out.

Search strategy

Following the primary literature search, the titles of each identified study were reviewed and determined to either be suitable for inclusion or excluded. Papers that were immediately excluded based on the title alone were studies that were clearly conducted in marine environments, were unavailable (e.g., unpublished symposium abstracts), were syntheses/reviews, or were not related to acidification. Abstracts of the included studies were then reviewed to determine the 'type' of acidification that the study was focused on (i.e., nitric, sulfuric, humic [organic], or carbonic). Any study that did not specifically investigate the effects of carbonic acid was excluded from further analysis. All remaining studies that investigated an effect of weak acidification, or elevated CO_2, on any freshwater organism were then accessed and reviewed.

To formulate a broad picture of the types of studies that were identified and to identify potential knowledge gaps, the following information was extracted from each paper: (1) pH range, (2) taxon (or taxa) assessed in the study, (3) life stage of the organism(s) assessed in the study, (4) the biological level of organization that was the focus of the study (i.e., organismal, population, community, or ecosystem), (5) the response level (i.e., physiological, behavioural, ecological, or evolutionary), and (6) the study type (i.e., laboratory, field, or microcosm/mesocosm). Studies were classified as demonstrating organismal-level outcomes if the study focused on individuals of a species (e.g., studies that monitored physiological or behavioural changes). Studies were considered to highlight populations if vital rates or population growth were determined. Studies that presented details about species richness/diversity or food webs were classified as focused on the community level. Studies that quantified broader ecological responses, such as whole ecosystem photosynthesis or respiration, nutrient cycling, etc., were classified as focused on ecosystems. With respect to the response levels, studies related to sub-organismal responses and whole body performance were considered to be physiological in nature, while studies that quantified or described changes to movement, habitat-use, or interactions with the environment or other organisms were considered to be behavioural. Types of responses that related to changes in species diversity, food webs, or broader ecosystem changes were considered as ecological responses, while evolutionary responses were considered to be multigenerational in nature or where heritability or adaptation was specifically assessed. Finally, studies where strict manipulations were carried out in a controlled setting were considered as laboratory studies, while studies that involved observations in natural settings were considered as field studies. Microcosm/mesocosm studies were studies that were designed to be experimental but sensitive to natural fluctuations.

Search results

In total, over 5000 citations were reviewed and 103 scientific studies published between 1913 and 2016 were identified as having investigated an effect of weak acidification, or elevated CO_2, in freshwater biota (Fig. 1). Of the included studies, the majority (81%) were completed under laboratory conditions, while the remaining were either field (13%) or microcosm/mesocosm (6%) studies. Over half (51%) of the studies were completed using fish, with 66% of these studies being completed on sexually mature fish (Fig. 2). Other taxa studied included macrophytes (19%), macroinvertebrates (12%), phytoplankton (11%), amphibians (3%), and zooplankton (1%) (Fig. 2). Three studies (3%) included more than one taxon.

The reviewed studies assessed a range of levels of biological organization. Most studies (86%) assessed the effect of weak acidification, or elevated CO_2, at the organismal-level, which mostly included a measurement of physiological and/or behavioural observations (Fig. 3). A further 10% of studies investigated community-level effects, with 80% of those studies measuring an ecological outcome of exposure to weak acidification or elevated CO_2 (Fig. 3). The remaining studies focused on population- (3%) and evolutionary-level responses (1%) (Fig. 3) to weak acidification or elevated CO_2.

Biological synthesis

Based on the above literature review, there are several potential consequences of weak acidification, induced by elevated free CO_2, for freshwater ecosystems. Several effects were found on a variety of biological scales including at the organismal-, population-, and community-levels. Organismal biology was the most studied discipline with respect to freshwater weak acidification, likely owing to the direct effect that a change in ambient (or environmental) water quality has on life processes. Of the more well-studied effects, impacts to growth rates, mortality and injuries, and behavioural responses were clear themes in the findings of the studies.

Growth rate

A primary consequence of weak acidification observed across freshwater taxa was an alteration in growth rate and/or biomass. The direction of this change in growth rate or biomass (i.e., reduction or increase) depended on whether the study organism was a primary producer or consumer. Overall, alterations in the typical energetic balance are a primary organismal response to weak acidification across freshwater taxa.

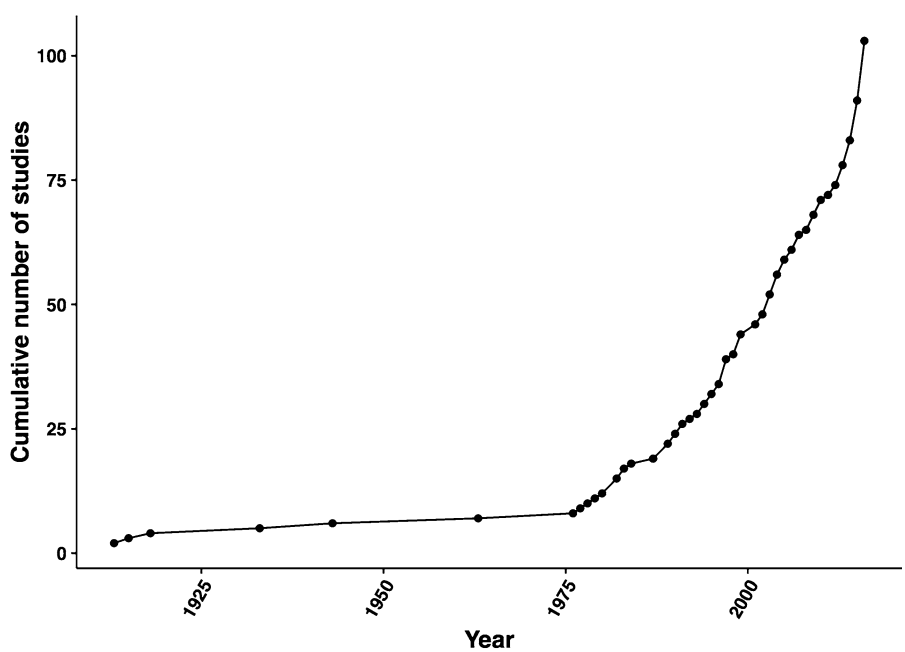

Fig. 1 Cumulative number of studies by year that focused on weak acidification and were included in the review

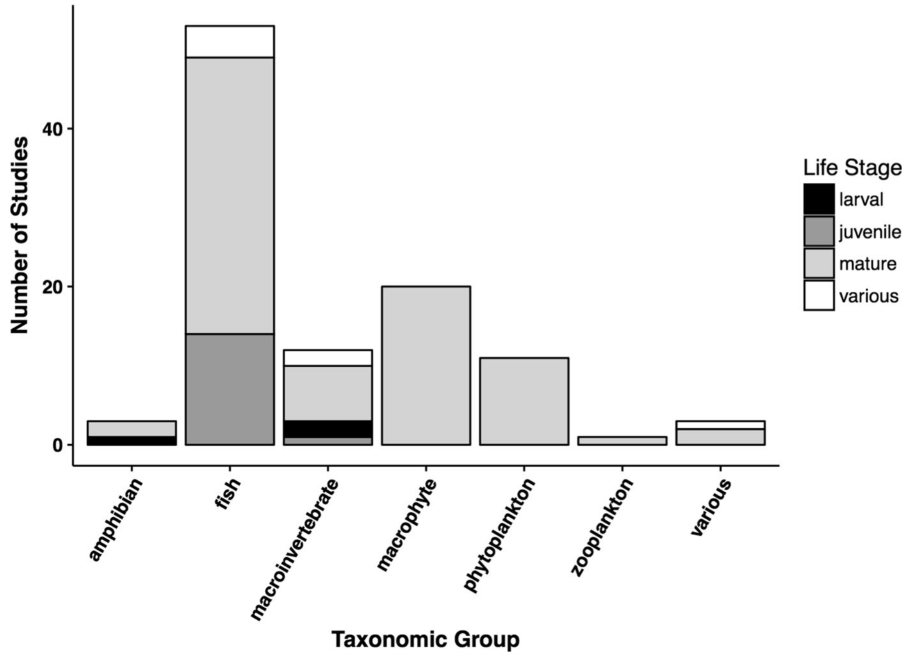

Fig. 2 Number of studies ($n = 103$) by taxonomic group (x-axis) and life stage (*grey bars*) that were reviewed for biological consequences of freshwater weak acidification caused by elevated CO_2. The taxonomic group/life stage "various" represents studies that included two or more taxonomic groups or life stages

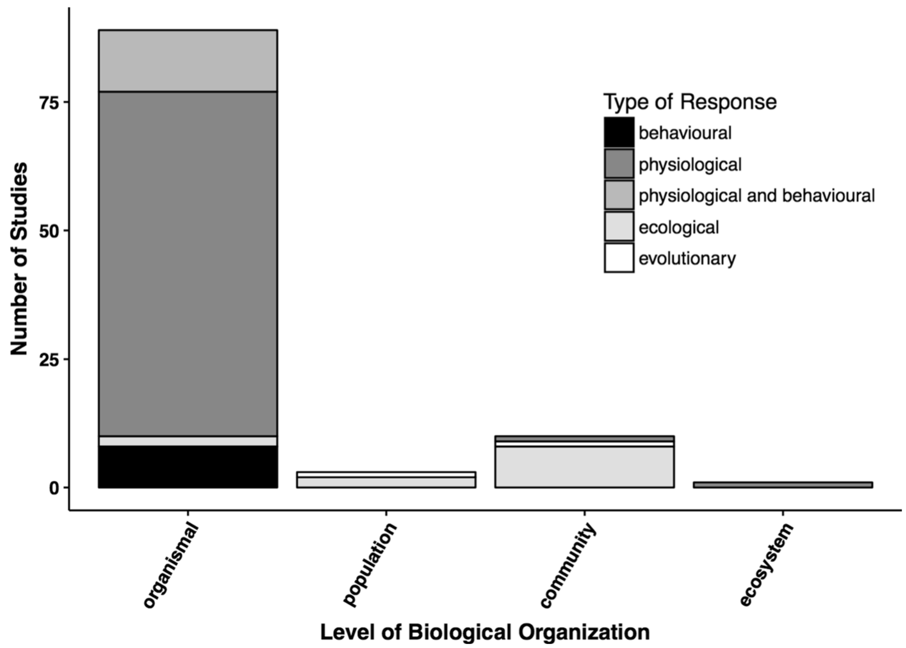

Fig. 3 Number of studies ($n = 103$) by level of biological organization (x-axis) and response type (*grey bars*) that were reviewed for biological consequences of freshwater weak acidification caused by elevated CO_2

In fish, amphibians, and macroinvertebrates, a reduction in growth rate has been observed in response to weak acidification. This decrease in growth rate likely resulted from the use of energetically expensive ion and acid–base regulatory mechanisms to combat acidification of fluids and tissues (e.g., Perry, 1982; Abbey-Lambertz et al., 2014; Hannan et al., 2016a). These regulatory mechanisms to buffer acidosis typically involve obtaining and retaining HCO_3^- from the environment while excreting accumulated H^+ (e.g., Cameron, 1978; Heisler et al., 1982; Busk et al., 1997; Brauner & Baker, 2009; Hannan et al., 2016a). In addition to buffering acidosis, many freshwater animals undergo a physiological stress response following exposure to weakly acidified water (e.g., Kates et al., 2012; Dennis et al., 2015a, b; Hannan et al., 2016a, b, c; Jeffrey et al., 2016) which also requires energy (Beyers et al., 1999). Thus, the energetic costs associated with maintaining homeostasis in situations of chronic exposure to weak acidification can alter the finite energy budgets of freshwater animals, and consequently result in a reduction in growth rates, calcification, and body mass (e.g., Fivelstad et al., 2003, 2007; Hosfeld et al., 2008; Lopes-Lima et al., 2009; Good et al., 2010; Abbey-Lambertz et al., 2014; Fivelstad et al., 2015). Additionally, in zooplankton, slower growth rates have been found in *Daphnia* spp. exposed to weak acidification; however, this response is likely due to a reduction in the nutritional quality of their food source, phytoplankton (Urabe et al., 2003). Overall, weak acidification can both directly and indirectly reduce growth rates of freshwater biota.

In contrast to animals, macrophytes and phytoplankton exposed to weak acidification demonstrated increased growth rates and biomass (Vadstrup & Madsen, 1995; Verspagen et al., 2014a, b; Low-Décarie et al., 2015). In macrophytes, increased growth under weak acidification is thought to result from an increase in free CO_2, which is less energetically costly to exploit than HCO_3^- (Vadstrup & Madsen, 1995). In phytoplankton, increased growth may be due to the low affinity that the RubisCO enzyme has for CO_2, and thus CO_2 assimilation can be more efficient in high CO_2 environments (Verspagen et al., 2014a). However, increased nutrient availability has also been found to be necessary for phytoplankton growth to increase in high pCO_2 environments (Low-Décarie et al., 2015). Thus, in situations where nutrient availability is not limited, macrophytes and phytoplankton can thrive in weakly acidified environments.

Mortality and sub-lethal injuries

Mortality and sub-lethal injuries have also been observed in animals exposed to weak acidification. Perhaps the most dramatic mortality event was described by Davidson (1933) observing a pink salmon (*Oncorhynchus gorbuscha*) spawning ground in an Alaskan stream. After sunset, a reach of the stream became acidified (pH 5.6, from 6.1) because of a rise in atmospheric CO_2, likely caused by an immediate cooling and stabilization of the air mass directly above the stream. Over 5000 fish (pink salmon, other trout species [*Salvelinus* or *Oncorhynchus* spp.], and other unidentified species) were estimated to have died during the approximately 30-min event. Other studies have also reported that experimentally induced weak acidification from high CO_2 that resulted in a drop in pH to 6.0–6.4 from approximately 7.0 induced mortality in freshwater fishes (Shelford & Allee, 1913; Wells, 1913; King, 1943; Ochumba, 1990; Bernier & Randall, 1998; Fivelstad et al., 1999, 2003). Likewise, fish mortality has also been observed during the use of carbonic acid as an anaesthetic (e.g., Gelwicks et al., 1998). Other freshwater species such as zebra mussels (*Dreissena polymorpha*; McMahon et al., 1995), Asian clams (*Corbicula fluminea*; McMahon et al., 1995), New Zealand mudsnails (*Potamopyrgus antipodarum*; Nielson et al., 2012), spring snails (*Pyrgulopsis montezumensis;* O'Brien & Blinn, 1999), juvenile fatmucket mussels (*Lampsilis siliquoidea*; Waller et al., 2017), and bullfrogs (Abbey-Lambertz et al., 2014) have also been reported to have increased mortality when exposed to weak acidification induced by high CO_2 (reported pH inducing mortality ranged from 5.0 to 6.3 and decreased from a range of 6.9–7.9).

Sub-lethal injury in animals exposed to weak acidification is also possible. For example, fish exposed to weak acidification from high CO_2 exposure may exhibit nephrocalcinosis (deposition of calcium salts in the kidney or stomach, Smart et al., 1979; Fivelstad et al., 1999; Hosfeld et al., 2008), lymphocytic portal hepatitis (liver inflammation, Good et al., 2010), gill epithelial hyperplasia (or gill lesions, Fivelstad et al., 2003; Good et al., 2010), and abnormalities in vertebrae (Martens et al., 2006). No studies found during our literature search suggested direct mortality or sub-lethal injury to macrophytes, phytoplankton, zooplankton, or aquatic insects.

Behavioural responses

Other types of responses at the organismal level that may be influenced by weak acidification include behavioural responses, particularly in fish, but also in invertebrates. For example, negative impacts to olfaction, alarm cue responses, and loss of predator avoidance behaviours in fishes have been observed in several studies (Leduc et al. 2004, 2010, 2013; Ou et al., 2015; Tix et al., 2017a). Furthermore, field experiments found that juvenile Atlantic salmon (*Salmo salar*) in weakly acidified streams experienced greater rates of predation, likely because of impaired chemosensory risk assessment as compared to fish in neutral pH streams (Elvidge & Brown, 2014). Other behavioural disturbances have also been observed in fish, including changes to personality (Jutfelt et al., 2013; Ou et al., 2015), altered diel movement behaviours (Hasler et al., 2016b), and altered activity patterns (Regan et al., 2016). Reported pH values that induced the above behavioural changes ranged from 5.8 to 7.7, and it is likely that these behavioural changes stem from physiological responses to acidification (Ou et al., 2015; Regan et al., 2016). However, not all studies have detected behavioural alterations following exposure to acidification, as fish personality and feeding behaviours were minimally impacted in freshwater fishes exposed to weakly acidified water (Midway et al., in press; Tix et al., 2017b). Furthermore, even when behavioural responses were observed, following exposure to weak acidification normal behaviour typically resumed in fish upon being returned to water at baseline pH (Hasler et al., 2016b; Tix et al., 2017a). These negative impacts to olfaction may not be exclusive to fish, as invertebrates, such as crayfish (*Cambarus bartonii*) also displayed reduced feeding responses due to impaired olfaction following exposure to strong acidification (pH range 4.5–7.5; Allison et al., 1992). In addition, freshwater mussels (*Lampsilis cardium*, *L. siliquoidea*, and *Pyganodon grandis*) have been found to alter gaping behaviour during periods exposure to weak acidification, which could increase their vulnerability to predation (Hasler et al., in press). Behavioural responses to weak acidification have not been reported for any other freshwater biota.

Population-level outcomes

Few studies have explicitly monitored population-level outcomes in natural populations following exposure to weakly acidified water, making it challenging to make broad conclusions pertaining to the effects of weak acidification on populations. More specifically, only two studies were found that focused on population-level endpoints, such as population growth (Alto et al., 2005) and historical abundances (Wolfe & Siver, 2013). Alto et al. (2005) found no change in mosquito populations grown in microcosms using leaf litter in weakly acidified water. Wolfe & Siver (2013) found that historic population sizes in chrysophytes showed positive relationships with summertime low pH induced by high $p\mathrm{CO_2}$. Despite the paucity of studies that specifically assessed population outcomes across a range of taxa, studies that focused on organismal biology did monitor reproductive output and mortality (see above), and thus we can infer how natural populations might change if freshwater ecosystems become acidified. For example, Titus & Hoover (1993) reported that freshwater macrophytes, *Najas flexilis* and *Vallisneria americana*, failed to sexually reproduce when held in water at pH 5.0 (a 1.5 decrease in pH compared to control conditions). Additionally, as described above, mortality increased in several fish and early-life stage invertebrate species in water below pH 6.3. A limitation of many of the studies in our literature review was that many experiments with weakly acidified water were completed over relatively short time periods (often less than a few weeks), and thus population-level endpoints could not be measured (i.e., require a longer timespan to become evident). It is likely that, given the organismal responses noted above (changes in growth, injury rates, physiological stress, etc.), survival rates and reproductive output may also be inherently altered, and thus weak acidification may lead to changes in population growth, although this requires further study.

Community-level dynamics

Few empirical studies have assessed community-level dynamics in weakly acidified freshwater. In Montezuma Well, Arizona, where the lake has been naturally acidified due to high concentrations of dissolved CO_2 (pH 6.5) (Cole & Barry, 1973), the aquatic insect community consists of 57 taxa in 16 families, and there are several endemic species. However, the unique conditions at Montezuma Well may also indicate that pH does have negative consequences for aquatic ecosystems, as larval stages for several aquatic insects, including Trichoptera, Lepidoptera, Megalopera, Neuroptera, Chironomidae, and Anisoptera, are absent (Blinn & Sanderson, 1989). Fish community changes may also occur should freshwater systems become weakly acidified. In an assessment of 138 northern Wisconsin lakes, some of which are naturally acidified from clear water seeps, there was an absence of many cyprinid and darter species in lakes with a pH below 6.2 (Rahel & Magnuson, 1983). In contrast, central mudminnow (*Umbra limi*), yellow perch (*Perca flavescens*), several centrachids, and black bullheads (*Inctalurus melas*) were found to inhabit a wide range of pH (Rahel & Magnuson, 1983).

Phytoplankton communities have also been altered by elevated pCO_2. In Montezuma Well (described above), 33 taxa of phytoplankton were collected, and almost 80% were classified as either Chlorophyta (green algae) or Cyanobacteria (blue-green algae) (Boucher et al., 1984). Most species collected were small (<5 μm diameter) in comparison to other freshwater phytoplankton, and Flagellates were absent from the Well (Boucher et al., 1984). Chlorophyta were also found to increase in abundance when mesocosms were artificially elevated in CO_2 (Low-Décarie et al., 2015), while abundances of cyanobacteria and diatoms were depressed (Low-Décarie et al., 2011). Lastly, by modelling competition in a toxic and non-toxic strain of freshwater cyanobacterium, *Microcystis aeruginosa*, in a high CO_2 environment Van de Waal et al. (2011) found that the toxic strain outcompeted the non-toxic strain, suggesting that either tolerance for low pH or ability to use free CO_2 resulted in dominance of the toxic strain. Projecting the above outcomes to a water body where CO_2 becomes elevated and weak acidification occurs suggests that freshwater ecosystems may be inundated with green algae and toxic cyanobacteria.

Conclusions and future directions

Overall, despite few empirical studies focused on weak acidification in the primary literature, some biological themes have emerged from our literature review. Most studies focused on physiological responses at the organismal level, and fish were the most studied taxa. Animals exhibited reduced growth, likely due to the high energetic costs of buffering acidosis and the physiological stress response. Primary producers (e.g., macrophytes and phytoplankton), in contrast, demonstrated increased growth, likely because of the lower energetic demand of exploiting free CO_2 gas rather than HCO_3^- during photosynthesis. In animals, mortality, sub-lethal injuries, and changes to behaviours such as predator avoidance were also observed. Negative consequences to reproduction in macrophytes were found as well. Relatively, few studies have focused on population, community, or ecosystem levels, though broad scale studies suggest that weak acidification can limit species community composition, specifically in invertebrates and fish. Broadly, many of the effects reported on in studies on weak acidification indicate that, like in the marine environment, weak acidification has the potential to cause harm to firewater biota, though future studies are needed.

Clear knowledge gaps exist in the primary literature focused on weak acidification. For example, studies that aimed to understand organismal level consequences of weak acidification on amphibians, macroinvertebrates, aquatic insects, zooplankton, phytoplankton, and macrophytes were either absent or poorly represented in our literature search. As were studies on evolutionary changes or transgenerational effects, which have not been studied in freshwater ecosystems, but recently has been the focus of acidification research in marine environments (e.g., Miller et al., 2012; Parker et al., 2013). Likewise, studies that focused on population, community, and ecosystem levels were also not prevalent in our literature search. Further, secondary impacts of weak acidification associated with changes in water chemistry [e.g., aluminium toxicity (Patrick et al., 1981)] and weak acidification as a multiple stressor were not found by our literature search. Moving forward, researchers need to continue to advance our understanding of the consequences of weak acidification (induced by carbonic acid) for freshwater biota given the potential for weak acidification in some freshwater ecosystems to persist due to climate change and other anthropogenic activities to affect these ecosystems. In a way, freshwater ecosystems are easier to test experimentally in comparison to marine ecosystems, as facilities such as the Experimental Lakes Area (ELA) in Ontario, Canada exist and offer the potential for long-term and whole ecosystem studies. Questions related to sensitivity of populations and communities to weak acidification and differences in species tolerances could be addressed using facilities such as the ELA. Other novel questions that should be prioritized include identifying geographical locations (i.e., lakes, rivers) that may be susceptible to weak acidification. There is also a need to move beyond simple species-level responses over the short-term and focus on longer-term studies—reproduction, survival, predator/prey dynamics, evolutionary (acclimation vs. adaptation), transgenerational, and community- or ecosystem-level responses. Studies that examine the role of weak acidification when multiple stressors are present (e.g., warming, hypoxia, eutrophication) should also be conducted to ensure that the possibility of interaction effects is known. Studies designed to assess the potential to influence outcomes that might be negative for humans, for example increase in abundance of toxic phytoplankton or will result in impacts to fisheries, should be given high priority. In conclusion, weak acidification is clearly a stressor for some taxa and freshwater ecosystems. With several potential factors that could increase dissolved CO_2 in freshwater ecosystems, such as climate change, invasive species, and land-use practices, it will be vital for scientists to immediately begin to understand the potential consequences of freshwater weak acidification. Further studies are required to ensure healthy and productive freshwater ecosystems.

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