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The effects of ocean acidification on fishes – history and future outlook

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Abstract

The effects of increased levels of carbon dioxide (CO_2) on the Earth's temperature have been known since the end of the 19th century. It was long believed that the oceans' buffering capacity would counteract any effects of dissolved CO_2 in marine environments, but during recent decades, many studies have reported detrimental effects of ocean acidification on aquatic organisms. The most prominent effects can be found within the field of behavioural ecology, *e.g.*, complete reversal of predator avoidance behaviour in CO_2-exposed coral reef fish. Some of the studies have been very influential, receiving hundreds of citations over recent years. The results have also been conveyed to policymakers and publicized in prominent media outlets for the general public. Those extreme effects of ocean acidification on fish behaviour have, however, spurred controversy, given that more than a century of research suggests that there are few or no negative effects of elevated CO_2 on fish physiology. This is due to sophisticated acid–base regulatory mechanisms that should enable their resilience to near-future increases in CO_2. In addition, an extreme "decline effect" has recently been shown in the literature regarding ocean acidification and fish behaviour, and independent research groups have been unable to replicate some of the most profound effects. Here, the author presents a brief historical overview on the effects of elevated CO_2 and ocean acidification on fishes. This historical recap is warranted because earlier work, prior to a recent (*c.* 10 year) explosion in interest, is often overlooked in today's ocean acidification studies, despite its value to the field. Based on the historical data and the current knowledge status, the author suggests future strategies with the aim to improve research rigour and clarify the understanding of the effects of ocean acidification on fishes.

KEYWORDS
carbon dioxide, climate change, observation bias, replication, warming

1 | INTRODUCTION

Anthropogenic release of carbon dioxide (CO_2) into the atmosphere is causing global warming, and it increases the amount of dissolved CO_2 in the world's oceans (Doney *et al.*, 2009; Hönisch *et al.*, 2012). Consequently, oceanic pH decreases, a process termed ocean acidification (Doney *et al.*, 2009, Hönisch *et al.*, 2012). Compared to the current-day CO_2 partial pressure (pCO_2) of about 400 µatm, a business-asusual scenario may lead to a pCO_2 increase to over 900 μatm by the year 2100, corresponding to a pH reduction of 0.3–0.5 pH units (Caldeira & Wickett, 2005). The field of ocean acidification has received considerable attention during the past 10–15 years. In fact, the research effort has been so vast that it has been proposed as being unprecedented in the marine sciences, and an exponential increase in number of publications is evident (Browman, 2016; Figure 1). Numerous reviews have also been published on the topic, including on the specific effects of ocean acidification on fish behaviour and physiology (Briffa *et al*., 2012; Clements & Hunt, 2015; Esbaugh, 2017; Heuer & Grosell, 2014; Tresguerres & Hamilton, 2017). The strongest and most detrimental effects have been reported within the field of behavioural ecology, *e.g*., complete reversal of predator avoidance in CO_2-exposed fish (Clements *et al*., 2022; Clements & Hunt, 2015). Some of those studies, published in high-profile journals, have been very influential, receiving hundreds of citations over recent years (Clements *et al*., 2022). The results have also been conveyed to policymakers, including the White House (Roberts, 2015), and have been publicized in prominent media outlets for the general public (Black, 2011; Yong, 2010). The extreme behavioural effects have, however, spurred a debate (Clark *et al*., 2020a, 2020b; Munday *et al*., 2020), because more than a century of research has shown that fish physiology is tolerant to CO_2 levels that vastly exceed those relevant in a climate change scenario (Ishimatsu *et al*., 2008; Ishimatsu & Kita, 1999; Pörtner *et al*., 2004). In addition, a recent meta-analysis has revealed that a "decline effect" phenomenon is present in this field, meaning that the initial strong effects reported in the literature have all but disappeared over a decade in subsequent studies (Clements *et al*., 2022).

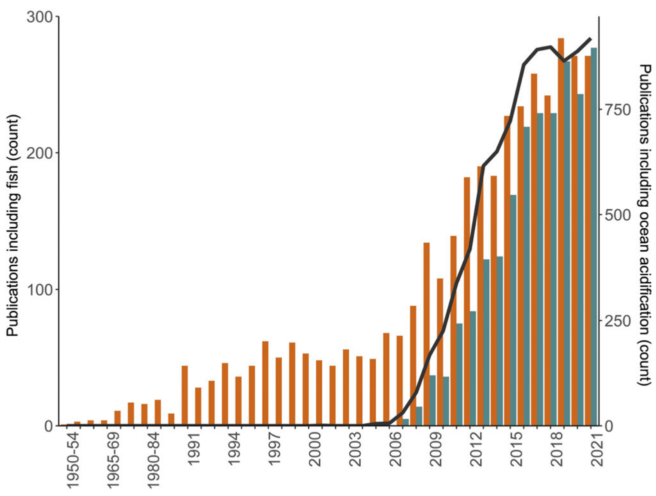

FIGURE 1 Number of publications over time on carbon dioxide, ocean acidification and fish. Orange bars (left *y*-axis) show number of publications based on the search term "carbon dioxide and fish," blue bars (left *y*-axis) show number of publications based on the search term "ocean acidification and fish" and the solid line (right *y*-axis) shows number of publications based on the search term "ocean acidification." Data were obtained from Web of Science Core Collection on 21 July 2022. For the years 1950–1989, data were pooled in bins of 5 years. Note the different scale on the *y*-axis, and that the orange and blue bars may contain the same study in instances where all three search terms were found within the same paper. No search hits prior to 1950 emerged for the carbon dioxide and fish search, none prior to 2007 for the ocean acidification and fish search and none prior to 2001 for the ocean acidification search. Nonetheless, the Rau and Caldeira (1999) paper, identified as the first mention of the term "ocean acidification," did not appear in the Web of Science Core Collection search. For detailed search data, see Electronic Supplementary Material in Appendix S1. Search terms ■ "carbon dioxide" AND fish; ■ "ocean acidification" AND fish; – "ocean acidification."

2 | CO_2 EMISSIONS AND OCEAN ACIDIFICATION – THE DEVELOPMENT OF A RESEARCH FIELD

Calculations on the amount of CO_2 required to alter the Earth's temperature were first presented towards the end of the 19th century (Arrhenius, 1896). Although it was acknowledged already at that time that "modern industry" was adding CO_2 into the atmosphere, it was believed that other processes, including CO_2 absorption by the oceans, would act in compensatory ways, and that the amount of industrial CO_2 added to the atmosphere would be minor (Arrhenius, 1896). The notion that anthropogenic CO_2 emissions could indeed have an impact on Earth's temperature, and had an impact already at that time, was proposed later (Callendar, 1938; Callendar, 1958). The 19th-century measurements of CO_2 were, however, uncertain, triggering a debate about the actual influence of CO_2 emissions on Earth's temperature, not the least due to the buffering capacity of marine environments (Bolin & Eriksson, 1959; Revelle & Suess, 1957). Although the effect of CO_2 on ocean chemistry was discussed in those early papers, it was only from a chemistry and mathematical point of view; potential effects of this change on aquatic organisms were not mentioned. A few studies did investigate the effects of CO_2 on fish and other organisms in the early 1900s; however, they did not concern the increased pCO_2 due to CO_2 emissions. Instead, they investigated the effects of "gas waste", *i.e*., pollution from several gasses from coal distillation and gas-washing in freshwater, mainly testing which pollution levels were fatal to freshwater fishes, with one of the tested gasses being CO_2 (Shelford, 1917). Later, the effects of ocean disposal of CO_2, also called ocean sequestration, received some research interest, when this method was proposed instead of atmospheric release (Caulfield *et al*., 1997; Marchetti, 1977; Takeuchi *et al*., 1997). A number of studies followed, testing the effects of elevated pCO_2 in this context in several species of fish (reviewed in Ishimatsu *et al*., 2004), and not the least in deep-sea species, because deep-sea areas were often suggested for CO_2 disposal (Freund & Ormerod, 1997; Haugan & Drange, 1992; Marchetti, 1977). Although very high levels of CO_2 were tested in these papers, corresponding to pH values of about 6–7 (which is far higher CO_2 than what is relevant in an ocean acidification context), it was suggested that such pH levels would overall be tolerated by fishes, at least temporarily (reviewed in Pörtner *et al*., 2004). The field of ocean sequestration later merged with that of ocean acidification (Barry & Drazen, 2007), with a 1999 study seeming to contain the first mention of the term "ocean acidification" (Rau & Caldeira, 1999).

Around 2005, ocean acidification started to pick up speed as its own research field, and it grew exponentially (Figure 1). To date, *i.e.*, in less than 20 years, more than 8500 papers have been published on ocean acidification (Figure 1). This fact has two important implications. Firstly, the vast amount of papers means that it is difficult to obtain a comprehensive overview of the accumulated results using classic tools, such as narrative reviews, systematic reviews and meta-analyses (Nakagawa *et al.*, 2019; see the "Future Outlook" section later). Secondly, the effects of CO_2 on fishes had been studied long before the concept of ocean acidification was introduced. Because the earlier work on fish and CO_2 was not written in a climate change context and such terminology was therefore not used, those papers are often overlooked in ocean acidification studies, although many of them might be highly relevant. Notably, in a review published in 1950, the authors state that the literature on the effects of CO_2 on fish was so extensive that it could not be fully reviewed, and papers dating back to the early 1900s are cited (Doudoroff & Katz, 1950). Hence, already in 1950, the accumulated scientific literature on the effects of CO_2 on fish was considered difficult to overlook (Doudoroff & Katz, 1950). Despite the long history of work on the effects of CO_2 and pH on fish, several relatively recent reviews reported that there was not enough information available to obtain any meta-analytical results (Kroeker *et al.*, 2010; Kroeker *et al.*, 2013; Wittmann & Pörtner, 2013). This may, in part, be due to the tendency that reviews only focus on the recent past, *e.g.*, only including search results from the past 20 years (Draper & Weissburg, 2019). It could also be due to difficulties in finding the relevant papers among the great number of studies, because many of the earlier results may not be applicable in the field of ocean acidification. Some studies (also on marine species) did not investigate the increased levels of CO_2, but rather lowered pH due to acid rain and/or by mineral acids, and the sensitivity to CO_2 *vs.* HCl (fixed acid)-induced water acidification may differ (Ishimatsu *et al.*, 2004). Furthermore, many studies tested acute or short-term exposure, although it can be argued that an ocean acidification scenario requires longer-term exposure (many ocean acidification studies, however, do use short-term exposure). Many early studies might be deemed irrelevant in a climate change scenario, as they often investigated very high levels of CO_2 (Ishimatsu *et al.*, 2008). Nonetheless, it seems counterintuitive that a relatively low level of CO_2 would have an effect, whereas a much higher level would have no effect. Therefore, despite the differences, several studies may still be relevant, highlighting the need to incorporate results from earlier work into the field of ocean acidification.

3 | HISTORY: THE EFFECTS OF CO_2 AND LOW pH ON FISHES

Some of the earliest work investigated the "reactions" of fishes to CO_2, using levels causing the death of the experimental animals to test CO_2 resistance, and to discuss the "physiological effects of gases in solution" (Shelford & Allee, 1913; Shelford & Powers, 1915; Wells, 1913). Many years of research then investigated the effects of elevated CO_2 or lowered pH on fish physiology, mainly focusing on toxicity, cardio-respiratory control and acid–base regulation (reviewed in Doudoroff & Katz, 1950, Fromm, 1980, Ishimatsu & Kita, 1999, Ishimatsu *et al.*, 2008). Those studies mainly involved freshwater fishes (Doudoroff & Katz, 1950; Fromm, 1980), but marine species were tested as well (Doudoroff & Katz, 1950; Ishimatsu *et al.*, 2008; Ishimatsu & Kita, 1999). Many studies were linked to aquaculture and therefore tested very high pCO_2 levels (Ishimatsu *et al.*, 2008). Despite testing extreme levels, those papers generally reported that fish physiology (cardio-respiratory control, acid–base regulation and growth) was tolerant to pCO_2 levels that vastly exceed those relevant in a climate change scenario (Ishimatsu *et al.*, 2008; Ishimatsu & Kita, 1999; Pörtner *et al.*, 2004). More recent studies, performed in an ocean acidification context and therefore using relevant pCO_2 levels, and testing marine species, confirm the pattern that many physiological traits are unaffected by elevated CO_2 (Cattano *et al.*, 2018; Esbaugh, 2017; Lefevre, 2016). Respiration is probably the physiological process that has been studied most extensively from an ocean acidification perspective, and a meta-analysis by Lefevre (2016) reported that CO_2 had no effect in the majority of studies testing resting oxygen uptake and absolute aerobic scope. Esbaugh (2017) confirms the view that the effects of ocean acidification on maximum metabolic rate and aerobic scope are ambiguous due to a high level of variability between species. Similar results are reported in Cattano *et al.* (2018), where CO_2 had no effect on metabolic scope, whereas resting metabolic rate was affected in some studies. The general pattern from the earlier papers on CO_2 and from the more recent ocean acidification literature, *i.e.*, that pH and/or pCO_2 has no or small effects on fish physiology, is in accordance with evidence that fishes are excellent acid–base regulators (Ishimatsu *et al.*, 2008). This also agrees with observations in the fossil record from mass extinction events where fishes showed great potential to adapt to new environmental conditions (Bush & Bambach, 2011; Chen & Benton, 2012).

4 | BEHAVIOURAL EFFECTS

Although the scientific literature on physiological effects of CO_2 and lowered pH is vast and expands far back in time, studies investigating behavioural effects are not that common, and in general appeared later (reviewed in Jones & Reynolds, 1997). There are, however, some studies, *e.g.*, a relatively early paper by Moss and McFarland (1970) where the effect of increasing levels of CO_2 on shoaling and swimming speed was investigated. No effects were found until pH reached a level of 6.2 (again, far more extreme than the levels used in an ocean acidification context) (Moss & McFarland, 1970). The paper tested the effects of increased levels of CO_2 based on a hypothesis that the concentration of oxygen and CO_2 could be altered within dense groups of schooling fish as a result of metabolism. The study is therefore not related to ocean acidification or anthropogenic increase of CO_2, but the results are nonetheless relevant due to the starting point pH and exposure duration. After some publications reporting blocking effects of low pH on the olfactory bulb (Hara, 1976; Thommesen, 1983), a large number of studies that focused on behaviour and chemoreception were published. For example, it was reported that fish did not respond behaviourally to chemical cues, such as food cues, sex pheromones or alarm cue substances from damaged skin, at low pH levels (6.0–6.5; Lemly & Smith, 1985, but see Smith & Lawrence, 1988). A large number of papers followed in the early 2000s, investigating behavioural responses to predator cues and alarm cues, reporting that fish did not respond when the cues had been produced in low pH (6.0), concluding that this was due to a covalent change of the alarm pheromone molecule itself rather than an effect on the behavioural response of the fish (Brown *et al*., 2002; Leduc *et al*., 2003). This theory was further strengthened by a study reporting that the observed lack of response to chemical cues was not due to the elevated physiological or behavioural stress (Leduc *et al*., 2003). Furthermore, no permanent olfactory damage occurred under reduced pH, and short-term reduction in olfactory sensitivity and degradation of the chemical alarm cues were therefore proposed as the likely mechanisms (Leduc *et al*., 2010). Importantly though, all of the mentioned studies on chemoreception were performed on freshwater or diadromous fishes, and in addition, they tested acidification, not the increased levels of CO_2. Results from studies using freshwater fishes cannot be directly applied to marine species due to differences in physiology and water chemistry, and the fact that the change in pH can be much more rapid in freshwater than in marine waters (*e.g*., due to acid rain) (reviewed in Ishimatsu *et al*., 2008). The concept of altered chemoreception due to changes in pH was tested on marine fishes in an ocean acidification context starting 2009, and a large number of studies followed. A number of different marine species were exposed to elevated pCO_2, with some of them reporting a complete reversal in the behavioural response to cues (*e.g*., attraction to predator chemical cues instead of avoidance) after CO_2 exposure (reviewed in Clements & Hunt, 2015). This led to an explosion of studies investigating the effects of pCO_2 on a range of behaviours, such as swimming activity, predator–prey interactions, behavioural lateralization and reproductive behaviours (Clements *et al*., 2022; Clements & Hunt, 2015).

5 | FISHY EFFECTS

Many of the behavioural studies reported very large effect sizes with little variation between and within individuals (Clark *et al*., 2020a; Clements *et al*., 2022). This fact, in combination with the large body of research showing that fish physiology is tolerant to elevated CO_2 (Ishimatsu *et al*., 2008; Ishimatsu & Kita, 1999; Pörtner *et al*., 2004), has spurred a debate (Clark *et al*., 2020a, 2020b; Munday *et al*., 2020). The identified "decline effect" in this field shows that the initial strong effects with large effect sizes have all but disappeared over a decade in the subsequent studies (Clements *et al*., 2022). The decline effect could not be explained by increasing the proportions of studies examining cold-water species, nonolfactory-associated behaviours or non-larval life stages (Clements *et al*., 2022). The decline effect was, however, no longer apparent when all papers authored or co-authored by at least one of the lead investigators of the early studies were removed from the dataset (Clements *et al*., 2022). A large-scale replication attempt from an independent research group also failed to replicate CO_2 effects in several behavioural traits of coral reef fishes, including predator cue avoidance (Clark *et al*., 2020a). Notably, some of the early studies published in 2009 and 2010, and some subsequent papers from the same authors, have recently been questioned for their scientific validity (Enserink, 2021), and a related paper has been retracted from *Science* due to data fabrication (Thorp, 2022), further fuelling the debate.

Although the discussion regarding the validity of some papers is recent, anomalies in the ocean acidification literature have been identified earlier. For example, some of the effects on behavioural traits do not seem to align with the results that other, related traits are unaffected. Cattano *et al*. (2018) report in their meta-analysis that there was no effect of ocean acidification on reproduction, cognition, audition, vision or habitat choice, whereas chemoreception (olfaction) and predator avoidance were affected. Given that chemoreception was affected (*via* altered $GABA_A$ receptor function, see further details later), it would be expected that other traits, for which the chemosensory system is important, would be affected as well. This has implications for the suggested mechanism behind the reported chemosensory effects, *i.e*., altered $GABA_A$ receptor function (Nilsson *et al*., 2012), which would be expected to cause effects also in other chemosensory-mediated behaviours. Additional concerns regarding the $GABA_A$ hypothesis have been raised. For example, many studies have reported that treating CO_2-exposed fish with gabazine, a $GABA_A$ receptor antagonist, completely restores CO_2-induced behavioural impairments (reviewed in Tresguerres & Hamilton, 2017). Nonetheless, most studies also reported that treating the control fish with the same dose of gabazine as the CO_2-exposed fish induced no measurable effects, although that would be expected because gabazine affects normal inhibitory GABA regulation, including neuronal excitation (reviewed in Esbaugh, 2017, Tresguerres & Hamilton, 2017).

Another anomaly in the CO_2 chemosensory literature is found in studies investigating the effects of CO_2 on learning, where chemical alarm cues and predator cues are typically utilized in the experimental design. An important assumption in some of these studies is that fish need to learn to respond to predator cues by pairing with chemical alarm cues, *i.e*., that it is not an innate response (Chivers *et al*., 2014a; Ferrari *et al*., 2012). In other studies, however, predator-naïve fish reportedly avoided predator cues without any prior learning (*e.g*., Dixson *et al*., 2010; Munday *et al*., 2010; Munday *et al*., 2012; Vail & McCormick, 2011). Some of the studies where learning was not required used the same or closely related species of the same life stage as those where learning was needed, and they were performed at the same time of the year and with fish collected from the same location (Munday *et al*., 2012, Vail & McCormick, 2011). Lack of cross-citation between these papers means that the cause and effect of those inconsistencies have not been discussed or resolved. An additional aspect regarding alarm cue research is the degradation rate of chemical alarm cues. Chivers *et al*. (2013) report that chemical alarm cue degrades rapidly, and that exposing the cues to CO_2 causes even faster degradation (Chivers *et al*., 2014b). Despite these findings, studies have used batches of alarm cues where the experimental duration far exceeded the degradation time, with no reported changes in fish preference/avoidance behaviour through time (Welch *et al*., 2014).

6 | FUTURE OUTLOOK

Throughout this paper, the author has referred to the extensive research field that ocean acidification has become. This great research effort comes with many benefits, but as discussed earlier, it may also lead to negative consequences as the literature by now is so vast that it is difficult or even impossible to oversee and papers are easily "lost." The study by Moss and McFarland (1970), mentioned earlier, is interesting in this respect, because it used a marine species and tested the effects of increasing levels of CO_2, with the starting point pH being relevant in an ocean acidification context. Despite the applicability of the results from this specific paper to more recent research, it has never been cited in an ocean acidification paper [based on a Google Scholar search on 21 July 2022, yielding 45 citations. For detailed search data, see Electronic Supplementary Material (ESM)]. This fuels selective reporting of results showing detrimental effects of ocean acidification, whereas studies investigating CO_2 exposure, often finding no effects, are left largely or completely uncited (Clements *et al*., 2022; Perry, 2022). Although narrative reviews, systematic reviews and meta-analyses can be useful tools, the field of ocean acidification is probably beyond the scope to fit in a single review or meta-analysis (Nakagawa *et al*., 2019). This is because issues such as heterogeneity between datasets, lack of data (data availability) and bias can make it difficult to assess an entire (large) research field within a review. To counteract this problem (which is, of course, relevant to many scientific fields), a new framework called research weaving, combining systematic mapping and bibliometrics, has recently been suggested (Nakagawa *et al*., 2019). Systematic mapping provides a snapshot of the current state of knowledge and identifies areas that need more research and areas where a full synthesis can be performed. Bibliometrics reveals the structure and development of a field, thereby enabling researchers to see how pieces of evidence are connected (Nakagawa *et al*., 2019). Research weaving may thus be a useful and powerful tool in the field of ocean acidification biology.

The anomalies and disparate findings across studies and research groups may point to methodological rather than biological explanations concerning the effects of elevated CO_2 on fishes, which have been suggested earlier (Heuer & Grosell, 2014). Given the ongoing replication crisis within many scientific fields, this is not a small issue. In the medical sciences, the ARRIVE (Animal Research: Reporting of In Vivo Experiments) guidelines were proposed as a means to overcome insufficient reporting of methods (McGrath *et al*., 2010). However good the incentive, most researchers do not use those guidelines, and many papers are still lacking in detail (Enserink, 2017), a problem not only true in the medical sciences. Many ocean acidification papers lack sufficient methodological details to allow replication. For example, a review of 15 papers investigating predator chemical cues showed that few contained enough information to allow replication (reviewed in Sundin *et al*., 2017). Basic data such as the number and size of the animals producing the chemical cues were missing, and it was common for method descriptions to be ambiguous such as "approximately 6–8," and "at least two," and unclear time descriptions such as "the following morning" and "overnight" (reviewed in Sundin *et al*., 2017). Journal word limits are sometimes used as an excuse as to why the methods were not fully reported; nonetheless, that is an insufficient explanation because full methods can be presented in the online supplementary material. For the sake of transparency and research rigour, it would be preferred if the full methods were included in the main paper, and some journals (*e.g*., *Journal of Experimental Biology*) apply an unrestricted word count on the material and methods section. Several journals mandate specific documentation where the authors must fill out method details of the study before final acceptance, such as "Checklist of key methodological and analytical information" in the *Journal of Experimental Biology* and "Editorial Policy checklist" and "Reporting Summary" mandated by *Nature*. Such incentives will help to ensure that the methodological description is sufficient to allow replication, but many journals do not have any such requirements. Instead, it is left to the authors, as well as the reviewers and editors, to ensure that the material and methods are adequately described, but this is poorly policed.

Another important aspect concerns the usage of blinded methods to avoid confirmation bias and other subjective data collection artefacts (Holman *et al*., 2015; Tuyttens *et al*., 2014). Many experiments are prone to observer bias, yet it is rarely stated in the paper whether blinded methods were used (Kardish *et al*., 2015). Some journals mandate statements noting whether blinding approaches were used (*e.g*., *Behavioral Ecology and Sociobiology*: Traniello & Bakker, 2015, and *Nature*). This is an important step forward. Nonetheless, statements of blinded data collection are rarely accompanied by details regarding how blinding was achieved. In experiments involving CO_2 exposure, complete blinding regarding treatment can be difficult, if not impossible, due to the CO_2 dosing system being both visually and auditorily noticeable to any human observer physically present during the experiments. It is not uncommon that blinding can be very difficult to obtain, and in such instances, video recording the experiments and using tracking software might be a solution (Clark, 2017). Video recording the experiments also allows fellow researchers to access the raw data of the study. It is worth noting that video recording of fish behaviour is a technique that has been used in CO_2 experiments since 1964 (Moss & McFarland, 1970), highlighting that we have little excuse not to use this method in modern times (Clark, 2017). Furthermore, automated tracking software was used in acidification studies already in 1985 (Lemly & Smith, 1985), and given the great range of free tracking software currently available (*e.g*., ToxTrack, Rodriguez *et al*., 2018 and Tracktor, Sridhar *et al*., 2019) there should not be any financial or methodological hindrance. For behaviours that are difficult to score using tracking software, there are free event-logging software options (*e.g*., BORIS, Friard & Gamba, 2016).

Overall, the controversy surrounding the impacts of ocean acidification on fish and other marine animals highlights the complexity of this issue and the need for continued research and further replication of previous studies (Clark *et al*., 2020a; Clements *et al*., 2022; Leung *et al*., 2022). Experiments should be systematically documented and transparent (Parker *et al*., 2016; Roche *et al*., 2015; Roche *et al*., 2022) so that we can reach a true understanding of any potential impacts of ocean acidification on fish behaviour and physiology. Although it might seem redundant to mention, this controversy does not, by any means, implicate that ocean acidification is an issue without concern. Negative effects of climate change and other human-induced stressors are well-established facts, and efforts must be made to mitigate these effects (Duarte *et al*., 2020).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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