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Impacts of climate-related stressors on social group cohesion and individual sociability in fish

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ABSTRACT

Group-living in animals comes with a number of benefits associated with predator avoidance, foraging, and reproduction. A large proportion of fish species display grouping behaviour. Fish may also be particularly vulnerable to climate-related stressors including thermal variation, hypoxia, and acidification. As climate-related stressors are expected to increase in magnitude and frequency, any effects on fish behaviour may be increased and affect the ability of fish species to cope with changing conditions. Here we conduct a systematic review of the effects of temperature, hypoxia, and acidification on individual sociability and group cohesion in shoaling and schooling fishes. Searches of the published and grey literature were carried out, and studies were included or excluded based on selection criteria. Data from studies were then included in a meta-analysis to examine broad patterns of effects of climate-related stressors in the literature. Evidence was found for a reduction in group cohesion at low oxygen levels, which was stronger in smaller groups. While several studies reported effects of temperature and acidification, there was no consistent effect of either stressor on sociability or cohesion. There was some evidence that marine fishes are more strongly negatively affected by acidification compared with freshwater species, but results are similarly inconsistent and more studies are required. Additional studies of two or more stressors in combination are also needed, although one study found reduced sociability following exposure to acidification and high temperatures. Overall, there is some evidence that hypoxia, and potentially other climate-related environmental changes, impact sociability and group cohesion in fishes. This may reduce survival and adaptability in shoaling and schooling species and have further ecological implications for aquatic systems. However, this synthesis mainly highlights the need for more empirical studies examining the effects of climate-related factors on social behaviour in fishes.

Key words: climate change, fish behaviour, shoaling, schooling, group behaviour, temperature, hypoxia, acidification.

CONTENTS

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I. INTRODUCTION

As global conditions change, ecosystems are increasingly affected by climate-related stressors (Doney, 2010; Nagelkerken & Connell, 2015). Fish populations may be particularly at risk; not only are they dependent on substances in solution for their metabolism, osmoregulation, and excretion, they are also very sensitive to changes in environmental temperature (Alfonso, Gesto & Sadoul, 2021; Heuer & Grosell, 2014; Herbert *et al.*, 2013). As atmospheric temperatures rise, bodies of water, particularly oceans, absorb much of the additional heat, leading to rising sea surface temperatures (von Schuckmann *et al.*, 2020). Warmer water has a lower capacity for dissolved oxygen, possibly contributing to increased occurrences of aquatic hypoxia (Gattuso *et al.*, 2015), which may exacerbate other sources of hypoxia including eutrophication resulting from nutrient run-off (Levin *et al.*, 2015). Atmospheric CO_2 may also enter into solution, leading to increased dissolved carbonic acid levels resulting in lower pH (Gattuso *et al.*, 2015). Even at sublethal levels, climate-related stressors may reduce fitness and affect inter- and intraspecific interactions (Domenici, Steffensen & Marras, 2017; Hurst, 2007). Changes in the magnitude and timing of these stressors has led to an urgent need to quantify the potential of aquatic organisms to cope with or adapt to changing conditions and combinations of stressors (Nagelkerken & Connell, 2015; Diaz & Rosenberg, 2008).

Climate-associated stressors can affect numerous aspects of fish physiology and behaviour. For example, temperature has plastic and evolutionary effects on metabolic rates in fish (Pilakouta *et al.*, 2020; Nati *et al.*, 2018; Clarke & Johnston, 1999). Hypoxia and elevated CO_2 may also affect metabolic traits and neural functioning (Heuer & Grosell, 2014; Jutfelt *et al.*, 2013). Moreover, climate-related stressors also cause changes to locomotor capacity, spontaneous activity, and foraging behaviours (Domenici *et al.*, 2017; Killen *et al.*, 2013). Individual physiological traits and performance can therefore change as a function of the environment, shaping physiological performance curves for traits such as metabolic rate or aerobic scope. At the individual level, changes in physiological traits due to climate-related factors may in turn alter behaviours associated with predator avoidance, foraging, or sociability (Metcalfe, Van Leeuwen & Killen, 2016; Killen *et al.*, 2017). Given that fish are the most diverse vertebrate taxa, being predators and prey in nearly every aquatic habitat on Earth, changes in the social behaviours of fish due to climate change may lead to altered food web dynamics or other inter- or intraspecific interactions (Domenici *et al.*, 2017; Killen *et al.*, 2017). The majority of fish species are highly social, and the challenges facing aquatic environments make these species an excellent model for studying the effects of climate change on social behaviour.

While studies on the effects of climate-related stressors on individual measures of behaviour are increasing, effects on group-level behaviours, including schooling and shoaling, are poorly understood. Schooling (synchronised and polarised group swimming) and shoaling (less-coordinated groups) (Palacios-Fuentes *et al.*, 2020; Miller & Gerlai, 2012) occur in many, if not most, fish species at some point in their lives, and are key for foraging, predator avoidance, and reproduction. Swimming in schools also confers hydrodynamic advantages, allowing fish to save energy while in groups (Marras *et al.*, 2015). For any given group member, the benefits and costs of group membership are dynamic, and will vary with the internal state of the individual and environmental conditions. Environmental factors may cause changes to individual sociability, defined as the tendency to associate with conspecifics in the absence of aggression or another external motivator such as a shared food source. Increased temperatures, for example, may cause an increase in energy requirements for fish *via* effects on metabolic rate, potentially decreasing the benefits of sociability due to increased competition for food or other resources (Webster & Hart, 2006; Killen *et al.*, 2016; Pilakouta *et al.*, 2022). Warming or hypoxia can also alter individual activity (Bartolini, Butail & Porfiri, 2015; Lefrancois *et al.*, 2009), which can affect group cohesion, generally measured in terms of among-individual distances within the group or the overall group area or volume occupied (Cooper, Adriaenssens & Killen, 2018; Angiulli *et al.*, 2020). The effects of temperature, hypoxia, and acidification may also affect neurological functioning (Toni *et al.*, 2019; Topal *et al.*, 2021; Andreassen *et al.*, 2022), and sensory systems (McKee *et al.*, 2020), directly affecting the mechanisms by which fish can sense conspecifics and coordinate behaviours

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with groupmates (McKee *et al.*, 2020; Corral-Lopez *et al.*, 2023) and potentially disrupting group functioning (Killen *et al.*, 2021). Therefore, increased spontaneous activity, decreased sociability, or disrupted neurological function could alter the cohesion of fish groups. Group disruption in hypoxic conditions may result from fish moving apart due to increased activity associated with attempts to escape hypoxic conditions (Domenici *et al.*, 2017), or altered neuromuscular or sensory functioning (Lucon-Xiccato *et al.*, 2014; Nilsson *et al.*, 1993; Partridge & Pitcher, 1980). Group cohesion may be further altered due to oxygen-seeking behaviours such as surfacing, as fish may perform risky behaviours such as surfacing in groups to reduce the risk of aerial or terrestrial predation (Domenici, Steffensen & Batty, 2000; Pineda *et al.*, 2020). Increased environmental and systemic carbon dioxide partial pressure ($p\mathrm{CO}_2$) corresponds to reduced pH (acidification) of water. To maintain blood pH under high $p\mathrm{CO}_2$ conditions, fish may alter blood ion concentrations and therefore cellular ion gradients, possibly leading to disrupted neuron functioning (Jutfelt *et al.*, 2013). The resulting change in cognitive ability may result in altered signalling capabilities and thus impaired shoaling or schooling (Maulvault *et al.*, 2018; Mitchell, Booth & Nagelkerken, 2022). Stress-related increases in metabolic rate stemming from homeostatic responses to acidification (Heuer & Grosell, 2014) could contribute to reductions in group cohesion and shoaling or schooling behaviour *via* reduced sociability.

As temperature, hypoxia, and acidification become increasingly prevalent stressors in aquatic ecosystems with the potential to impact fish behaviour, a thorough understanding of our current knowledge of the effects of these stressors would be beneficial for directing future research efforts. While there have been attempts to examine the effects of climate-related stressors on fish sociability and group cohesion, there has been no attempt to synthesise current studies in this area. As such, it has been challenging to identify general trends and uncover potential biases and knowledge gaps in the ongoing study of how climate change is affecting fish social behaviour. We aimed systematically to review the current literature covering the singular and interactive effects of temperature, hypoxia, and acidification on individual sociability and group cohesion in shoaling and schooling fish species. In addition to summarising the overall trends for the effects of climate-related stressors on fish sociability and group cohesion, we analysed the existing literature for geographical and taxonomic patterns, and identified existing knowledge gaps and avenues for future research.

II. METHODS

(1) Literature searches

Searches of the literature were carried out in *Web of Science*, *Scopus*, *ProceedingsFirst*, and *Google Scholar* from October to December 2022, using the terms "temperature", "hypoxia", "acidity" or "acidification" combined with the terms "social* behaviour", "sociability" or "group cohesion". The term "fish" was also used in *Google Scholar*, in order to improve the relevance of the first 100 results which were examined from each search (Fig. 1; Table 1). Searches were limited to English language publications and those within the field of Zoology. Studies used included those published in peer-reviewed journal articles (95.5% of total studies) as well as unpublished PhD and Masters theses (4.5%). Relevant studies that were missed by these literature searches were also identified from citations within the sourced publications. A total of 39 studies were found from searches (Table 1). A further six relevant studies were identified from references in studies found from searches (Fig. 1). Data from all but two studies (Clark, 2022; Stienessen, 2015) had been published as peer-reviewed articles. Sources were only included for analyses if shoaling or schooling were examined in relation to climate-related stressors, specifically temperature, oxygen availability, and/or acidification. Where species were not specified as shoaling or schooling in relevant studies, for example in trials of individual sociability or aggregation, searches of the literature were conducted to ascertain that each species displays shoaling or schooling behaviour. As this review focused on the effects of anthropogenic climate change, thermocline effects were excluded as these represent consistent natural variation in temperature, rather than climate or seasonal fluctuations. As climate change is generally associated with increases in temperature, we focused on studies of the effects of high temperatures, either at the high end of or above the thermal optimum of the studied species. Studies of hyperoxia were excluded as it is likely that comparisons between high and low oxygen for these studies would have different results to studies of hypoxia. Studies were excluded if they did not directly quantify either sociability or group cohesion, meaning studies of sexual behaviour, aggression, dominance hierarchies, migration, social learning, and social recognition were excluded. Interactions with non-climate-related stressors (e.g. predation cues) were also excluded. Studies using numerical models (theoretical studies) were excluded, as were conspecific *versus* heterospecific preference tests. Studies focused on "aggregation" were not included (Pitcher, 1983), with one exception where "aggregation" was specifically used as a proxy for wild shoaling in a shoaling species (Clark, 2022). All studies were considered independently by one author (I.C.T.), and then blind reviewed by one of two other authors (A.M or D.C.). Studies that were disagreed upon were discussed and included or excluded by consensus.

(2) Data collection

Following study inclusion, data were extracted directly from descriptions of study methods and results, or from supplementary material provided, and entered into a single database (see online Supporting Information, Table S1) before further processing and analysis. In cases where data were not available in tables or supplementary data, data were extracted from graphs using *WebPlotDigitizer* version

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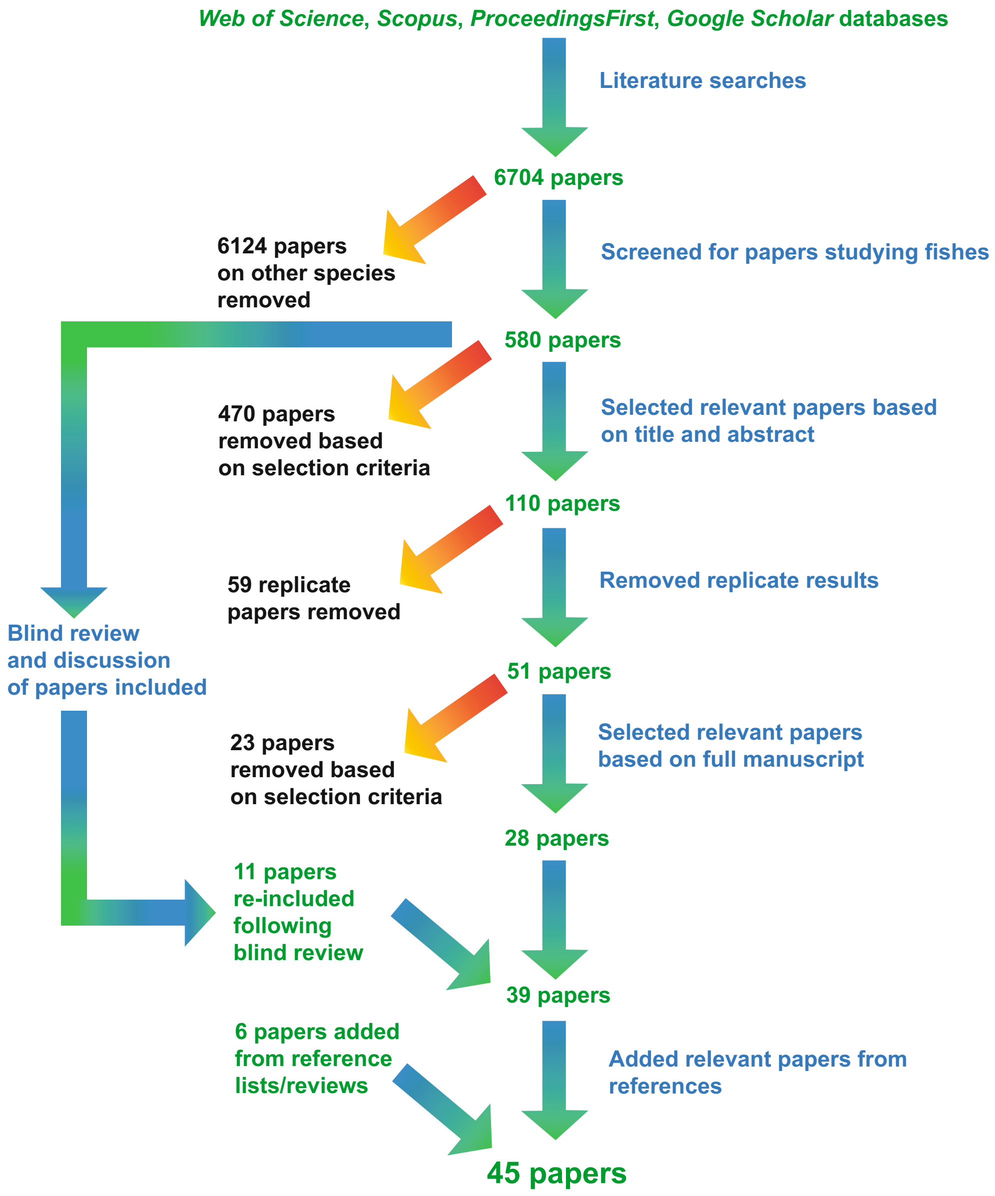

Fig. 1. Flow diagram illustrating paper selection process for systematic review.

4.6 (Rohatgi, 2022). Data on the following variables were collected for each study:

(1) *Effect size of each treatment on group cohesion or sociability, relative to the control*. As studies used different metrics to assess sociability and group cohesion, direct comparison using the units given in studies was not possible. Therefore, any change in behaviour was converted to a standardised measure, effect size, that could then be used in models to compare results among studies. Effect size (Hedges' *g*, a standardised difference of means between groups) of all treatment levels (i.e. climate-related stressors) were calculated for 36 studies and 347 data points, as all treatments from nine studies (Duteil *et al*., 2016; Stienessen, 2015; Israeli & Kimmel, 1996; Palacios-Fuentes *et al*., 2020; Mameri *et al*., 2020; Fahlman *et al*., 2021; O'Driscoll & McClatchie, 1998; Olla, Studholme & Bejda, 1985; Swartzman, 1997) were excluded where some or all data needed to calculate an effect size were not available. Some treatments from an additional two studies (Colchen *et al*., 2017; Mehdi *et al*., 2022) were excluded for the same reason. Effect sizes were calculated as a standardised measure of change in sociability or group cohesion, as various metrics may be used to measure each. Effect sizes were transformed (multiplied by 1 or −1) according to the metric used to measure group cohesion or sociability, so that positive effect sizes indicate an increase in sociability or group cohesion and negative effect sizes indicate a decrease.

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Table 1. Search terms and sources used to find papers included in this review.

Database	Search term	Results	Results examined	Results included in analysis
Web of Science	Temperature AND "social* behaviour"	2669	All	23
Web of Science	Hypoxia AND "social* behaviour"	76	All	1
Web of Science	Temperature AND "group cohesion"	15	All	0
Web of Science	Hypoxia AND "group cohesion"	5	All	0
Web of Science	Temperature AND "sociability"	84	All	3
Web of Science	Hypoxia AND "sociability"	10	All	0
Web of Science	Acidity AND "social* behaviour"	13	All	1
Web of Science	Acidity AND "group cohesion"	0	All	0
Web of Science	Acidity AND "sociability"	3	All	0
Web of Science	Acidification AND "social* behaviour"	33	All	3
Web of Science	Acidification AND "group cohesion"	3	All	0
Web of Science	Acidification AND sociability	0	All	0
Scopus	Temperature AND "social* behaviour"	1238	All	1
Scopus	Hypoxia AND "social* behaviour"	102	All	0
Scopus	Temperature AND "group cohesion"	12	All	0
Scopus	Hypoxia AND "group cohesion"	2	All	0
Scopus	Temperature AND "sociability"	57	All	0
Scopus	Hypoxia AND "sociability"	7	All	0
Scopus	Acidity AND "social* behaviour"	11	All	0
Scopus	Acidity AND "group cohesion"	0	All	0
Scopus	Acidity AND "sociability"	1	All	0
Scopus	Acidification AND "social* behaviour"	9	All	0
Scopus	Acidification AND "group cohesion"	2	All	0
Scopus	Acidification AND sociability	1	All	0
ProceedingsFirst	Temperature AND "social* behaviour"	101	All	0
ProceedingsFirst	Hypoxia AND "social* behaviour"	13	All	0
ProceedingsFirst	Temperature AND "group cohesion"	7	All	0
ProceedingsFirst	Hypoxia AND "group cohesion"	2	All	0
ProceedingsFirst	Temperature AND "sociability"	20	All	0
ProceedingsFirst	Hypoxia AND "sociability"	1	All	0
ProceedingsFirst	Acidity AND "social* behaviour"	1	All	0
ProceedingsFirst	Acidity AND "group cohesion"	0	All	0
ProceedingsFirst	Acidity AND "sociability"	0	All	0
ProceedingsFirst	Acidification AND "social* behaviour"	3	All	0
ProceedingsFirst	Acidification AND "group cohesion"	0	All	0
ProceedingsFirst	Acidification AND sociability	3	All	0
Google Scholar	Effects of temperature on social behaviour in fish	485,000	Top 100 by relevance	1
Google Scholar	Effects of temperature on group cohesion in fish	91,100	Top 100 by relevance	2
Google Scholar	Effects of temperature on sociability in fish	21,500	Top 100 by relevance	0
Google Scholar	Effects of hypoxia on social behaviour in fish	26,400	Top 100 by relevance	0
Google Scholar	Effects of hypoxia on group cohesion in fish	19,900	Top 100 by relevance	1
Google Scholar	Effects of hypoxia on sociability in fish	1860	Top 100 by relevance	2
Google Scholar	Effects of acidity on social behaviour in fish	30,600	Top 100 by relevance	0
Google Scholar	Effects of acidity on group cohesion in fish	21,100	Top 100 by relevance	0
Google Scholar	Effects of aciditiy on sociability in fish	1430	Top 100 by relevance	0
Google Scholar	Effects of acidification on social behaviour in fish	32,800	Top 100 by relevance	0
Google Scholar	Effects of acidification on group cohesion in fish	22,300	Top 100 by relevance	0
Google Scholar	Effects of acidification on sociability in fish	1360	Top 100 by relevance	0

The effect size for each treatment level (Cohen's *d*) on each metric of cohesion or sociability was calculated according to the formula:

$$\mathrm{C}d=\frac{\overline{x}_1-\overline{x}_2}{\mathrm{PSD}} \qquad (1)$$

where C*d* is Cohen's *d*, $\overline{x}$ is the mean of each group, and PSD is the pooled standard deviation of both groups, calculated as:

$$\mathrm{PSD}=\sqrt{\frac{\left(N^1-1\right)\mathrm{SD}_1^2+\left(N^2-1\right)\mathrm{SD}_2^2}{N^1+N^2-2}} \qquad (2)$$

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where N is the number of replicates of each group, and SD is the standard deviation of each group. Cohen's d values were converted to Hedges' g values (sample-size-corrected effect size) using the formula:

$$\text{Hg} = \left(1 - \frac{3}{\left(4 \times \left(N^1 + N^2\right)\right) - 9}\right) \times \text{C}d \tag{3}$$

where Hg is Hedges' g. When standard error (SE) rather than SD was reported in a study, SD was calculated according to:

$$\sigma = \text{SE}\sqrt{n} \tag{4}$$

Where the SE of the difference between groups was given (but not the SE of both groups separately), pooled SE was converted to SD which was then used as pooled SD. Where confidence intervals were reported, SD was calculated according to:

$$\sigma = \frac{\sqrt{N} \times (\text{upper limit} - \text{lower limit})}{3.92} \tag{5}$$

Where median and quartile values were reported, these were used in place of mean and SD according to Greco *et al.* (2015). Effect size was calculated for each treatment level, for example where trials were carried out at three temperature treatments, the effect size for each of these treatments was calculated relative to the control. Where multiple measurements were carried out within each treatment level, for example across time, means at each sampling point were recorded and used to calculate the overall mean and SD for that treatment level. Raw data, where available, were used to calculate means and SDs if these were not reported in the study. For forest plot construction, mean and SE of effect size for each study was calculated from effect sizes calculated for all treatment levels.

(2) *Focal species used in each study*. Species names differed in some studies from the currently accepted scientific name; in these cases, the current accepted name was used according to the *World Register of Marine Species* database (WoRMS, 2023). Species habitat was also recorded as marine, freshwater, brackish, or any combination of these, based on the WoRMS database.

(3) *Treatment levels of variables of interest*. For variables with more than one treatment level (e.g. temperature tested at control, control +2 °C, control +4 °C), effect size was calculated for each treatment level relative to the control, or relative to the highest or lowest level (depending on the variable) for uncontrolled comparisons. For combined stressors, effect sizes for all treatments with non-control values of both or all stressors were calculated relative to treatments using control values for both or all stressors. Where treatments were introduced partway through a behavioural assay, or where treatments were compared to different control treatments within a study, changes were compared by subtracting Hedges' g values for control before *versus* after from treatment before *versus* after (Morris, 2008). Where this was not possible due to data presentation, values derived after treatment introduction were compared to the control values. Actual (not nominal) treatment levels were recorded where these were given. For fluctuating treatments (two studies: Davis *et al.*, 2019; Kwan, Hamilton & Tresguerres, 2017), the effect size was calculated between the control and the maximum treatment level. Here, only maximum treatment level was used (rather than maximum and minimum levels) as in both studies of fluctuating treatments minimum treatment level was close to control level and calculating an average treatment level accurately was not possible without precise time data, which were not available.

(4) *Group sizes used in trials*. A trial refers to a single behavioural assay of a group or individual under a given set of conditions. Where group size varied, the minimum number of fish per group in a given treatment was used. Minimum group size was used as it was not always possible to produce average values due to the way group size was reported in some papers (e.g. Domenici *et al.*, 2002).

(5) *Number of replicates* (n). Number of replicates was recorded as number of groups per treatment. Where the number of replicates per treatment varied, for example between control and treatment groups, the replicates value for treatment groups was recorded (or the average value if this was reported). If trials were repeated on the same groups, n was recorded as the number of groups. In effect size calculations, number of groups was also used, unless only one replicate was present in which case number of fish in the group was used as the calculations do not allow for a sample size of 1.

(6) *Sex of fish(es) used in each study*. If sex was not specified this was recorded as "unsexed".

(7) *Period over which fishes were exposed to each treatment*. Exposure time was recorded in days, with appropriate fractions for hours and minutes (e.g. 1 h = 1/24 = 0.0417 days). Where a range of exposure times was reported (e.g. 3–4 days), the minimum exposure period was recorded. Exposure times include acclimation/gradual reduction or increase times. Where individuals were raised under treatment conditions, age at assessment of social behaviour was used. Recovery period (if applicable) following exposure but prior to assessment of social behaviour was also recorded. Exposure period was then designated as "acute" (<7 days), "acclimated" (≥7 days) (Islam, Kunzmann & Slater, 2022), "developmental" (fish exposed during larval or egg development but not during adulthood), or "uncontrolled" (including fish observed in the wild, or farmed fish observed under natural conditions where exposure period was not controlled and/or reported).

(8) *Metrics used to assess cohesion or sociability*. In the majority of studies, individual sociability (defined as the tendency of individual fish to move towards or associate with conspecifics) was quantified using some variant of the three-chamber test (Xia, Niu & Pei, 2010) or shoal preference test (Salahinejad *et al.*, 2022), while group cohesion (defined as the degree of coordination in movement and activity within groups of fish)

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was quantified in group shoaling trials (Lanzarin *et al.*, 2020; Santos *et al.*, 2021). Cohesion within groups of fish was commonly measured as inter-individual distance (IID), nearest-neighbour distance (NND), shoal polarity, or mean distance from the centre of the shoal (MDCS; Table 2). Individual sociability was often measured as the frequency of approach to a conspecific shoal (ACS), time spent near a conspecific shoal (TCS), latency to approach a conspecific shoal (LCS), or distance to a conspecific shoal (DCS) (Table 2). Other studies measured sociability as time spent away from the conspecific shoal, or sociability score, a function of time and distance from a conspecific shoal (Table 2). Various studies used time spent in different tank "zones" to measure social behaviour in shoal choice tests, however exact study designs varied slightly. Therefore, "time away from social zone" was used to refer to trials in which tanks were divided into only two zones. "Time in far zone" was used in studies with three or more zones, and refers to furthest zone from shoal. Far-zone variables were only recorded where more than two zones were present, or where these were the only variables reported. Where zone times were statistically compared, for example near *versus* far zone, but time in each zone was not compared between treatments, results were recorded as statistically significant if a difference in the relationship between treatments was found, for example if fish spent more time near the shoal in the control treatment, but had no preference in other treatments.

(9) *Reported statistical significance (or lack thereof) of the effect of each treatment.* Statistical significance as reported in each study was recorded as $p < 0.05$. Where only the overall relationship between a continuous stressor and cohesion or sociability was tested, individual treatment levels were marked as significant (or not) according to the result of the overall relationship.

(10) *Location (country) where each study was carried out.*

(3) Statistical analysis

A meta-analysis was then carried out in R using the *MCMCglmm* package (Hadfield, 2010) to run phylogeny-adjusted linear models for each climate-related stressor. *MCMCglmm* was used in place of a phylogenetic least-squares regression (PGLS) model as multiple data points (representing multiple treatments and/or studies) were present for many of the species, and this data format is not supported by PGLS modelling. To account for phylogenetic relatedness among fish species, a phylogenetic tree was constructed including all species, using the R packages *phytools* (Revell, 2012) and *phylobase* (Hackathon *et al.*, 2020) which allow trees to be constructed from the *Tree of Life* database (Tree of Life Web Project, 2023). This tree was then incorporated into a data set with effect size and variable data using *mulTree* package (Guillerme & Healy, 2020), which combines a data table with a phylogenetic tree object to form a data list. This data list was then used to run a phylogeny-adjusted model. Significance level for explanatory variables was set at $p < 0.05$. The response variable in these models was effect size, while the explanatory variables were level of the relevant stressor (percentage oxygen for each treatment in the case of hypoxia, and difference from control in °C and pH respectively for temperature and acidification), exposure period, number of replicates, group size, exposure type (acute, acclimated, developmental, or uncontrolled), and metric (group cohesion or sociability). For studies of uncontrolled populations, that is where exposure period and group size were not known, 100 days and a group size of 10 individuals respectively were used in order to allow inclusion of uncontrolled studies in models. Sex of fish(es) used in each trial was included as a random effect variable. Specimen, referring to different treatments utilising the same species, was also included as a random effect variable to account for the effects of different trials using the same species. Species was also included as a random effect variable, as required to include phylogeny effects in *MCMCglmm* models. Stressors were modelled separately due to the difficulty associated with standardising treatment levels for stressors measured in different units. Multi-stressor interactions were not modelled due to the small number of studies that investigated stressor combinations. Lambda (λ) value for phylogenetic signal was calculated using the *phytools* package. Graphs and figures were plotted using the *ggplot* (Wickham, 2016), *ggraph* (Pedersen, 2022), and *ggtree* (Yu *et al.*, 2017) packages in R.

III. RESULTS

(1) Overview of the literature

In total, we identified 45 studies encompassing 391 data points (observations) that investigated the effects of climate-related stressors on sociability or group cohesion in shoaling or schooling fishes (Table 3), of which 347 data points from 36 studies were included in the meta-analysis (Fig. 2A). For the remainder, some or all data required for inclusion in our meta-analysis were missing. The majority of studies took place in Europe (20) and North America (15), with four studies from Asia, two from the Caribbean, two in Oceania, and two in South America (Fig. 3). No studies were carried out in Africa. A total of 43 species were utilised in studies (Fig. 4), with no particular bias towards any species or group, although marine species were more commonly used than freshwater or estuarine/anadromous species (Fig. 5A). The most popular species was the three-spined stickleback *Gasterosteus aculeatus* L. 1758, which was used in four studies (Fig. 4). Exposure period to stressors ranged from <10 min to 300 days (Fig. 5B).

A funnel plot indicated that publication bias may be present, with fewer studies with a low number of replicates than would be expected showing near-zero or positive effect sizes, that is a bias in favour of studies finding negative effect sizes (Fig. 2B). This may be due to a publication bias against

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Table 2. Metrics used in studies included in this review to measure group cohesion or sociability.

Term	Definition	Associated metrics
Group cohesion		
Inter-individual distance (IID)	Mean distance between each individual and all other individuals in a shoal	Variance in IID, oscillation frequency (time between peaks in IID), amplitude variability (mean standard deviation of measured IID), maximum IID
Nearest neighbour distance (NND)	Distance between the focal fish and the nearest neighbouring fish	1st, 2nd, 3rd NND, Clark-Evans Index (CEI) (calculated by comparing theoretical with observed NND to find a measure of school distribution)
Polarity	The extent to which fish face in the same direction, indicating coordinated movement. Sometimes measured as the difference in orientation angle between neighbouring fish (inverse polarity)	Orientation (yaw/pitch)
Mean distance from the centre of the shoal (MCDS)	The mean distance of each fish from the central point of the shoal i.e. the point at which the distance to each fish is as low as possible without increasing the distance to other shoal members	
Shoal density	Area or volume of shoal	Aggregation, school length, school width, school depth, school area, school volume, total school volume, number of near neighbours, density (fish per unit area), convex hull area, number of fish with NND <1 body length
Cohesion score	Score calculated as the product of distance between individuals and number of interactions	Cohesion score
Willingness to shoal	Extent to which fish show shoaling behaviour	Latency to school, duration of schooling, shoaling/schooling behaviour (number of individuals displaying shoaling/schooling behaviour), elective group size, sociability index (% occurrence of different group sizes)
Interaction	Degree of interaction among individuals within a shoal or school	Number of physical contacts, frequency of approach–withdrawal behaviour, time spent associating
Sociability		
Time near conspecific shoal (TCS)	Time a fish spends near a shoal of conspecifics during a shoal choice test	Time interacting with conspecifics, time away from conspecific shoal (inverse TCS), time in far zone (inverse TCS, used where near, middle, and far zones were present in choice chamber), time interacting with a conspecific (where a stimulus individual was used rather than a shoal), time near a conspecific
Latency to approach conspecific shoal (LCS)	Time a fish takes to approach a conspecific shoal during a shoal choice test	
Number of approaches to a conspecific shoal (ACS)	Number of times a fish approached a conspecific shoal or entered the nearest zone to the conspecific shoal during a shoal choice test	Number of times moving away from a shoal (inverse ACS)
Distance to a conspecific shoal (DCS)	Distance of a focal fish from a conspecific shoal during a shoal choice test	
Distance travelled near a conspecific shoal (DtCS)	Distance swum by a fish when near a conspecific shoal during a shoal choice test	
Shoal size choice	Tendency to choose a larger conspecific shoal during a shoal choice test	
Sociability score	Measure of sociability calculated based on the product of distance to the shoal and time spent at a certain distance from the shoal	

Group cohesion is defined as the degree of coordination of movement and activity within groups of fish, and is often measured as distance or polarity between groupmates. Sociability is defined as the tendency of individual fish to move towards or associate with conspecifics.

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Table 3. Summary of all studies included in this review.

Climate variable	Metric	Reference	Species	Treatments	Exposure period	Reported results	Results summary (mean effect size)
Temperature	Sociability	Angiulli *et al.* (2020)	*Danio rerio*	26, 24 °C	21 days; acclimated	Reduced time near and distance travelled near conspecifics; no effect on latency to approach or number of approaches to conspecifics	–
		Cooper *et al.* (2018)	*Gasterosteus aculeatus*	Increasing or decreasing temperature	30 min; acute	Stronger association with shoal when shoal was located in a cool environment	+
		Maulvault *et al.* (2018)	*Argyrosomus regius*	19, 24 °C	28 days; acclimated	Increased time near conspecifics. No effect on latency of approach or number of approaches.	+
		Mehdi *et al.* (2022)	*Pimephales promelas*	4, 20 °C	21 days; acclimated	No effect on time near or time spent interacting with a conspecific	–
		Monnet *et al.* (2023)	*Salmo trutta*	12.41, 12.72, 15.02 °C	100 days; uncontrolled	No effect on sociability score	–
		Pilakouta *et al.* (2022)	*Gasterosteus aculeatus*	10, 12, 18 °C	30 days; acclimated	No effect on distance to conspecific shoal in parental generation, increased distance in F2	0
		Tang & Fu (2021)	*Zacco platypus*	21.7, 25.6, 26.23, 27.3, 28.73, 29.07 °C	100 days; uncontrolled	No effect of temperature on sociability score	–
		Weetman *et al.* (1999)	*Poecilia reticulata*	22, 26 °C	28 days; acclimated	No effect on shoal size choice	–
	Group cohesion	Bartolini *et al.* (2015)	*Devario aequipinnatus*	22, 25, 28 °C	15 days; acclimated	Increased polarity at 25 °C, no effect on NND	0
		Clark (2022) (thesis)	*Gasterosteus aculeatus*	13.4, 14.7, 16.3, 16.5 °C	100 days; uncontrolled	Reduced aggregation (used as a proxy for shoaling)	–
		Colchen *et al.* (2017)	*Salmo trutta*	4, 6, 8, 10, 12 °C	9 days; acclimated	Increased NND at 8 and 10 °C, increased IID at 10 *versus* 6 °C, reduced physical contacts and variance in IID at 6 and 8 °C, increased approach-withdrawal frequency at 12 °C	0
		Davis *et al.* (2019)	*Hypomesus transpacificus*	17.1, 21 °C Increasing or fluctuating	7 days; acclimated	Increased IID and increased variance in IID under increasing temperature. No effect on NND. No effect of fluctuating temperature	–
		Elkins & Grossman (2014)	*Luxilus coccogenis*	12, 17 °C	2 days; acute	Reduced group cohesion	–

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Table 3. *(Cont.)*

Climate variable	Metric	Reference	Species	Treatments	Exposure period	Reported results	Results summary (mean effect size)
		Fahlman *et al.* (2021)	*Perca fluviatilis*	Natural temperature fluctuations	14 days; uncontrolled	Reduced NND with increasing temperature	+ reported
		Holubova *et al.* (2021)	*Abramis brama* *Alburnus alburnus* *Cyprinus carpio* *Aspius aspius* *Perca fluviatilis* *Rutilus rutilus*	12, 13, 17, 18, 19, 21, 21.5, 23 °C	100 days; uncontrolled	Increased group cohesion at higher temperatures	+
		Hurst (2007)	*Gadus chalcogramma* (*Theragra chalcogramma*)	2, 5, 9 °C	60 days; acclimated	Increased NND	−
		Kuruvilla *et al.* (2023)	*Notemigonus crysoleucas*	9, 13, 17, 21, 25, 29 °C	7 days; acclimated	No effect on NND or convex hull area	0
		Mameri *et al.* (2020)	*Luciobarbus bocagei*	24.5, 29.7 °C	9 h, repeated six times; acute	No effect on number of fish within 1 body length	No effect reported
		Mitchell *et al.* (2022)	*Abudefduf vaigiensis* *Atypichthys strigatus*	20, 23, 26 °C	6 days; acute	No effect on group cohesion	−
		O'Driscoll & McClatchie (1998)	*Allothunnus fallai* *Thyrsites atun* *Trachurus murphyi*	Natural temperature fluctuations	100 days; uncontrolled	No effect on horizontal school area	No effect reported
		Olla & Studholm (1971)	*Pomatomus saltatrix*	Increasing temperature (20–29 °C)	29–32 days; acclimated	Increased sociability index as temperature increases	+
		Olla *et al.* (1985)	*Pomatomus saltatrix*	1, 14.8, 19.1 °C	11 days (14.8 °C), 23 days (19.1 °C); acclimated	Reduced group cohesion	– reported
		Palacios-Fuentes *et al.* (2020)	*Helcogrammoides chilensis*	Natural temperature fluctuations	100 days; uncontrolled	More shoaling behaviour and fewer solitary individuals at higher temperatures. No effect on schooling behaviour.	+ reported
		Petitjean *et al.* (2020)	*Gobio occitaniae*	17, 24 °C	30 days; acclimated	No effect on group cohesion score	+
		Pineda *et al.* (2020)	*Corydoras aeneus*	25, 30 °C	14 days; acclimated	No effect on IID	−
		Steinessen (2015)	*Gadus chalcogramma* (*Theragra chalcogramma*)	Natural temperature fluctuations	100 days; uncontrolled	Reduced school density	– reported
		Swartzman (1997)	*Merluccius productus*	Natural temperature fluctuations	100 days; uncontrolled	Reduced group cohesion	– reported
		Theodorou *et al.* (2012)	*Gadus morhua*	3, 13 °C	13 days; acclimated	No effect on IID	−
		Weetman *et al.* (1998)	*Poecilia reticulata*	22, 26 °C	14 days; acclimated	Reduced NND and increased elective group size. No effect on polarity	0
				20, 28.5 °C			0

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Table 3. *(Cont.)*

Climate variable	Metric	Reference	Species	Treatments	Exposure period	Reported results	Results summary (mean effect size)
		Williams & Coutant (2003)	*Atherina boyeri* (*Atherina mochon*)		80 min during larval and/or egg stage; developmental	Increased approach-withdrawal frequency and latency to school formation. Reduced polarity and school duration	
Hypoxia	Sociability	Sommer-Trembo *et al.* (2017)	*Poecilia vivipara*	Wild-caught fish from populations at 100%, ~88%, ~87%, ~71%, and ~47% O_2	100 days; uncontrolled	No effect on time near conspecifics	0
	Group cohesion	Alfonso *et al.* (2020)	*Dicentrarchus labrax*	100%, 95%, 50%, 21% O_2	90 min; acute	Increased IID at 21% SO_2	–
		Anders *et al.* (2019)	*Scomber scombrus*	100%, 70%, 50%, 40% O_2	10 min; acute	No effect on NND or orientation	–
		Cook *et al.* (2014)	*Embiotoca lateralis*	100%, 15–75% measured at 5% intervals	5 h; acute	No effect on NND or polarity	–
		Domenici *et al.* (2002)	*Clupea harengus*	15–95% O_2, measured at 5% intervals	4 h; acute	Increased school length, width, and depth at 20–25% O_2	–
		Hayes *et al.* (2019)	*Luciobarbus bocagei*	100%, 48.4%, 16.5% O_2	8 min, acute	Increased maximum IID at 16.5% O_2. No effect on mean IID or NND	0
		Israeli & Kimmel (1996)	*Carassius auratus*	~88%, 11% O_2	5.5 h; acute	Increased school depth, no effect on school width or length	– reported
		Moss & Mcfarland (1970)	*Engraulis mordax*	89%, 7.6%, 6.9% O_2	2 h; acute	Increased MDCS and reduced polarity at low O_2	–
		Pineda *et al.* (2020)	*Corydoras aeneus*	100%, 60%, 30% O_2	4 h; acute	No effect on IID	0
Acidification	Sociability	Kleinhappel *et al.* (2019)	*Gasterosteus aculeatus*	pH 6.25, 6.3, 8.4	2 days; acute	No effect on time spent associating with a conspecific	+
		Maulvault *et al.* (2018)	*Argyrosomus regius*	pH 7.6, 8	28 days; acclimated	Reduced time near conspecific shoal. No effect on latency of approach or number of approaches to a conspecific shoal	–
		Regan *et al.* (2016)	*Pangasianodon hypophthalmus*	pH 7.2, 5.8	7 days; acclimated	No effect on time near conspecifics	–
	Group cohesion	Cattano *et al.* (2019)	*Chromis viridis*	pH 7.9, 8.1	5 days; acute	No effect on IID	–
		Duteil *et al.* (2016)	*Dicentrarchus labrax*	pH 7.82, 8.03	59 days; acclimated	No effect on number of nearest neighbours or IID	No effect reported
		Kwan *et al.* (2017)	*Chromis punctipinnis*	pH 7.7, 7.9, increasing and fluctuating pH	11 days; acclimated	No effect on IID	+

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Table 3. *(Cont.)*

Climate variable	Metric	Reference	Species	Treatments	Exposure period	Reported results	Results summary (mean effect size)
		Lopes *et al.* (2016)	*Atherina presbyter*	pH 7.6, 8.1	7, 21 days; developmental	Increased NND and CEI following 7 days exposure; reduced NND following 21 days exposure	−
		Mitchell *et al.* (2022)	*Abudefduf vaigiensis*, *Atypichthys strigatus*	pH 7, 8.1	6 days; acute	Increased IID in mixed-species pairs. No effect on amplitude variability or oscillation frequency	–
		Moss & Mcfarland (1970)	*Engraulis mordax*	pH 6, 6.1, 7.75	90 min; acute	Increased MDCS and reduced polarity at low pH	–
		Ross *et al.* (2001)	*Rhinichthys atratulus*	pH 6.6, 6.8	1 day; acute	No effect on number of contacts between conspecifics	0
Combined stressors	Sociability	Maulvault *et al.* (2018)	*Argyrosomus regius*	19 °C + pH 7.6, 24 °C + pH 8	28 days; acclimated	Reduced time near conspecifics, increased latency of approach No effect on number of approaches.	–
	Group cohesion	Mitchell *et al.* (2022)	*Abudefduf vaigiensis*, *Atypichthys strigatus*	23 °C + pH 8.1, 26 °C + pH 8.1 pH 7, 8.1, combinations	6 days; acute	No effect on group cohesion	−
		Pineda *et al.* (2020)	*Corydoras aeneus*	30 °C + 60%, 30 °C + 30% O_2	Temperature 14 days; acclimated + hypoxia 4 h; acute	No effect on IID	0

"Results summary (mean effect size)" indicates the overall results found by the present study based on mean effect size for each stressor (across treatments if applicable), as shown in Fig. 2A. + indicates a positive effect on sociability or cohesion, − indicates a negative effect on sociability or cohesion, and 0 indicates no effect. "reported" indicates that effect size could not be calculated, and therefore the results summary reflects the result reported by the study itself.
CEI, Clark-Evans Index; IID, inter-individual distance; MDCS, mean distance from centre of shoal; NND, nearest-neighbour distance.

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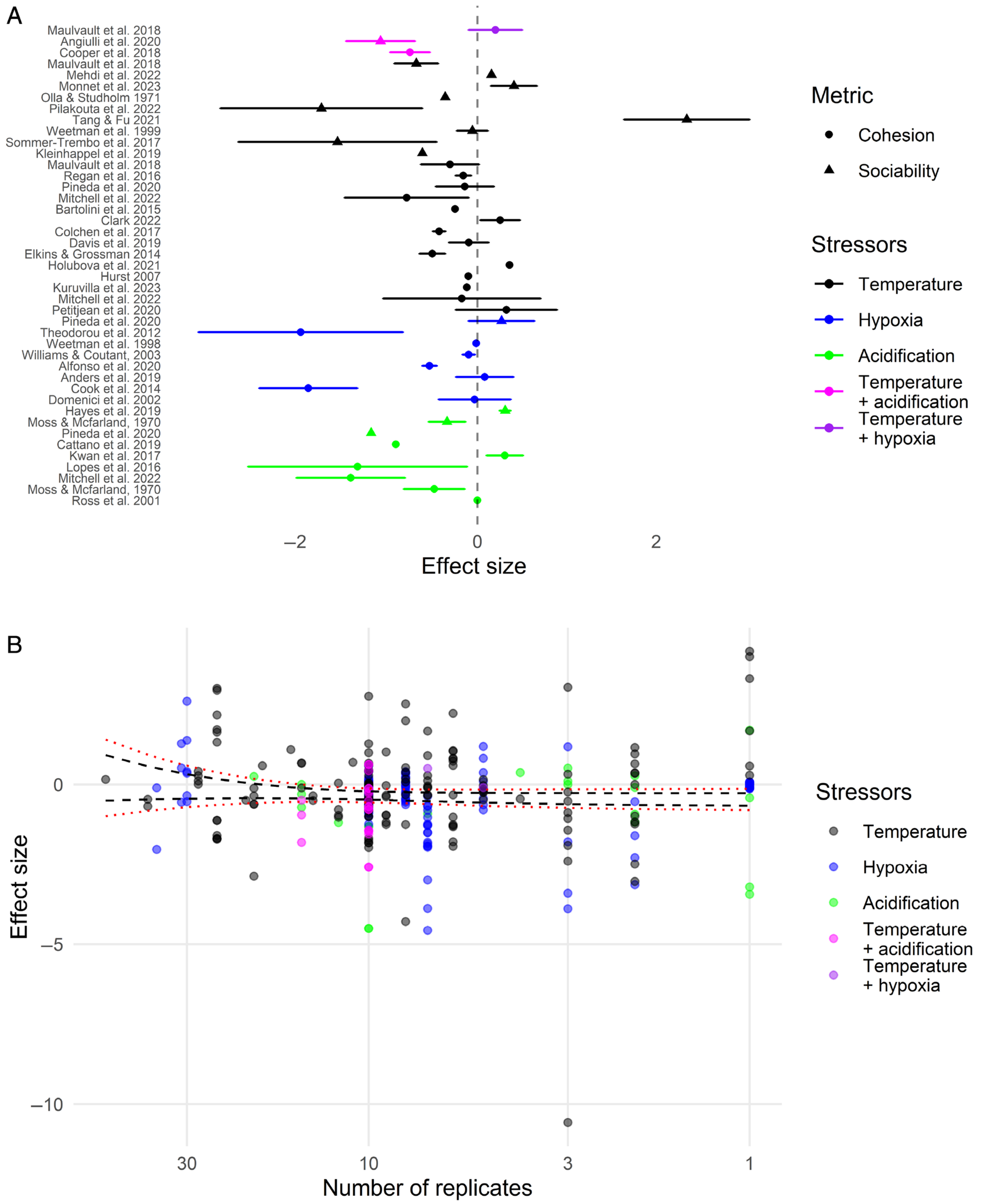

Fig. 2. (A) Forest plot showing mean effect sizes (Hedges' *g*) of climate stressors on group cohesion and sociability in fishes. Mean and standard error of effect size for each study was calculated from effect sizes calculated for all treatment levels. (B) Funnel plot showing effect size plotted against number of replicates per treatment utilised in each study. Red dashed lines show upper and lower 99% confidence interval; black dashed lines show upper and lower 95% confidence interval.

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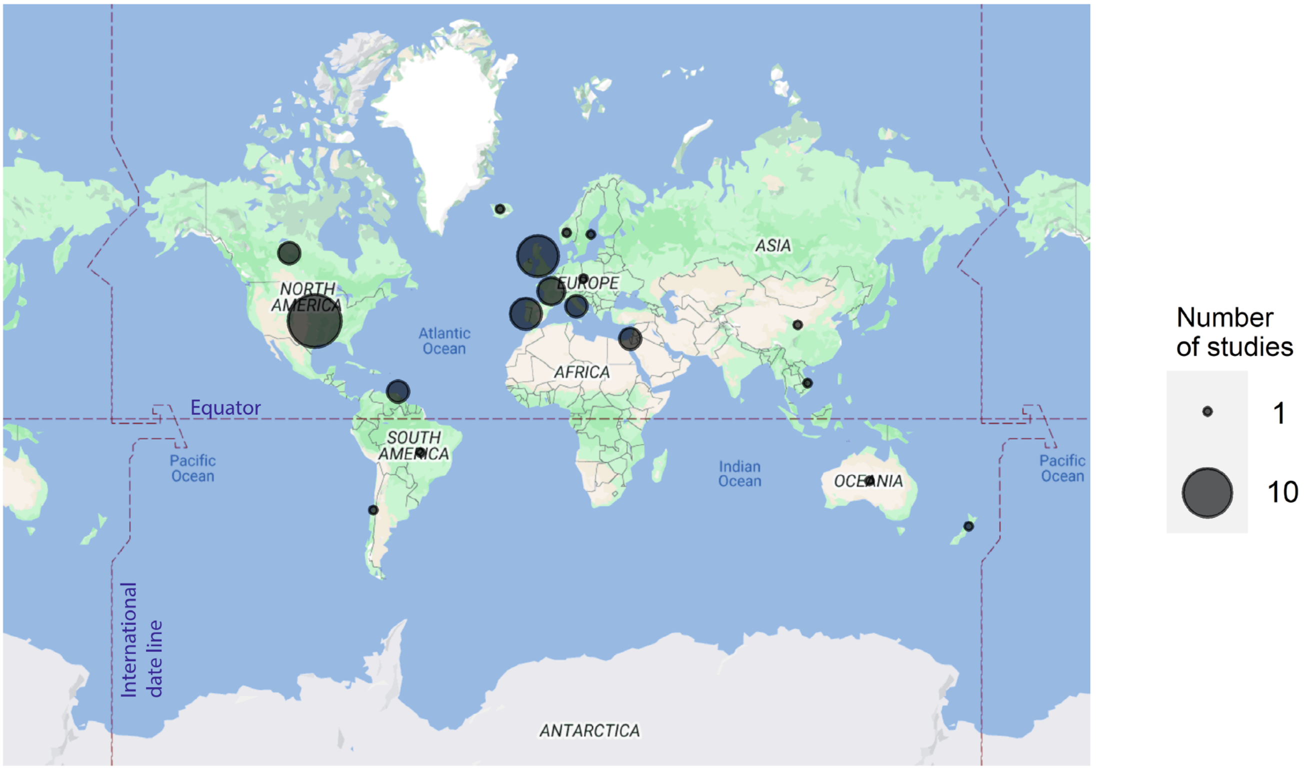

Fig. 3. Geographical distribution of studies of the effect of climate-related variables on sociability and group cohesion in fishes. In cases where the location of the research institute differed from the location of the study, the location is recorded as the location where the study was carried out. Larger circles indicate more studies.

studies with small sample sizes that reported either null results or positive results. There was a minimal phylogenetic signal across studies ($\lambda = 0.101$; $p = 0.241$).

(2) Temperature change

In total, 30 studies (representing 32 species) investigated the effects of temperature, with 22 studies quantifying group cohesion and eight studies quantifying individual sociability (Table 3). Temperature change from control levels ranged from <+1 to +20 °C (Fig. 6A). For a total of 10 studies on group cohesion, including three uncontrolled studies, we found increased temperature to be associated with reduced cohesion. For five studies (three uncontrolled and two laboratory) we found increased temperature to be linked with increased cohesion, while for seven studies, including one uncontrolled study, we found no effect of temperature on cohesion (Table 3).

A similar pattern was found for individual sociability: for five studies, including two uncontrolled studies, we found that increased temperature was linked with decreased sociability, for two studies we found a positive association between temperature and sociability, and for one study we found no effect (Table 3). Our meta-analysis found no correlation of effect size for sociability or cohesion with any explanatory variables tested, including degree of temperature change and exposure period (Table 4).

(3) Oxygen availability

The effect of hypoxia on group cohesion was examined in eight studies (representing eight species), for six of which we found reduced cohesion at lower oxygen levels, and for two we found no effect (Table 3). One additional study investigated effects on individual sociability, for which we found no significant effect (Table 3). Reduction in oxygen level for hypoxia treatments ranged from <1% to >95% (Fig. 6B). Meta-analysis revealed no consistent effect of hypoxia exposure, but there was a significant positive correlation between magnitude of change in oxygen availability and the effect on group cohesion, that is at greater levels of hypoxia there was a greater reduction in cohesion (Fig. 7A). The correlation between oxygen availability and effect on sociability was non-significant (Table 5). Group size was also positively correlated with the effects of hypoxia on cohesion, indicating that fish tested in larger groups were more cohesive under hypoxic conditions. This relationship was not entirely linear, however, with the positive correlation only being apparent in groups containing 7–19 individuals (Fig. 7B), while small groups (≤7 individuals) had similar cohesion to large groups (≥19 individuals) following exposure to hypoxia. No other variables were found to be significantly correlated with effect size.

(4) Acidification

Seven studies investigated the effects of acidification on group cohesion, for four of which we found negative effects

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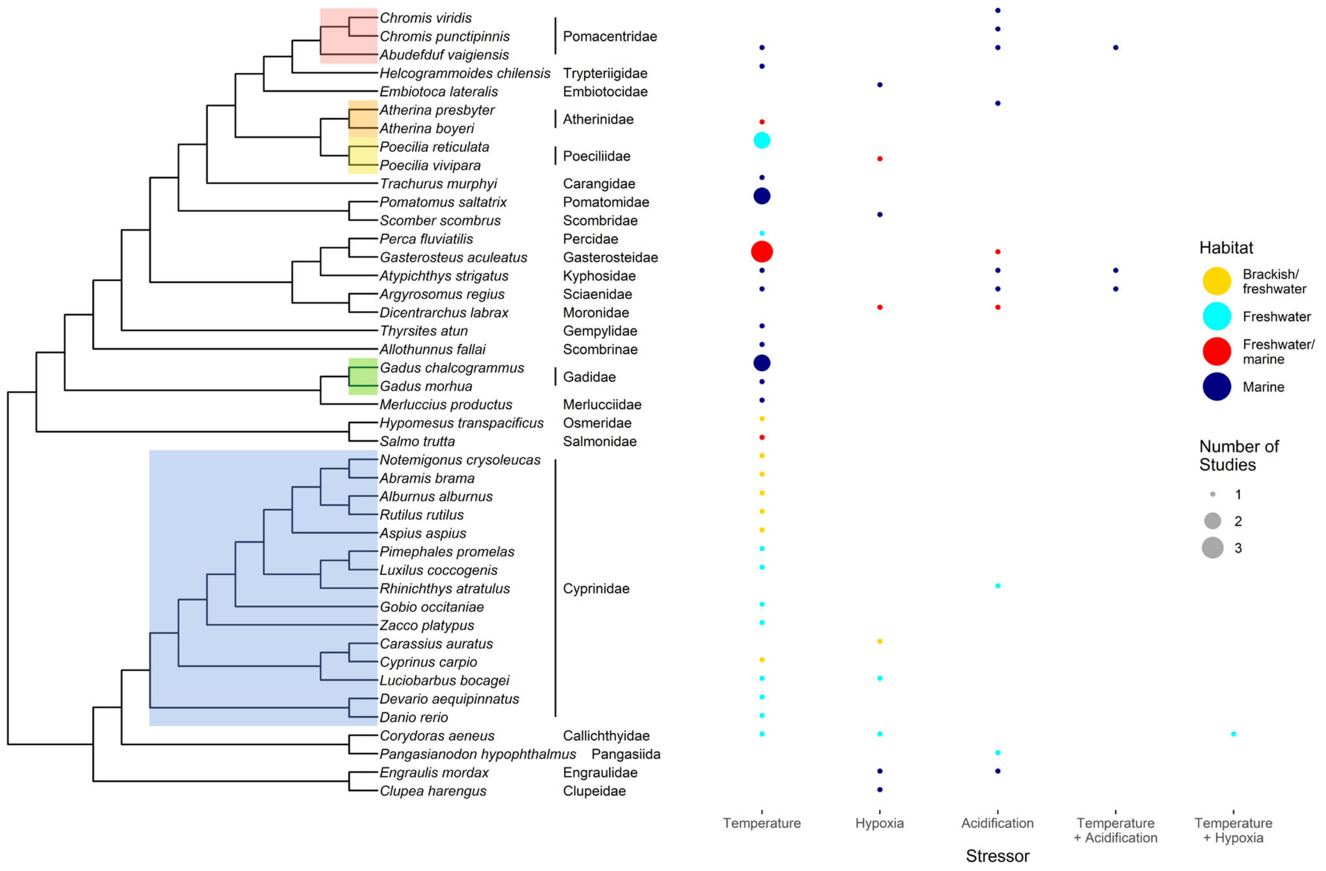

Fig. 4. Dendrogram showing species and families (coloured where multiple species are present in a family) included in the meta-analysis, with dot plot showing stressors studied for each species and the number of studies carried out on each species. Species habitat is indicated by dot colour.

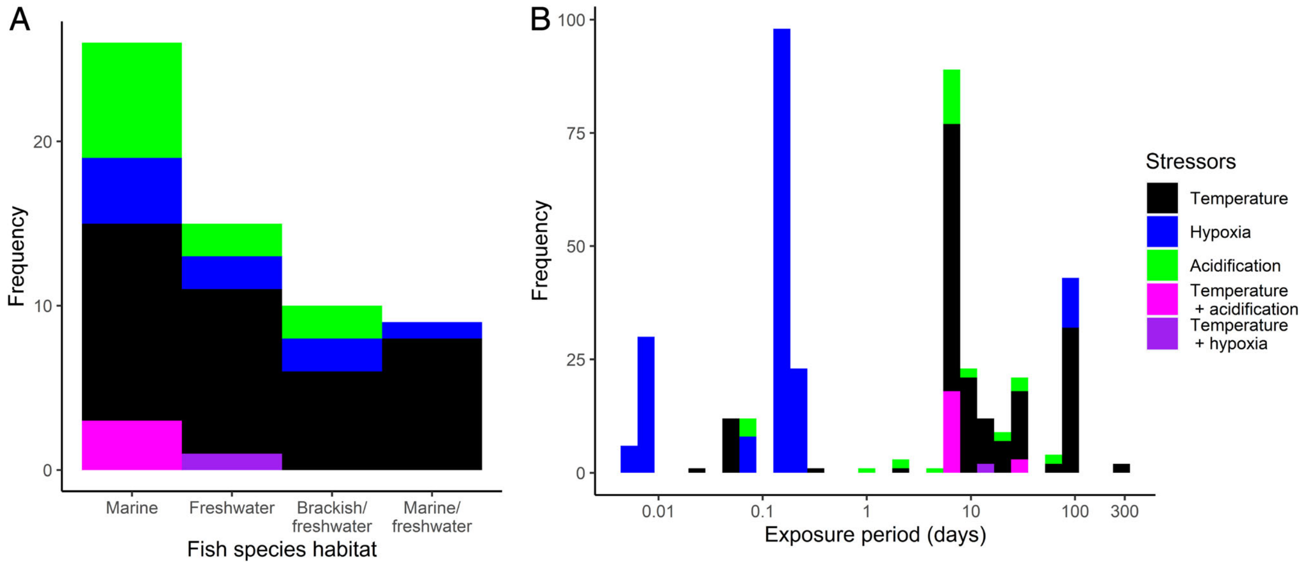

Fig. 5. Frequency histograms of (A) species included in all studies in our database according to their habitat, and (B) exposure periods and stressors used in all studies included in our database.

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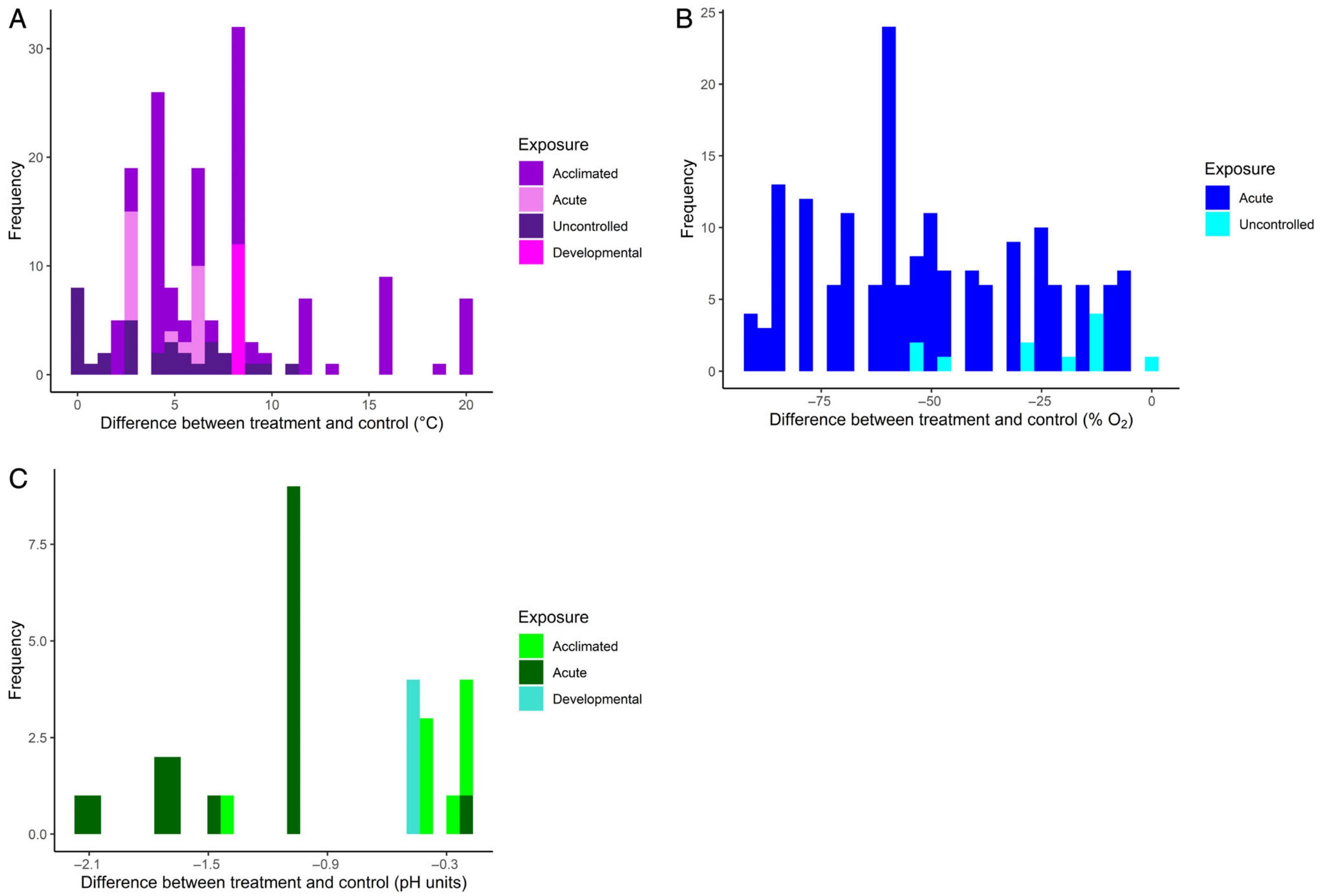

Fig. 6. Frequency histograms of trials of sociability or group cohesion according to degree of change in (A) temperature, (B) oxygen concentration and (C) pH (acidification).

Table 4. Results of phylogeny-adjusted *MCMCglmm* model investigating the effects of temperature on sociability and group cohesion.

	Posterior mean	Lower 95% CI	Upper 95% CI	Effective sample size	*p*MCMC
Intercept	0.494	−1.960	1.793	1655	0.995
Temperature change (*versus* control)	−0.001	−0.068	0.059	1800	0.960
Group size	0.001	−0.014	0.018	1800	0.866
Replicates	0.016	−0.036	0.062	1800	0.497
Exposure period (days)	−0.0003	−0.010	0.008	1386	0.971
Metric (sociability)	−1.155	−2.799	0.544	1800	0.194
Exposure type (Acute)	−0.584	−1.392	0.282	1444	0.178
Exposure type (Developmental)	−0.041	−1.273	1.280	1800	0.927
Exposure type (Uncontrolled)	−0.394	−1.502	0.648	1800	0.488
Temperature change × sociability	0.066	−0.169	0.276	1800	0.557

of acidification on group cohesion and for one a positive effect. For the remaining two studies, we found no effects of pH on cohesion (Table 3). An additional three studies investigated individual sociability, for which we found a negative effect for two studies and a positive effect of acidification for one study on sociability (Table 3). Changes in pH during treatments ranged from −0.21 to −2.15 pH units (Fig. 6C). Our meta-analysis revealed no consistent effect of acidification, or any other explanatory variable included in the model on group cohesion or sociability, although the relatively small number of studies (10 in total) and number of data points (29 treatments with sufficient data) investigating acidification limited the power of the analysis (Table 6). There is some evidence for greater effects on marine species compared with freshwater species, with no studies finding effects of acidification on freshwater species ($n = 2$ studies) while half of studies ($n = 4$) on marine species found significant effects (Lopes *et al*., 2016; Maulvault *et al*., 2018; Mitchell *et al*., 2022; Moss & McFarland, 1970).

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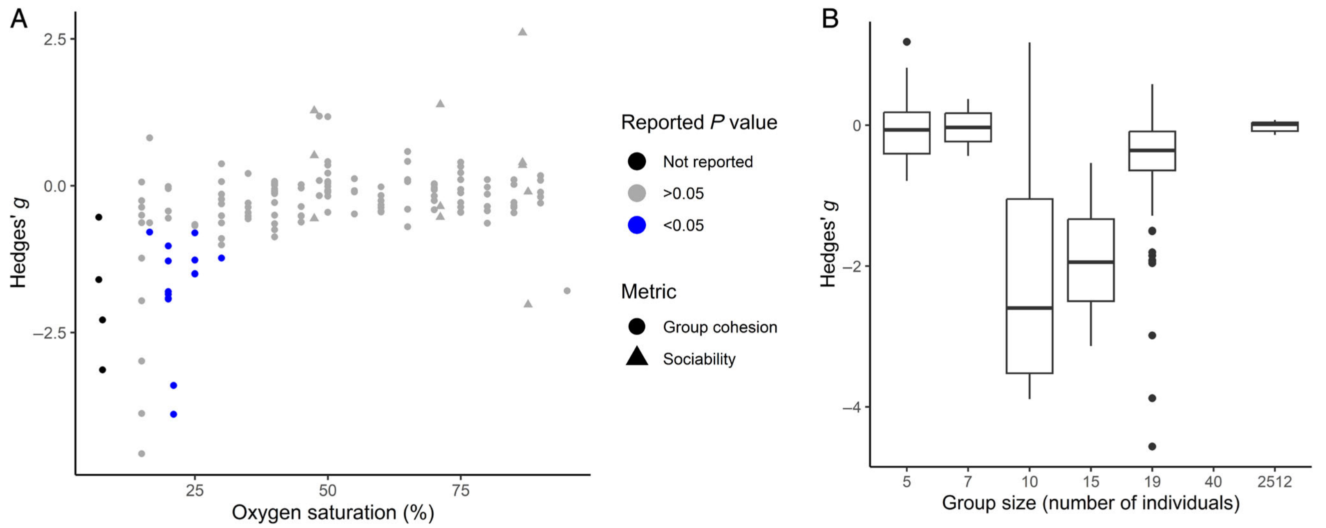

Fig. 7. (A) Effect size (Hedges' *g*) of hypoxia on group cohesion and sociability in fishes. Reported *p* values from the original studies are also indicated. (B) Effect of group size on mean effect sizes for changes in group cohesion in response to hypoxia in fishes. Black lines show the median, boxes show the interquartile range. Whiskers show values ≤1.5 times the interquartile range from the box. Outliers indicate values >1.5 times the interquartile range from the box.

Table 5. Results of phylogeny-adjusted *MCMCglmm* model investigating the effects of hypoxia on sociability and group cohesion.

	Posterior mean	Lower 95% CI	Upper 95% CI	Effective sample size	*p*MCMC
Intercept	560.5	−44854	57484	1800	0.846
Change in oxygen availability (*versus* control)	0.012	0.005	0.018	1313	<0.001***
Group size	0.0005	0.0002	0.001	1549	<0.001***
Replicates	0.080	−0.001	0.167	1800	0.070
Exposure period (days)	0.055	−4.005	3.480	1800	0.990
Metric (sociability)	−511.1	−139571	144089	1655	0.996
Exposure type (uncontrolled)	−28.28	−145527	140946	1800	0.998
Oxygen availability × sociability	−0.020	−0.046	0.009	1800	0.178

*** indicates significance at $p < 0.001$.

(5) Multi-stressor interactions

Only three studies investigated the effects of multiple stressors, specifically combinations of temperature with acidification and temperature with hypoxia. No effect was found of temperature with hypoxia, however for both studies of temperature with acidification we found a negative effect (Table 3), one on sociability (Maulvault *et al.*, 2018) and one on cohesion (Mitchell *et al.*, 2022).

IV. DISCUSSION

While climate-related stressors can affect various facets of fish behaviour (Domenici *et al.*, 2017; Killen *et al.*, 2013), the present meta-analysis reveals that the effects of temperature, hypoxia, and acidification on social behaviour are complex and in need of further study. Despite the known effects of climate-related stressors on fish metabolism (Pilakouta *et al.*, 2020; Nati *et al.*, 2018) and neural functioning (Heuer & Grosell, 2014; Jutfelt *et al.*, 2013), we found no strong evidence for consistent effects of temperature or acidification on group cohesion or individual sociability. While reduced cohesion under conditions of hypoxia was observed, the low number of studies and lack of standardised metrics limits the conclusions that can be drawn. Although our review highlights some statistical trends in the existing data, we emphasise that further study, including replication of existing studies, is needed to gain a more complete understanding of how climate-related stressors affect fish social behaviours. Likewise, while no consistent trends were found for temperature or acidification, this may also be a result of low sample size, a lack of standardisation of measurements, variability in responses among species, and variation in the magnitudes of the changes in temperature and pH examined and the durations of exposure. Nevertheless, we discuss potential mechanisms whereby trends across studies

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Table 6. Results of phylogeny-adjusted *MCMCglmm* model investigating the effects of acidification on sociability and group cohesion.

	Posterior mean	Lower 95% CI	Upper 95% CI	Effective sample size	*p*MCMC
Intercept	−2.220	−5.992	2.065	1800	0.284
pH change (*versus* control)	−0.693	−2.556	1.157	1793	0.469
Group size	0.095	−0.174	0.377	1698	0.464
Replicates	−0.038	−0.368	0.236	1640	0.787
Exposure period (days)	0.127	−0.054	0.296	1800	0.149
Metric (sociability)	−0.610	−5.095	3.630	1649	0.776
Exposure type (Acute)	−0.174	−3.616	3.119	1800	0.930
Exposure type (Developmental)	−2.076	−4.962	0.863	1653	0.144
pH change × sociability	0.391	−4.220	5.889	1653	0.897

observed in this review may be explained, and suggest directions in which much-needed further research may proceed.

(1) Temperature

As increasing temperature leads to an elevation in metabolic rate and spontaneous activity level in many fish species (Davis *et al.*, 2019; Colchen *et al.*, 2017), it has been hypothesised that warming may lead to reduced group cohesion and lower individual sociability due to an increase in risk-taking related to individual foraging motivation (Killen *et al.*, 2016; Conrad *et al.*, 2011). We found that the results to date do not indicate a consistent relationship between temperature and either group cohesion or individual sociability across studies. In some species where original studies reported no effect of temperature, such as the corydoras catfish *Corydoras aeneus* Gill 1858, behaviours such as air-breathing may allow fish to compensate in part for the increased metabolic costs and oxygen demands that accompany higher temperatures while remaining in groups (Pineda *et al.*, 2020). In addition, for some non-air-breathing species, including the Iberian barbel *Luciobarbus bocagei* Steindachner 1864, the Indo-Pacific sergeant *Abudefduf vaigiensis* Quoy and Gaimard 1825, and the Australian mado *Atypichthys strigatus* Günther 1860, studies reported no effect of temperature, indicating that some species may be robust to temperature changes in terms of effects on social behaviour without utilising air-breathing as a coping strategy (Mameri *et al.*, 2020; Mitchell *et al.*, 2022). Inter- and intra-specific comparisons are severely limited, however, by the low number of studies available, and by the lack of standardisation among studies.

The effects of temperature on sociability and cohesion were also not influenced by the duration of exposure to the treatment temperatures. However, as the majority of studies used only acclimated (≥7 days; $n = 16$) or uncontrolled exposure periods ($n = 9$), the effects of shorter-term exposure are underrepresented in our data set (Fig. 6A). Fish may be more likely to respond to acute thermal effects, showing exaggerated immediate changes in metabolism, aerobic scope and blood glucose levels (Johansén *et al.*, 2021). Studies of acute exposure are needed to identify how these changes may affect behaviour in the short term. Many of these physiological parameters return to baseline levels within days or weeks of acclimation (Johansén *et al.*, 2021). As metabolic factors have been found to affect social behaviour (Killen *et al.*, 2016), metabolic thermal compensation during acclimation may also reduce behavioural changes following acclimation to stressors.

Given the lack of consistent patterns in our results, this begs the question of how changes in sociability and cohesion in fish species are regulated, and to what extent behavioural plasticity or metabolic acclimation are responsible for a lack of response following long-term exposure to different temperatures. Although a relatively small number of studies have investigated modes of social behaviour change in response to temperature in fish species, evidence has been found for both plasticity and trans-generational adaptation. For example, Pilakouta *et al.* (2020) showed that allopatric populations of *G. aculeatus* from warm environments are less sociable than their colder-origin counterparts regardless of acclimation temperature, indicating genetic change in sociability with temperature, but these same populations showed minimal capacity for within-generational plasticity. However, the F2 generation of these fish showed changes in sociability according to rearing temperature. Specifically, warmer temperatures led to reduced sociability, indicating that developmental plasticity may play a role in shaping sociability in response to thermal variation. This indicates a degree of heritability in sociability, as well as potentially plastic effects of rearing temperature, although these may also be explained by parental or epigenetic effects (Pilakouta *et al.*, 2022). Developmental exposure to high temperatures also influenced group cohesion in *Atherina boyeri* Risso 1810, indicating plasticity (Williams & Coutant, 2003). Further studies of multi-generation or developmental effects of temperature on social behaviour would be beneficial, and would likely help to identify the role of plasticity and heritability in temperature tolerance in different species.

While the magnitude of temperature change did not influence cohesion or sociability, there may be complex interactions between the magnitude of a thermal shift and the duration of exposure that would require additional studies and a larger data set to interpret. While a greater temperature change may be expected to have a larger effect on measures of social behaviour, thermal acclimation can allow fish to adjust expression of various physiological traits to

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compensate for the change in temperature, at least partially. The effects of temperature on social behaviour may also be non-linear or vary depending on the temperature range of the exposure, and the thermal optimum of the species concerned. Small or moderate increases in temperature may increase metabolic costs and therefore increase boldness and reduce sociability (Angiulli *et al.*, 2020; Colchen *et al.*, 2017; Davis *et al.*, 2019). With temperatures above a species' optimum for aerobic scope or locomotor performance, however, fish may remain in cohesive groups due to a reduced capacity for activity and predator avoidance associated with a limited aerobic scope or altered neuromuscular functioning (Maulvault *et al.*, 2018; Weetman, Atkinson & Chubb, 1998). The effects of a given increase in temperature above the thermal optimum are also very likely to vary among species. At present, too few studies exist to allow comparison among species in terms of the effect of a given temperature increase above a species' thermal optimum, but future research could focus on examining how social behaviour changes in relation to thermal optima for physiological traits and behaviour at both the species and individual levels (Killen *et al.*, 2021).

Depending on their native habitat and migration patterns, different species experience different levels of spatial and temporal thermal variation under natural conditions. It may therefore be expected that the effects of temperature on social behaviour would vary among species due to evolutionary effects on thermal sensitivity or capacity for thermal acclimation. Interestingly, however, there was very little effect of phylogeny on our measures of social behaviour. Overall, the number of species that have been measured for thermal effects on social behaviour (or indeed the effects of any variable on social behaviour) relative to the extreme diversity across teleost fishes is very low, with little replication of studies across species. Low interspecific diversity within the data set also precludes a thorough understanding of how habitat characteristics and life histories may interact with evolutionary changes in social behaviour and sensitivity to environmental stressors. Intertidal species and some riverine fishes may experience rapid changes in conditions such as temperature and hypoxia, and are adapted to deal with these conditions (Bennett, 2010; Campos *et al.*, 2017). These species may therefore show reduced responses to temperature, but the effects of habitat on social behaviours have not been studied and so have not been included in our meta-analysis.

Shoal dynamics, meaning the organisation of individuals within a shoal, may also play a role in determining the behavioural responses of fish to changes in temperature and whether these changes can be detected. For example, while average IID was greater with increasing temperature in delta smelt, *Hypomesus transpacificus* McAllister 1963, NND did not change (Davis *et al.*, 2019). In this study, fish formed smaller clusters at higher temperatures, possibly due to increased swimming speed, which caused groups to fragment. Thus, while the overall group was more spread out, fish were still equally close to their nearest neighbours within the newly formed smaller groups (Davis *et al.*, 2019). If groups increase swimming speed due to a change in temperature, active or passive sorting may also cause individuals with similar maximum swimming speeds to group together, thus fragmenting large groups into smaller ones (Jolles *et al.*, 2017; Killen *et al.*, 2017). This demonstrates the importance of using multiple metrics to analyse group cohesion, as studies using only one metric may underestimate or overlook important effects on group organisation. Standardising methods and units when measuring group cohesion by different metrics is important, however, in allowing comparisons among species and laboratories. Factors such as intra-group familiarity may also contribute to shoal dynamics, and may be more important for coordinating group movement at temperature extremes when physiological responses are challenged (Weetman *et al.*, 1998). Whether fish tested in groups have previously been held together, as in most studies to date, may therefore influence propensity to shoal in response to varying conditions (Weetman *et al.*, 1998). Recognition of conspecifics may also itself be affected by temperature through metabolic changes, or changes in spontaneous activity, and thus alter responses to cues based on factors such as habitat and diet. In addition to shoaling dynamics, there is evidence that individual social preference and temperature preference may play a significant role in determining behavioural responses to temperature in individual sociability trials. Fish may be willing to compromise individual temperature preference to remain with a shoal, but this is likely to depend on the degree to which an individual prioritises group membership over occupying their own preferred thermal regime (Cooper *et al.*, 2018). In *G. aculeatus* given a temperature choice test, while fish changed space use in the presence of a shoal in order to spend time with conspecifics, fish with a warmer water preference consistently spent more time in a warm environment, even when the shoal was presented in a cool environment (Cooper *et al.*, 2018).

(2) Oxygen availability

As oxygen saturation decreases to hypoxic levels, fish in groups may move apart or become less coordinated and cohesive due to increases in activity level associated with individual attempts to escape areas of low oxygen (Lefrancois *et al.*, 2009; Domenici *et al.*, 2017). Neural processing may also play a role in any breakdown in cohesion at low environmental oxygen levels, as neuromuscular processes can become impaired or non-functional due to oxygen starvation (Nilsson *et al.*, 1993; Schellart & Wubbels, 1998; Domenici, Lefrancois & Shingles, 2007; Lucon-Xiccato *et al.*, 2014). While we found evidence of reduced group cohesion in response to hypoxia, this was based on relatively few studies, and appreciable changes in group cohesion were generally only observed at levels below 35% saturation (Fig. 7A). In air-breathing species such as *C. aeneus*, breathing air when aquatic dissolved oxygen is limited may allow group cohesion to persist, with the number of air breaths taken by fish at the group level increasing in this species at lower levels of dissolved oxygen (Pineda *et al.*, 2020). However, at least one non-air-breathing species, the striped surfperch *Embiotoca*

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lateralis Agassiz 1854, maintains shoal cohesion when exposed to hypoxic conditions as low as 15% saturation (Cook *et al*., 2014). This species reduced swim speeds and turning rates at low oxygen levels, which may allow them to reduce their oxygen demand while also maintaining group cohesion. Swimming speed of Atlantic herring *Clupea harengus* L. 1758 prior to hypoxia exposure was positively correlated with the oxygen concentration at which school disruption occurred (15–35% saturation), indicating that faster-swimming schools were less tolerant to hypoxia (Domenici *et al*., 2000). Having a low swimming speed may therefore be an effective coping strategy for hypoxia, potentially by reducing active metabolic needs and thus oxygen demand. However, if increasing activity is a mechanism to escape hypoxia, it is possible that having low swimming speed as a coping strategy would have costs in natural settings by hindering attempts to escape hypoxia. Both swim speed and polarity relate to group cohesion, as fish swimming at similar speeds and in similar directions can form more cohesive groups and *vice versa*. We found no studies of interindividual differences in routine swim speed within shoals, while studies of polarity are also relatively underrepresented. Studies of shoal dynamics in terms of differences or similarities in interindividual swim speed and directionality within a shoal may therefore help to resolve the factors that contribute to shoal disruption at very low oxygen levels, and the reasons why extreme levels of hypoxia may be required to disrupt group cohesion.

The effects of environmental stressors on cohesion may also be affected by group size. For example, we found that groups containing an intermediate number of individuals showed a greater reduction in cohesion when exposed to hypoxia as compared to groups with fewer individuals, possibly due to a greater increase in activity under hypoxic conditions (Fig. 7B). The presence of additional conspecifics when faced with a limitation to a resource such as oxygen may increase the urgency with which fish attempt to escape their situation, as limited oxygen will be consumed more quickly in the presence of more individuals. Any change in spontaneous activity among a subset of individuals may also be more likely to spread throughout larger groups. In addition, oxygen level at the centre or rear of larger shoals may be more limited as oxygen is consumed more rapidly within the shoal, leading to spreading out of individuals from the centre outward, an effect that may be magnified in larger groups with greater oxygen consumption (Moss & Mcfarland, 1970; Domenici *et al*., 2017). Cohesion appeared to be similar in small (≤7) and large (≥19) groups, possibly because fish in large social groups may experience a "calming effect" of social group membership, whereby individuals experience reduced stress and possibly a reduced routine metabolic rate and oxygen demand (Nadler *et al*., 2016), which would be predicted to increase resilience to hypoxia. In an experimental setting, increased density of individuals within behavioural arenas may also have effects that are separate from the effects of group size *per se*. When fish are contained within an enclosed experimental arena, the size of the shoal interacts with the size and/or shape of enclosures used for behavioural tests, although this was not included in our analysis. A review of the methodology used in behavioural trials with regard to space available would be useful in standardising methodology and making results more comparable and reproducible.

While degree of hypoxia and group size may have effects on group cohesion, no effect of exposure period on hypoxia was found. It should be noted, however, that exposure period varied little across studies with none examining the effects of hypoxia on sociability or cohesion after a period of acclimation. The longest laboratory-based hypoxia exposure was 5.5 h, and as the only uncontrolled study exposed fish to relatively high oxygen levels even in "hypoxic" conditions (minimum 47% air saturation) the long-term effects of more severe hypoxia (<35% air saturation) on social behaviour remain unstudied (Fig. 6B). The frequency, severity, and duration of hypoxic episodes in aquatic habitats are all increasing (Diaz & Breitburg, 2009). While longer exposures to hypoxia may result in some degree of acclimation, they may also lead to worsened neurosensory functioning, including that involved in lateral line sensing (Schellart & Wubbels, 1998), or other adverse effects of prolonged reductions in blood and tissue oxygen availability on physiological functions. Hypoxia has been found to impair ciliated inner ear cell function in bullfrogs *Rana catesbeiana* Shaw 1802 (Sitko & Honrubia, 1986), and while these cells have not been studied in fish in connection with hypoxia, similar structures are present in fish lateral lines (Domenici *et al*., 2007; Schellart & Wubbels, 1998). Lateral line stimulation appears to be involved in the coordination of fish schools, and especially in the maintenance of IIDs. Overall, more work is needed to understand the effects of hypoxia, including varying periods of hypoxia, on group cohesion or sociability. The impacts of developmental exposure to hypoxia are also relatively unknown, although one study found no effect of dissolved oxygen level on individual sociability in *Poecilia vivipara* Bloch and Schneider 1801 captured from environments varying in oxygen availability but tested under normoxia (Sommer-Trembo *et al*., 2017). As these fish had been exposed to differing oxygen levels during adulthood, however, it is unknown what effect exposure during only larval or egg phases would have.

(3) Acidification

Acidification may be expected to alter sociability and/or group cohesion in fishes due to changes to neuromuscular function, respiratory impairment, or compromised osmoregulation. Contrary to this prediction, and despite finding negative effect sizes for the majority of studies, our meta-analysis revealed no overall effect on group cohesion or individual sociability. The power of this analysis may have been limited as only 29 observations from 10 studies were available. In addition, some studies found different results for different metrics of cohesion or sociability or different treatment levels (e.g. Lopes *et al*., 2016; Maulvault *et al*., 2018), which may not be reflected in the mean effect sizes. All studies that found an effect investigated marine species, consistent with the greater sensitivity of marine fishes to acidification relative to freshwater fishes (Kwong, Kumai & Perry, 2014; Ishimatsu

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et al., 2004). However, the literature was also strongly biased in favour of studies on marine species. Therefore, to determine whether freshwater species are indeed more resilient to acidification, further studies on these species are needed. The literature is also sparse regarding the effects of acidification on individual sociability, an area that would benefit from further research to understand better interindividual and interspecific variation in tolerance to acidification.

As for temperature and hypoxia, the period over which fish were exposed to acidification was not related to the magnitude of effect on shoaling or social behaviour. Similarly to temperature, the majority of studies used longer exposure periods, which may allow fish time to acclimate (Table 3). The only study of acidity using an exposure lasting <1 day found a significant reduction in cohesion (Moss & Mcfarland, 1970), although more research is needed to understand fully the effects of acute acidification on fish social behaviour. While understanding of long-term effects of acidification is vital in a changing climate, events such as coastal upwellings can lead to acute exposure to acidification in the wild, and so studies focused on acute effects are also important (Lopes *et al.*, 2016). Another understudied area is the effects of developmental exposure to acidity on social behaviour, especially considering the increasing evidence for the role of developmental plasticity in adapting to stressors (Schunter *et al.*, 2018). One study indicated a delay in the development of shoaling behaviour following larval exposure to acidification (Lopes *et al.*, 2016), potentially leaving juvenile fishes vulnerable to predation. Evidence of effects of parental exposure to acidification on offspring physiology have also been found, although this is yet to be investigated with regards to social behaviour (Schunter *et al.*, 2018).

(4) Multi-stressor interactions

While individual stressors may significantly impact group behaviour and sociability in fish species, fish in the wild are likely to experience multiple stressors, either concurrently or in rapid succession (Doney, 2010; Nagelkerken & Connell, 2015). The majority of studies to date, however, have examined the effects of single stressors on sociability and group cohesion, and those that exist have shown mixed results. The combination of hypoxia with high temperatures is becoming increasingly common in ecosystems, not only because warmer water has a lower carrying capacity for oxygen, but also due to the increasing coincidence of eutrophication with warmer temperatures. In theory, increased temperature could exacerbate the adverse effects of hypoxia on social group cohesion, if fish experience an increase in oxygen demand due to an increased metabolic rate or increased spontaneous activity. Similarly, for species that decrease spontaneous activity during exposure to moderate hypoxia, as a means of energy conservation, warming could promote increased spontaneous activity that opposes this response and again causes greater disruption to group cohesion than would otherwise be observed. We identified only one study that examined the combined effects of hypoxia and temperature, and this study found no effects of temperature, hypoxia, or their combination on group cohesion. Notably, however, this study was carried out on airbreathing *C. aeneus*, and the ability to extrapolate results to non-air-breathing species is limited (Pineda *et al.*, 2020). Additional studies are needed to understand better the combined effects of temperature and hypoxia on non-air-breathing fishes.

Temperature and acidification may also have interactive effects on sociability and group cohesion in fish that are yet to be fully understood. Mechanistically, increased metabolic rate due to warming may result in a more rapid proliferation of ionic imbalances caused by acidification (Lucon-Xiccato *et al.*, 2014; Nilsson *et al.*, 1993). Only one study found a significant effect on sociability at high temperature and low pH (Maulvault *et al.*, 2018); this study found a greater reduction in sociability with the combination of heat and acidification compared to either stressor alone. A second study reported no effect of a combination of temperature and pH on group cohesion, though the effect size calculated for this study was negative (Mitchell *et al.*, 2022). It is possible that these differing results are due to interspecific differences in responses due to different physiological or behavioural capacity to cope with environmental changes, although further research is needed to identify which species may be more vulnerable or robust. Multi-stressor research would benefit from further attention, as very few studies have investigated acidification or hypoxia with temperature, and studies of acidification with hypoxia or of all three stressors together have been entirely neglected. These conditions are increasingly likely to be experienced together in natural settings, as combinations of eutrophication and heat anomalies resulting from climate change become ubiquitous. Replicating ecologically relevant stressor combinations in the laboratory may be challenging (Munson, Cortese & Killen, 2024), and studies of naturally occurring differences or fluctuations in conditions affecting wild-living populations, that is observations of populations in the wild, may help to elucidate the effects of these interactions, although these present additional issues in terms of controlling for other variables. We suggest that a more collaborative "many-labs" approach to studying the effects of climate stressors on social behaviour may help to elucidate this increasingly relevant topic of research. If multiple laboratories were able to coordinate study of the effects of climate-related variables on social behaviour, this may make comparisons among experiments and standardisation of variables measured more feasible. Such an approach has been utilised in studying behaviour in corvids (Miller *et al.*, 2022) and primates (Kopiske *et al.*, 2016) but has yet to be used in the study of fish social behaviour. This approach could focus particularly on multi-stressor interactions, inter- and intraspecific variation in responses, and on the effects of exposure period to different stressors.

V. FUNCTIONAL IMPLICATIONS

Direct benefits of shoaling and schooling in fishes include protection from predators and swimming energetics. Being

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part of a group dilutes the risk to any one individual of being targeted by a predator; groups of prey are also better able to detect potential predators at greater distances and identify whether they pose a risk with greater accuracy (Ward & Webster, 2016). If a predator attacks, grouped fish can benefit from the confusion effect, where predators find it difficult to identify and follow lone individuals against a background of moving groupmates. Members of less-cohesive groups, and individuals whose behaviour is less coordinated with that of their group members, may be at heightened risk of predation (Ioannou, Guttal & Couzin, 2012). If fish experiencing hypoxic conditions form less-cohesive shoals, as we found for six of the eight studies included in our meta-analysis, then they may lose some of the anti-predator benefits of shoaling. Susceptibility to capture by predators may be further exacerbated by effects of hypoxia on individual perception of predator cues. While fast-start responses (such as C-start responses) are anaerobic and should not be affected by hypoxia, probability of initiating a fast-start response (responsiveness) has been shown to be reduced at very low oxygen levels (Lefrancois & Domenici, 2006; Lefrancois, Shingles & Domenici, 2005). In addition, endurance in the event of a sustained pursuit by a predator may be affected (Domenici *et al.*, 2007), and recovery from anaerobic metabolism used during an escape may be impaired by hypoxia or thermal stress (Killen *et al.*, 2015). The interactions among hypoxia, shoal cohesion and predation risk also will depend upon the type of predator involved. Predatory fishes may themselves be affected by hypoxia, reducing their perception of prey responses, agility when pursuing prey, and also their overall motivation to hunt. For example, juvenile naked gobies *Gobiosoma bosc* Lacepède 1800 were attacked less often by fish predators, striped bass *Morone saxatilis* Walbaum 1792 and adult *G. bosc*, as oxygen concentration decreased (Breitburg *et al.*, 1994). If responses to hypoxia differ among species, this may also affect predator avoidance in mixed-species shoals, thus affecting survival success in both robust as well as susceptible species.

While piscine predation has been focused on by the majority of hypoxia studies to date, other predator species may also have a significant effect on fish in hypoxic conditions. Hypoxia-tolerant and air-breathing predators such as birds and mammals (e.g. river otters *Lutra lutra* Linnaeus 1758), and fish predators that can breathe air at the surface will be less affected by hypoxia, with their fish prey likely at greater risk of capture under hypoxic conditions (Domenici *et al.*, 2007). Under hypoxic conditions, juvenile naked gobies and larvae of red sea bream *Pagrus major* Temminck and Schlegel 1843 were both more vulnerable to capture by hypoxia-tolerant cnidarian predators, sea nettles *Chrysaora quinquecirrha* Desor 1848 and moon jellyfish *Aurelia aurita* L. 1758 respectively (Shoji *et al.*, 2005; Breitburg *et al.*, 1994), which may reflect hypoxia-diminished escape responses. Opportunistic predation of air-breathing fishes by avian predators at the surface is also well documented (Domenici *et al.*, 2007). However, the relationship between hypoxia-induced changes in shoal cohesion and predation risk has not, to our knowledge, been investigated directly. Research in this area would be useful in determining how changes in shoaling behaviour observed for some species might interact with vulnerability to predation.

While fish swimming in schools can typically save energy while swimming compared to solitary fish, any changes in group cohesion as a result of climate-related stressors could diminish these energy savings. Trailing fish can save energy by exploiting wave vortices generated by others swimming ahead of them, while anterior fish can gain forward momentum from the wave of higher pressure produced by schoolmates behind them (Hemelrijk *et al.*, 2015; Liao *et al.*, 2003). For example, grey mullet *Liza aurata* Risso 1810 groups in a laboratory swimming tunnel expended less energy, measured as tail-beat frequency and amplitude, than did lone fish (Marras *et al.*, 2015). This was true for three different swimming speeds and was independent of position relative to schoolmates. While those swimming behind others benefited the most, fish in forward positions, including those at the front of the school, had lower tail-beat frequencies than fish that swam alone (Marras *et al.*, 2015). A hypoxia-related reduction in shoal cohesion could have implications for swimming energetics if it leads fish to disperse beyond the vortices or pressure waves produced by schoolmates. Even a reduction in NNDs could cause a decrease in hydrodynamic efficiency for individuals, because areas proximate to neighbours can have a high degree of turbulence which reduces the opportunity for phase-matching of body undulations while swimming (Li *et al.*, 2020). Increased swimming effort resulting from travelling independently of others may be particularly costly under hypoxic conditions if it increases oxygen demand. On the other hand, dense groups of fish can lead to localised depletion of dissolved oxygen (McFarland & Moss, 1967; Steffensen, 1995). The costs and benefits of travelling in a cohesive group under hypoxic conditions, in terms of oxygen demand, are therefore likely to be complex and to interact with other factors including swimming speed and water current speed, water temperature, the body size of the fish and the size and density of the group (Halsey *et al.*, 2018).

VI. CONCLUSIONS

(1) While climate-related stressors have been shown to have significant effects on physiology and behaviour in fish species, our literature review only found evidence for an effect of hypoxia on group behaviour.

(2) Our meta-analysis was limited by the lack of research available on this topic to date, and further study is urgently needed to provide more robust evidence for observed trends and to elucidate how factors such as species, habitat, ontogeny, exposure period, and degree of change in conditions may predict effects.

(3) Empirical studies investigating the interactions of two or more climate-related stressors are also relatively sparse in

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the literature, although one study indicates significant interactions between temperature and acidification that warrant further investigation.

(4) Studies investigating the reproducibility and mechanisms of robustness in species that are apparently resilient to climate-related stressors would aid understanding of the impacts of these stressors and how organisms may adapt.

(5) A more collaborative approach would benefit this area of research and allow more targeted studies to be carried out globally.

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VIII. REFERENCES

Alfonso, S., Gesto, M. & Sadoul, B. (2021). Temperature increase and its effects on fish stress physiology in the context of global warming. *Journal of Fish Biology* **98**(6), 1496–1508.

Alfonso, S., Sadoul, B., Cousin, X. & Begout, M.-L. (2020). Spatial distribution and activity patterns as welfare indicators in response to water quality changes in European sea bass, *Dicentrarchus labrax*. *Applied Animal Behaviour Science* **226**, 104974.

Anders, N., Howarth, K., Totland, B., Handegard, N. O., Tenningen, M. & Breen, M. (2019). Effects on individual level behaviour in mackerel (*Scomber scombrus*) of sub-lethal capture related stressors: crowding and hypoxia. *PLoS One* **14**(3), e0213709.

Andreassen, A. H., Hall, P., Khatibzadeh, P., Jutfelt, F. & Kermen, F. (2022). Brain dysfunction during warming is linked to oxygen limitation in larval zebrafish. *Proceedings of the National Academy of Sciences of the United States of America* **119**(39), e2207052119.

Angiulli, E., Pagliara, V., Cioni, C., Frabetti, F., Pizzetti, F., Alleva, E. & Toni, M. (2020). Increase in environmental temperature affects exploratory behaviour, anxiety and social preference in *Danio rerio*. *Scientific Reports* **10**(1), 5385.

Bartolini, T., Butail, S. & Porfiri, M. (2015). Temperature influences sociality and activity of freshwater fish. *Environmental Biology of Fishes* **98**(3), 825–832.

Bennett, W. (2010). Extreme physiology of intertidal fishes of the Wakatobi. In *Marine Research and Conservation in the Coral Triangle: The Wakatobi National Park* (eds J. Clifton, R. K. F. Unsworth and D. J. Smith), pp. 111–128. NOVA Science Publishers, New York, NY.

Breitburg, D. L., Steinberg, N., Dubeau, S., Cooksey, C. & Houde, E. D. (1994). Effects of low dissolved-oxygen on predation on estuarine fish larvae. *Marine Ecology Progress Series* **104**(3), 235–246.

Campos, D. F., Jesus, T. F., Kochhann, D., Heinrichs-Caldas, W., Coelho, M. M. & Almeida-Val, V. M. F. (2017). Metabolic rate and thermal tolerance in two congeneric Amazon fishes: *Paracheirodon axelrodi* Schultz, 1956 and *Paracheirodon simulans* Gery, 1963 (Characidae). *Hydrobiologia* **789**(1), 133–142.

Cattano, C., Fine, M., Quattrocchi, F., Holzmand, R. & Milazzo, M. (2019). Behavioural responses of fish groups exposed to a predatory threat under elevated CO_2. *Marine Environmental Research* **147**, 179–184.

Clark, M. A. (2022). *Investigating the Impacts of Environmental Change on Social Behaviour in Fish*. Masters by Research. University of Bristol, Bristol.

Clarke, A. & Johnston, N. M. (1999). Scaling of metabolic rate with body mass and temperature in teleost fish. *Journal of Animal Ecology* **68**(5), 893–905.

Colchen, T., Teletchea, F., Fontaine, P. & Pasquet, A. (2017). Temperature modifies activity, inter-individual relationships and group structure in a fish. *Current Zoology* **63**(2), 175–183.

Conrad, J. L., Weinersmith, K. L., Brodin, T., Saltz, J. B. & Sih, A. (2011). Behavioural syndromes in fishes: a review with implications for ecology and fisheries management. *Journal of Fish Biology* **78**(2), 395–435.

Cook, D. G., Brown, E. J., Lefevre, S., Domenici, P. & Steffensen, J. F. (2014). The response of striped surfperch *Embiotoca lateralis* to progressive hypoxia: swimming activity, shoal structure, and estimated metabolic expenditure. *Journal of Experimental Marine Biology and Ecology* **460**, 162–169.

Cooper, B., Adriaenssens, B. & Killen, S. S. (2018). Individual variation in the compromise between social group membership and exposure to preferred temperatures. *Proceedings of the Royal Society B-Biological Sciences* **285**(1880), 20180884.

Corral-Lopez, A., Kotrschal, A., Szorkovszky, A., Garate-Olaizola, M., Herbert-Read, J., van der Bijl, W., Romenskyy, M., Zeng, H.-L., Buechel, S. D., Fontrodona-Eslava, A., Pelckmans, K., Mank, J. E. & Kolm, N. (2023). Evolution of schooling drives changes in neuroanatomy and motion characteristics across predation contexts in guppies. *Nature Communications* **14**(1), 6027.

Davis, B. E., Hansen, M. J., Cocherell, D. E., Nguyen, T. X., Sommer, T., Baxter, R. D., Fangue, N. A. & Todgham, A. E. (2019). Consequences of temperature and temperature variability on swimming activity, group structure, and predation of endangered delta smelt. *Freshwater Biology* **64**(12), 2156–2175.

Diaz, R. J. & Breitburg, D. L. (2009). The hypoxic environment. In *Hypoxia Fish Physiology* (eds J. G. Richards, A. P. Farrell and C. J. Brauner), pp. 1–23. Academic Press, Cambridge, MA.

Diaz, R. J. & Rosenberg, R. (2008). Spreading dead zones and consequences for marine ecosystems. *Science* **321**(5891), 926–929.

Domenici, P., Ferrari, R. S., Steffensen, J. F. & Batty, R. S. (2002). The effect of progressive hypoxia on school structure and dynamics in Atlantic herring *Clupea harengus*. *Proceedings of the Royal Society B-Biological Sciences* **269**(1505), 2103–2111.

Domenici, P., Lefrancois, C. & Shingles, A. (2007). Hypoxia and the antipredator behaviours of fishes. *Philosophical Transactions of the Royal Society B-Biological Sciences* **362**(1487), 2105–2121.

Domenici, P., Steffensen, J. F. & Batty, R. S. (2000). The effect of progressive hypoxia on swimming activity and schooling in Atlantic herring. *Journal of Fish Biology* **57**(6), 1526–1538.

Domenici, P., Steffensen, J. F. & Marras, S. (2017). The effect of hypoxia on fish schooling. *Philosophical Transactions of the Royal Society B-Biological Sciences* **372**(1727), 20160236.

Doney, S. C. (2010). The growing human footprint on coastal and open-ocean biogeochemistry. *Science* **328**(5985), 1512–1516.

Duteil, M., Pope, E. C., Perez-Escudero, A., de Polavieja, G. G., Furtbauer, I., Brown, M. R. & King, A. J. (2016). European sea bass show behavioural resilience to near-future ocean acidification. *Royal Society Open Science* **3**(11), 160656.

Elkins, D. & Grossman, G. D. (2014). Invasive rainbow trout affect habitat use, feeding efficiency, and spatial organization of warpaint shiners. *Biological Invasions* **16**(4), 919–933.

Fahlman, J., Hellstrom, G., Jonsson, M., Fick, J. B., Rosvall, M. & Klaminder, J. (2021). Impacts of oxazepam on perch (*Perca fluviatilis*) behavior: fish familiarized to lake conditions do not show predicted anti-anxiety response. *Environmental Science and Technology* **55**(6), 3624–3633.

Gattuso, J. P., Magnan, A., Bille, R., Cheung, W. W. L., Howes, E. L., Joos, F., Allemand, D., Bopp, L., Cooley, S. R., Eakin, C. M., Hoegh-Guldberg, O., Kelly, R. P., Portner, H. O., Rogers, A. D., Baxter, J. M., *et al.* (2015). Contrasting futures for ocean and society from different anthropogenic CO_2 emissions scenarios. *Science* **349**(6243), aac4722.

Greco, T., Biondi-Zoccai, G., Gemma, M., Guerin, C., Zangrillo, A. & Landoni, G. (2015). How to impute study-specific standard deviations in meta-analyses of skewed continuous endpoints? *World Journal of Meta-Analysis* **3**(5), 215–224.

Guillerme, T. & Healy, K. (2020). mulTree: performs MCMCglmm on m ultiple phylogenetic trees. R package version 1.3.7.

Hackathon, R., Bolker, B., Butler, M., Cowan, P., de Vienne, D., Eddelbuettel, D., Holder, M., Jombart, T., Kembel, S., Michonneau, F., Orme, D., O'Meara, B., Paradis, E., Regetz, J. & Zwickl, D. (2020). Phylobase: base package for phylogenetic structures and comparative data. R package version 0.8.10.

Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software* **33**(2), 1–22.

Halsey, L. G., Wright, S., Racz, A., Metcalfe, J. D. & Killen, S. S. (2018). How does school size affect tail beat frequency in turbulent water? *Comparative Biochemistry and Physiology A - Molecular and Integrative Physiology* **218**, 63–69.

Hayes, D. S., Branco, P., Santos, J. M. & Ferreira, T. (2019). Oxygen depletion affects kinematics and shoaling cohesion of cyprinid fish. *Water* **11**(4), 642.

Hemelrijk, C. K., Reid, D. A. P., Hildenbrandt, H. & Padding, J. T. (2015). The increased efficiency of fish swimming in a school. *Fish and Fisheries* **16**(3), 511–521.

Herbert, N. A., Domenici, P., Lefrancois, C., Steffensen, J. F. & McKenzie, D. J. (2013). The effect of hypoxia on fish swimming performance and behaviour. In *Swimming Physiology of Fish: Towards Using Exercise to Farm a Fit Fish in Sustainable Aquaculture* (eds A. Palstra and J. Planas), pp. 129–159. Springer, Berlin, Heidelberg.

Heuer, R. M. & Grosell, M. (2014). Physiological impacts of elevated carbon dioxide and ocean acidification on fish. *American Journal of Physiology-Regulatory Integrative and Comparative Physiology* **307**(9), 1061–1084.

1469185x, 2024, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.13111 by Swedish University Of, Wiley Online Library on [12/11/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Holubova, M., Hejzlar, J., Cech, M., Vasek, M., Blabolil, P. & Peterka, J. (2021). Fluctuations in pelagic fish density linked to ambient conditions. *Journal of Fish Biology* **98**(3), 756–767.

Hurst, T. P. (2007). Thermal effects on behavior of juvenile walleye pollock (*Theragra chalcogramma*): implications for energetics and food web models. *Canadian Journal of Fisheries and Aquatic Sciences* **64**(3), 449–457.

Ioannou, C. C., Guttal, V. & Couzin, I. D. (2012). Predatory fish select for coordinated collective motion in virtual prey. *Science* **337**(6099), 1212–1215.

Ishimatsu, A., Kikkawa, T., Hayashi, M., Lee, K. S. & Kita, J. (2004). Effects of CO_2 on marine fish: larvae and adults. *Journal of Oceanography* **60**(4), 731–741.

Islam, M. J., Kunzmann, A. & Slater, M. J. (2022). Responses of aquaculture fish to climate change-induced extreme temperatures: a review. *Journal of the World Aquaculture Society* **53**(2), 314–366.

Israeli, D. & Kimmel, E. (1996). Monitoring the behavior of hypoxia-stressed *Carassius auratus* using computer vision. *Aquacultural Engineering* **15**(6), 423–440.

Johansén, J. L., Nadler, L. E., Habary, A., Bowden, A. J. & Rummer, J. (2021). Thermal acclimation of tropical coral reef fishes to global heat waves. *eLife* **10**, e59162.

Jolles, J. W., Boogert, N. J., Sridhar, V. H., Couzin, I. D. & Manica, A. (2017). Consistent individual differences drive collective behavior and group functioning of schooling fish. *Current Biology* **27**(18), 2862–2868.

Jutfelt, F., de Souza, K. B., Vuylsteke, A. & Sturve, J. (2013). Behavioural disturbances in a temperate fish exposed to sustained high-CO_2 levels. *PLoS One* **8**(6), e65825.

Killen, S. S., Cortese, D., Cotgrove, L., Jolles, J. W., Munson, A. & Ioannou, C. C. (2021). The potential for physiological performance curves to shape environmental effects on social behavior. *Frontiers in Physiology* **12**, 754719.

Killen, S. S., Fu, C., Wu, Q., Wang, Y.-X. & Fu, S.-J. (2016). The relationship between metabolic rate and sociability is altered by food deprivation. *Functional Ecology* **30**(8), 1358–1365.

Killen, S. S., Marras, S., Metcalfe, N. B., McKenzie, D. J. & Domenici, P. (2013). Environmental stressors alter relationships between physiology and behaviour. *Trends in Ecology and Evolution* **28**(11), 651–658.

Killen, S. S., Marras, S., Nadler, L. & Domenici, P. (2017). The role of physiological traits in assortment among and within fish shoals. *Philosophical Transactions of the Royal Society B-Biological Sciences* **372**(1727), 20160233.

Killen, S. S., Reid, D., Marras, S. & Domenici, P. (2015). The interplay between aerobic metabolism and antipredator performance: vigilance is related to recovery rate after exercise. *Frontiers in Physiology* **6**, 111.

Kleinhappel, T. K., Burman, O. H. P., John, E. A., Wilkinson, A. & Pike, T. W. (2019). The impact of water pH on association preferences in fish. *Ethology* **125**(4), 195–202.

Kopiske, K. K., Bruno, N., Hesse, C., Schenk, T. & Franz, V. H. (2016). The functional subdivision of the visual brain: is there a real illusion effect on action? A multi-lab replication study. *Cortex* **79**, 130–152.

Kuruvilla, M., Dell, A., Olson, A. R., Knouft, J., Grady, J. M., Forbes, J. & Berdahl, A. M. (2023). The effect of temperature on fish swimming and schooling is context dependent. *Oikos* **2023**(2), e09202.

Kwan, G. T., Hamilton, T. J. & Tresguerres, M. (2017). CO_2-induced ocean acidification does not affect individual or group behaviour in a temperate damselfish. *Royal Society Open Science* **4**(7), 170283.

Kwong, R. W. M., Kumai, Y. & Perry, S. F. (2014). The physiology of fish at low pH: the zebrafish as a model system. *Journal of Experimental Biology* **217**(5), 651–662.

Lanzarin, G. A. B., Venancio, C. A. S., Monteiro, S. M. & Felix, L. M. (2020). Behavioural toxicity of environmental relevant concentrations of a glyphosate commercial formulation - RoundUp (R) UltraMax - during zebrafish embryogenesis. *Chemosphere* **253**, 126636.

Lefrancois, C. & Domenici, P. (2006). Locomotor kinematics and behaviour in the escape response of European sea bass, *Dicentrarchus labrax* L., exposed to hypoxia. *Marine Biology* **149**(4), 969–977.

Lefrancois, C., Ferrari, R. S., da Silva, J. M. & Domenici, P. (2009). The effect of progressive hypoxia on spontaneous activity in single and shoaling golden grey mullet *Liza aurata*. *Journal of Fish Biology* **75**(7), 1615–1625.

Lefrancois, C., Shingles, A. & Domenici, P. (2005). The effect of hypoxia on locomotor performance and behaviour during escape in *Liza aurata*. *Journal of Fish Biology* **67**(6), 1711–1729.

Levin, L. A., Liu, K.-K., Emeis, K.-C., Breitburg, D. L., Cloern, J., Deutsch, C., Giani, M., Goffart, A., Hofmann, E. E., Lachkar, Z., Limburg, K., Liu, S.-M., Montes, E., Naqvi, W., Ragueneau, O., et al. (2015). Comparative biogeochemistry-ecosystem-human interactions on dynamic continental margins. *Journal of Marine Systems* **141**, 3–17.

Li, L., Nagy, M., Graving, J. M., Bak-Coleman, J., Xie, G. M. & Couzin, I. D. (2020). Vortex phase matching as a strategy for schooling in robots and in fish. *Nature Communications* **11**(1), 5408.

Liao, J. C., Beal, D. N., Lauder, G. V. & Triantafyllou, M. S. (2003). The Karman gait: novel body kinematics of rainbow trout swimming in a vortex street. *Journal of Experimental Biology* **206**(6), 1059–1073.

Lopes, A. F., Morais, P., Pimentel, M., Rosa, R., Munday, P. L., Goncalves, E. J. & Faria, A. M. (2016). Behavioural lateralization and shoaling cohesion of fish larvae altered under ocean acidification. *Marine Biology* **163**(12), 243.

Lucon-Xiccato, T., Nati, J. J. H., Blasco, F. R., Johansen, J. L., Steffensen, J. F. & Domenici, P. (2014). Severe hypoxia impairs lateralization in a marine teleost fish. *Journal of Experimental Biology* **217**(23), 4115–4118.

Mameri, D., Branco, P., Ferreira, M. T. & Santos, J. M. (2020). Heatwave effects on the swimming behaviour of a Mediterranean freshwater fish, the Iberian barbel *Luciobarbus bocagei*. *Science of the Total Environment* **730**, 139152.

Marras, S., Killen, S. S., Lindstrom, J., McKenzie, D. J., Steffensen, J. F. & Domenici, P. (2015). Fish swimming in schools save energy regardless of their spatial position. *Behavioral Ecology and Sociobiology* **69**(2), 219–226.

Maulvault, A. L., Santos, L. H. M. L. M., Paula, J. R., Camacho, C., Pissarra, V., Fogaca, F., Barbosa, V., Alves, R., Ferreira, P. P., Barcelo, D., Rodriguez-Mozaz, S., Marques, A., Diniz, M. & Rosa, R. (2018). Differential behavioural responses to venlafaxine exposure route, warming and acidification in juvenile fish (*Argyrosomus regius*). *Science of the Total Environment* **634**, 1136–1147.

McFarland, W. N. & Moss, S. A. (1967). Internal behaviour in fish schools. *Science* **156**(3772), 260–262.

McKee, A., Soto, A. P., Chen, P. & McHenry, M. J. (2020). The sensory basis of schooling by intermittent swimming in the rummy-nose tetra (*Hemigrammus rhodostomus*). *Proceedings of the Royal Society B* **287**(1937), 20200568.

Mehdi, H., Morphet, M. E., Lau, S. C., Bragg, L. M., Servos, M. R., Parrott, J. L., Scott, G. R. & Balshine, S. (2022). Temperature modulates the impacts of wastewater exposure on the physiology and behaviour of fathead minnow. *Chemosphere* **294**, 133738.

Metcalfe, N. B., Van Leeuwen, T. E. & Killen, S. S. (2016). Does individual variation in metabolic phenotype predict fish behaviour and performance? *Journal of Fish Biology* **88**(1), 298–321.

Miller, N. & Gerlai, R. (2012). From schooling to shoaling: patterns of collective motion in zebrafish (*Danio rerio*). *PLoS One* **7**(11), e48865.

Miller, R., Lambert, M. L., Frohnwieser, A., Brecht, K. F., Bugnyar, T., Crampton, I., Garcia-Pelegrin, E., Gould, K., Greggor, A. L., Izawa, E.-I., Kelly, D. M., Li, Z., Luo, Y., Luong, L. B., Massen, J. J. M., et al. (2022). Socio-ecological correlates of neophobia in corvids. *Current Biology* **32**(1), 74–85.

Mitchell, A., Booth, D. J. & Nagelkerken, I. (2022). Ocean warming and acidification degrade shoaling performance and lateralization of novel tropical-temperate fish shoals. *Global Change Biology* **28**(4), 1388–1401.

Monnet, G., Rosenfeld, J. S. & Richards, J. G. (2023). Growth variation along a dispersal gradient in juvenile rainbow trout. *Ecology of Freshwater Fish* **32**(2), 247–256.

Morris, S. B. (2008). Estimating effect sizes from pretest-posttest-control group designs. *Organizational Research Methods* **11**(2), 364–386.

Moss, S. A. & McFarland, W. N. (1970). Influence of dissolved oxygen and carbon dioxide on fish schooling behaviour. *Marine Biology* **5**(2), 100–107.

Munson, A., Cortese, D. & Killen, S. S. (2024). Multiple stressors. In *Behavioural Responses to a Changing World: Challenges and Applications* (eds B. Wong and U. Candolin). Oxford University Press, Oxford.

Nadler, L. E., Killen, S. S., McClure, E. C., Munday, P. L. & McCormick, M. I. (2016). Shoaling reduces metabolic rate in a gregarious coral reef fish species. *Journal of Experimental Biology* **219**(18), 2802–2805.

Nagelkerken, I. & Connell, S. D. (2015). Global alteration of ocean ecosystem functioning due to increasing human CO_2 emissions. *Proceedings of the National Academy of Sciences of the United States of America* **112**(43), 13272–13277.

Nati, J. J. H., Lindstrom, J., Yeomans, W. & Killen, S. S. (2018). Physiological and behavioural responses to hypoxia in an invasive freshwater fish species and a native competitor. *Ecology of Freshwater Fish* **27**(3), 813–821.

Nilsson, G. E., Perezpinzon, M., Dimberg, K. & Winberg, S. (1993). Brain sensitivity to anoxia in fish as reflected by changes in extracellular K^+ activity. *American Journal of Physiology* **264**(2), 250–253.

O'Driscoll, R. L. & McClatchie, S. (1998). Spatial distribution of planktivorous fish schools in relation to krill abundance and local hydrography off Otago, New Zealand. *Deep-Sea Research Part II-Topical Studies in Oceanography* **45**(7), 1295–1325.

Olla, B. L. & Studholm, A. (1971). Effect of temperature on activity of bluefish, *Pomatomus saltatrix* L. *Biological Bulletin* **141**(2), 337–349.

Olla, B. L., Studholme, A. L. & Bejda, A. J. (1985). Behaviour of juvenile bluefish *Pomatomus saltatrix* in vertical thermal gradients - influence of season, temperature acclimation, and food. *Marine Ecology Progress Series* **23**(2), 165–177.

Palacios-Fuentes, P., Diaz-Astudillo, M., Antonia Recule, M., Patricio Ojeda, F. & Landaeta, M. F. (2020). Presettlement schooling behaviour of a rocky fish in a shallow area. Is it related to local environmental conditions? *Scientia Marina* **84**(3), 243–252.

Partridge, B. L. & Pitcher, T. J. (1980). The sensory basis of fish schools - relative roles of lateral line and vision. *Journal of Comparative Physiology* **135**(4), 315–325.

Pedersen, T. L. (2022). ggraph: An implementation of grammar of g raphics for graphs and networks. R package version 2.1.0.

1469185x, 2024, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/brv.13111 by Swedish University Of, Wiley Online Library on [12/11/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Petitjean, Q., Jean, S., Cote, J., Lamarins, A., Lefranc, M., Santos, R., Perrault, A., Laffaille, P. & Jacquin, L. (2020). Combined effects of temperature increase and immune challenge in two wild gudgeon populations. *Fish Physiology and Biochemistry* **46**(1), 157–176.

Pilakouta, N., Killen, S. S., Kristjansson, B. K., Skulason, S., Lindstrom, J., Metcalfe, N. B. & Parsons, K. J. (2020). Multigenerational exposure to elevated temperatures leads to a reduction in standard metabolic rate in the wild. *Functional Ecology* **34**(6), 1205–1214.

Pilakouta, N., O'Donnell, P. J., Crespel, A., Levet, M., Claireaux, M., Humble, J. L., Kristjansson, B. K., Skulason, S., Lindstrom, J., Metcalfe, N. B., Killen, S. S. & Parsons, K. J. (2022). A warmer environment can reduce sociability in an ectotherm. *Global Change Biology* **29**, 206–214.

Pineda, M., Aragao, I., McKenzie, D. J. & Killen, S. S. (2020). Social dynamics obscure the effect of temperature on air breathing in Corydoras catfish. *Journal of Experimental Biology* **223**(21), jeb222133.

Pitcher, T. J. (1983). Heuristic definitions of fish shoaling behavior. *Animal Behaviour* **31**, 611–613.

Regan, M. D., Turko, A. J., Heras, J., Andersen, M. K., Lefevre, S., Wang, T., Bayley, M., Brauner, C. J., Do Thi Thanh, H., Nguyen Thanh, P. & Nilsson, G. E. (2016). Ambient CO_2, fish behaviour and altered GABAergic neurotransmission: exploring the mechanism of CO_2-altered behaviour by taking a hypercapnia dweller down to low CO_2 levels. *Journal of Experimental Biology* **219**(1), 109–118.

Revell, L. (2012). Phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* **3**, 217–223.

Rohatgi, A. (2022). WebPlotDigitizer (Version 4.6). Available at: https://automeris.io/WebPlotDigitizer.

Ross, R. M., Krise, W. F., Redell, L. A. & Bennett, R. M. (2001). Effects of dissolved carbon dioxide on the physiology and behavior of fish in artificial streams. *Environmental Toxicology* **16**(1), 84–95.

Salahinejad, A., Attaran, A., Meuthen, D., Rachamalla, M., Chivers, D. P. & Niyogi, S. (2022). Maternal exposure to bisphenol S induces neuropeptide signaling dysfunction and oxidative stress in the brain, and abnormal social behaviors in zebrafish (Danio rerio) offspring. *Science of the Total Environment* **830**, 154794.

Santos, D., Luzio, A., Matos, C., Bellas, J., Monteiro, S. M. & Felix, L. (2021). Microplastics alone or co-exposed with copper induce neurotoxicity and behavioral alterations on zebrafish larvae after a subchronic exposure. *Aquatic Toxicology* **235**, 105814.

Schellart, N. A. M. & Wubbels, R. J. (1998). The auditory and mechanosensory lateral line system. In *The Physiology of Fishes*, 2 (ed. D. H. Evans), pp. 283–312. CRC Press, Boca Raton, NY.

Schunter, C., Welch, M. J., Nilsson, G. E., Rummer, J. L., Munday, P. L. & Ravasi, T. (2018). An interplay between plasticity and parental phenotype determines impacts of ocean acidification on a reef fish. *Nature Ecology and Evolution* **2**(2), 334–342.

Shoji, J., Masuda, R., Yamashita, Y. & Tanaka, M. (2005). Effect of low dissolved oxygen concentrations on behavior and predation rates on red sea bream *Pagrus major* larvae by the jellyfish *Aurelia aurita* and by juvenile Spanish mackerel *Scomberomorus niphonius*. *Marine Biology* **147**(4), 863–868.

Sitko, S. & Honrubia, V. (1986). Differential effect of ischemia on spontaneous and sinusoidal evoked activity in semicircular canal afferents in the bullfrog. *Acta Oto-Laryngologica* **102**(3–4), 179–185.

Sommer-Trembo, C., Petry, A. C., Silva, G. G., Vurusic, S. M., Gismann, J., Baier, J., Krause, S., Cardoso Iorio, J. d. A., Riesch, R. & Plath, M. (2017). Predation risk and abiotic habitat parameters affect personality traits in extremophile populations of a neotropical fish (*Poecilia vivipara*). *Ecology and Evolution* **7**(16), 6570–6581.

Steffensen, J. F. (1995). Possible limitations of speed and size of swimming fish schools, based on oxygen-consumption of herring, *Clupea harengus*, measured at different swimming speeds. *Journal of Physiology-London* **483P**, 192.

Stienessen, S. (2015). *Information transfer, heterogeneity, and local environmental effects on emergent group patterns defining fish schools: perspectives from different scales of observation*. PhD: University of Washington, Washington, USA.

Swartzman, G. (1997). Analysis of the summer distribution of fish schools in the Pacific Eastern Boundary Current. *ICES Journal of Marine Science* **54**(1), 105–116.

Tang, Z. H. & Fu, S. J. (2021). Effects of habitat conditions on the boldness and sociability of wild-caught fish (*Zacco platypus*) along a river. *Journal of Ethology* **39**(3), 379–391.

Theodorou, P., Olafsdottir, G. A. & Snorrason, S. S. (2012). Reaching the limit: constrained behavioural flexibility of juvenile Atlantic cod (*Gadus morhua*) at current coastal temperatures. *Journal of Experimental Marine Biology and Ecology* **413**, 192–197.

Toni, M., Angiulli, E., Miccoli, G., Cioni, C., Alleva, E., Frabetti, F., Pizzetti, F., Scalvini, F. G., Nonnis, S., Negri, A., Tedeschi, G. & Maffioli, E. (2019). Environmental temperature variation affects brain protein expression and cognitive abilities in adult zebrafish (*Danio rerio*): a proteomic and behavioural study. *Journal of Proteomics* **204**, 103396.

Topal, A., Ozdemir, S., Arslan, H. & Comakli, S. (2021). How does elevated water temperature affect fish brain? (A neurophysiological and experimental study: assessment of brain derived neurotrophic factor, cFOS, apoptotic genes, heat shock genes, ER-stress genes and oxidative stress genes). *Fish & Shellfish Immunology* **115**, 198–204.

Tree of Life Web Project (2023). *Tree of Life*. Available at: http://tolweb.org/tree/phylogeny.html Accessed 8.6.2023.

von Schuckmann, K., Cheng, L., Palmer, M. D., Hansen, J., Tassone, C., Aich, V., Adusumilli, S., Beltrami, H., Boyer, T., Cuesta-Valero, F. J., Desbruyeres, D., Domingues, C., Garcia-Garcia, A., Gentine, P., Gilson, J., *et al.* (2020). Heat stored in the earth system: where does the energy go? *Earth System Science Data* **12**(3), 2013–2041.

Ward, A. & Webster, M. M. (2016). *Sociality: The Behaviour of Group-Living Animals*. Springer, Zurich.

Webster, M. M. & Hart, P. J. B. (2006). Kleptoparasitic prey competition in shoaling fish: effects of familiarity and prey distribution. *Behavioral Ecology* **17**(6), 959–964.

Weetman, D., Atkinson, D. & Chubb, J. C. (1998). Effects of temperature on anti-predator behaviour in the guppy, *Poecilia reticulata*. *Animal Behaviour* **55**, 1361–1372.

Weetman, D., Atkinson, D. & Chubb, J. C. (1999). Water temperature influences the shoaling decisions of guppies, *Poecilia reticulata*, under predation threat. *Animal Behaviour* **58**, 735–741.

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York.

Williams, M. A. & Coutant, C. C. (2003). Modification of schooling behavior in larval atherinid fish *Atherina mochon* by heat exposure of eggs and larvae. *Transactions of the American Fisheries Society* **132**(4), 638–645.

WoRMS (2023). *World Register of Marine Species*. Available at: https://www.marinespecies.org/index.php Accessed 8.6.2023.

Xia, J., Niu, C. & Pei, X. (2010). Effects of chronic exposure to nonylphenol on locomotor activity and social behavior in zebrafish (*Danio rerio*). *Journal of Environmental Sciences* **22**(9), 1435–1440.

Yu, G., Smith, D., Zhu, H., Guan, Y. & Lam, T. T.-Y. (2017). ggtree: an R package for visualization and annotation of phylogenetic trees with their covariates and other associated data. *Methods in Ecology and Evolution* **8**(1), 28–36.

IX. SUPPORTING INFORMATION

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

Table S1. Full data set of studies used in the systematic review.

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