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Review

Impacts of anthropogenic pollutants on social group cohesion and individual sociability in fish: A systematic review and meta-analysis[☆]

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ABSTRACT

Anthropogenic pollutants are near-ubiquitous in aquatic systems. Aquatic animals such as fishes are subject to physiological stress induced by pollution present in aquatic systems, which can translate to changes in behaviour. Key adaptive behaviours such as shoaling and schooling may be subject to change as a result of physiological or metabolic stress or neurosensory impacts of pollution. This can result in fitness and ecological impacts such as increased predation risk and reduced foraging success. Here, we conducted a systematic metanalysis of the existing literature, comprising 165 studies, on the effects of anthropogenic pollution on sociability and group cohesion in fish species. Both organic (number of studies = 92, posterior mean (PM) = −0.483, $p < 0.01$) and inorganic ($n = 24$, PM = −1.453, $p < 0.001$) chemical pollutants, as well as light exposure ($n = 21$, PM = −3.038, $p < 0.01$) were found to reduce sociability. These pollutants did not reduce group cohesion, indicating that effects may be masked in group settings, though fewer studies were carried out on group cohesion and this is a key area for future research. Mixtures of chemical pollutants ($n = 16$) were found to reduce cohesion (PM = −43.71, $p < 0.01$), but increase sociability (PM = 44.27, $p < 0.01$). Evidence was found that fish may behaviourally acclimate to two forms of pollutant, namely mixed chemical pollutants (PM = −0.668, $p < 0.01$) and noise exposure ($n = 22$, PM = −4.043, $p < 0.01$). While aquatic systems are often subject to pollution from multiple sources and of multiple types, very few studies investigated the effects of multiple stressors concurrently. This review identifies trends in the existing literature, and highlights areas where further research is required in order to understand the behavioural and ecological impacts of anthropogenic pollutants in aquatic systems.

1. Introduction

It is increasingly difficult to identify ecosystems that are not subject to anthropogenic pollution. While chemical pollutants are near-ubiquitous in most environments (Hong et al., 2021), organisms must also contend with other forms of anthropogenic disturbance. These include noise pollution (Hubert et al., 2020; Neo et al., 2018), light pollution (Kurvers et al., 2018; Lafoux et al., 2023), and, in aquatic environments, turbidity associated with anthropogenic pollutants, industrial activities, and eutrophication (Borner et al., 2015; Fischer and Frommen, 2013). While many of these are potentially lethal, they also have a variety of effects on animals at sublethal concentrations (Saaristo et al., 2018). Toxicants may also accumulate, following absorption through permeable epithelial surfaces and dietary consumption (Weber et al., 2013). The ability of fish and other aquatic organisms to cope with these stressors is key to ecosystem functioning (Killen et al., 2021; Simpson et al., 2016). Understanding the impacts of pollutants is important for predicting how organisms may cope with or adapt to these stressors (Bertram et al., 2022a).

Chemical pollutants vary in their toxicity and structure, but general classifications can be useful to predict effects. Organic toxicity depends on the ability of the organism to biologically transform the product and reduce bioaccumulation. Organic pharmaceuticals such as antidepressants may have similar modes of action in aquatic species as in humans,

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with behavioural changes resulting from altered levels of neurological signalling molecules such as serotonin (Valenti et al., 2012). Other organic pollutants such as organophosphates interfere with functioning of enzymes such as acetylcholinesterase (ACHe) (Escher et al., 2011), which also plays a role in neurotransmitter function (Colovic et al., 2013). Many organic pollutants, such as 17α-ethinylestradiol (EE2), the main active ingredient in birth control, can act as endocrine disrupting chemicals. These often mimic or alter normal hormonal function causing a cascade of issues with social behaviour, reproduction, survival and growth (Bertram et al., 2022b; Fenske et al., 2020; Kidd et al., 2007).

Inorganic chemical pollutants like metals cannot be biologically transformed, and are oftenacutely toxic, with the potential for endocrine disruption after chronic exposure (Vieira et al., 2009; Shahjahan et al., 2022). The mechanisms of toxicity of inorganic compounds are conserved across species. In fishes, metal ions (e.g., nickel (Ni), cadmium (Cd), copper (Cu), zinc (Zn) etc.) target the active ionic uptake pathways in the gills and intestines, via ionic mimicry thereby reducing the uptake of essential nutrients and ions. Indirect effects of this ion imbalance can include reduced respiratory gas exchange, increased oxidative stress, and changes to the basolaterally located sodium/potassium ATPase, where metals affect amino acid moieties and the metal cofactor (Wood et al., 2012). Metals can also impair sensory function (i.e., olfaction and mechanoreception), including lateral line function in fishes (Chaput et al., 2023). Additionally, many inorganic pollutants interfere with neurological processes (Maulvault et al., 2018) and indirectly affect the endocrine system. Inorganic pollutants can increase metabolic rate, thereby altering energy needs due to the increased cost of maintaining homeostasis and eliminating toxic substances (Thomas et al., 2013).

While mode of action and chemical pollutant concentration may impact the level of toxicity experienced by aquatic organisms, environmental water parameters also influence toxicant uptake and toxicity. Metals can be bound to dissolved organic carbon or other organic molecules, which may affect absorption rates, while differences in toxicity may be observed for some substances in salt as compared with freshwater environments (Paquin et al., 2002). Further, most chemical pollutants are not present in the environment in isolation. Mixture effects of chemical pollutants, whether organic, inorganic, or a combination, is not a new concept but understanding the complex relationship between mixtures and environment has not been fully developed (Orr et al., 2024).

Non-chemical pollutants such as noise and artificial light may also increase physiological stress, resulting in increased circulating glucocorticoids (Simpson et al., 2016; Wysocki et al., 2006). While changes in metabolic traits, neurological function, and circulating glucocorticoids due to stress may have their own effects on fitness, growth, and survival (Pickering and Pottinger, 1989; Simpson et al., 2016), they have also been found to affect various forms of behaviour (Mickle and Higgs, 2018; Neo et al., 2015a; b; Peng et al., 2015). Other non-chemical pollutants such as overall turbidity, defined as the total dissolved matter in the water, may also impact sensory perception of both conspecifics and other environmental cues. Despite a large body of research examining the toxic mechanisms and sublethal effects of chemical and non-chemical pollutants on aquatic animals, we still lack a synthesised understanding of the effects on ecologically relevant behaviours.

Group-living species rely on social behaviour as a defence against predators and to facilitate finding food and mates (Pitcher et al., 1982). Groups of fish can be organised as shoals or schools. A shoal is an unpolarised social group of fish, while schooling is characterised by polarity and coordinated swimming within a social group (Pitcher, 1983). In social fishes, changes to neurological capabilities caused by chemical pollutants may disrupt interactions with conspecifics, altering group behaviour by, for example, reducing group cohesion (Chaput et al., 2023; Michelangeli et al., 2022; Partridge and Pitcher, 1980). If metabolic needs increase due to pollutant exposure, individuals may become less sociable to prioritise foraging and reduce competition (Killen et al., 2016). Behavioural traits such as boldness and activity may also be affected by the direct and indirect effects of chemical pollutants (Polverino et al., 2021), which may in turn affect social behaviour (Michelangeli et al., 2022). Both increased boldness and greater activity may cause individuals to move away from a shoal, due to reduced risk-perception and increased overall movement (Bartolini et al., 2015; Jolles et al., 2015). In group-living species, these changes in individual behaviour and physiology could affect how groups respond to changes in abiotic conditions, with associated changes to emergent collective behaviours (Killen et al., 2021; Michelangeli et al., 2022). The exact response likely depends on the class of chemical pollutant(s) encountered. Antidepressants, for example, may reduce anxiety in fish, making them less sociable and potentially increasing predation risk (Maulvault et al., 2018; Salahinejad et al., 2022). In contrast, noise pollution may provoke an anxiety or stress response, causing fish to move closer together (Currie, 2021; Neo et al., 2015a; b).

Here we review the effects of environmentally relevant concentrations of various anthropogenic chemical and non-chemical pollutants on individual sociability and group cohesion in gregarious fish species and identify key issues that remain poorly understood. While different chemical and non-chemical pollutants have different modes of action, a generalised overview and metanalysis of their effects on social behaviour is lacking in the literature and may be a useful tool in developing predictive frameworks (Orr et al., 2024). Fish are ideal for studying effects of chemical and non-chemical pollutants on social behaviour because the majority of species exhibit shoaling or schooling behaviour at some point in their lives. In addition, fish are widespread in a diverse range of habitats, with over 35000 known species (Froese and Pauly, 2023), and may thus be exposed to almost every aquatic environmental pollutant.

2. Methods

A concise overview of the methods is provided here, with detailed methodology available in the supplementary material (Supp. 1).

2.1. Literature searches

Searches of the literature were carried out from October to December 2022 (Fig. 1). Sources were only included for analyses if shoaling or schooling were examined in relation to anthropogenic pollutants, including chemical pollutants, noise, light, and turbidity. All papers were considered independently by one author of the current study (I.C.T.), and then blind reviewed by one of two other authors (D.C. or A.M.). Papers that were disagreed upon were discussed and included or excluded by consensus, based on the above-mentioned considerations.

2.2. Data collection

Following paper inclusion, data on the following variables were collected for each paper. The effects of individual- and multiple-stressor trials were recorded separately.

1. Effect size (Hedges' *g*, a standardize difference of means between groups) of each treatment on cohesion or sociability, relative to the control.
2. Focal species used in each paper.
3. Class of pollutant to which fish were exposed (Table 1).
4. Treatment levels of variables of interest, converted to z scores.
5. Group sizes. This was defined as the number of fish used per group trial in group cohesion studies.
6. Sex of fish(es) used in each experiment.
7. Number of replicates. Number of replicates was recorded as number of groups per treatment.
8. Period over which fishes were exposed to each treatment, in days.

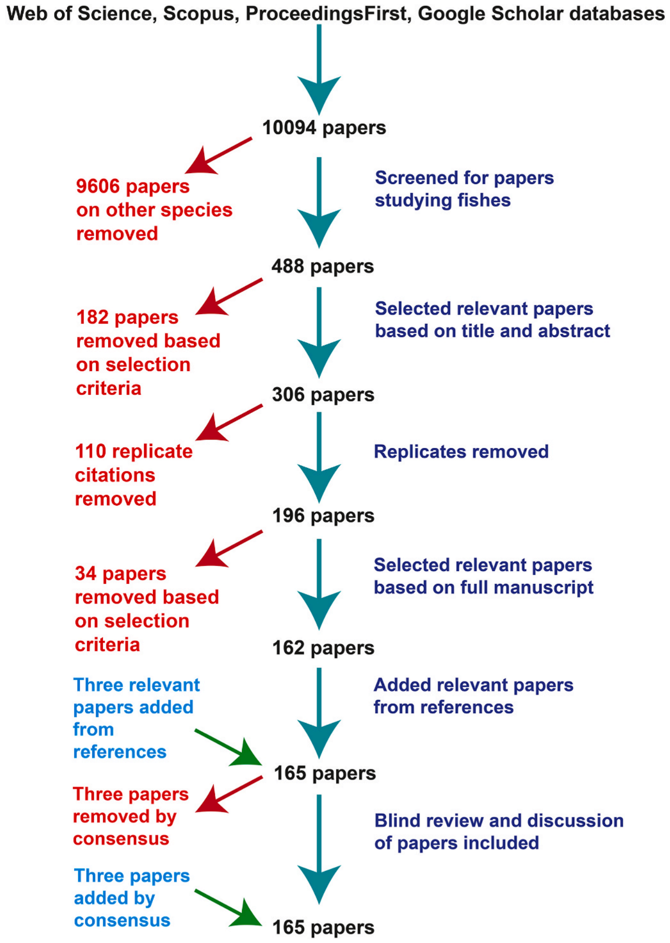

Fig. 1. Flow diagram illustrating paper selection process for systematic review.

Table 1
Classes into which pollutants were divided in our study, with description of how pollutants were classified and examples of each pollutant class.

Pollutant class	Criteria	Examples
Organic	Chemical pollutants consisting of organic (carbon-based) compounds	Pharmaceuticals, organically-derived fertilizers and pesticides, oils, microplastics
Inorganic	Chemical pollutants consisting of inorganic compounds	Metal salts, heavy metals
Mixtures	Any combination of multiple chemical pollutants	Untreated effluent, combinations of multiple substances
Noise	Studies of anthropogenic sounds	Boat noise, pile-driving sounds
Light	Studies of light pollution or varying levels of light exposure.	
Turbidity	Studies of turbidity level, a measure of the amount of suspended matter in the water	

9. Exposure type. Categories of exposure type were uncontrolled (including populations exposed in the wild, and farmed fish exposed in a natural setting), developmental, parental, acute, or acclimated.
10. Metrics used to assess cohesion or sociability.
11. Reported statistical significance (or lack thereof) of the effect of each treatment were recorded for each paper. Statistical significance was recorded as $p < 0.05$.
12. Country where each study was carried out (geographical location).

2.3. *Statistical analysis*

Metanalysis was carried out in R using the MCMCglmm package (Hadfield, 2010) to run phylogenetically-adjusted linear models. Pollutant classes were modelled separately, to reduce model complexity and allow interactions among explanatory variables for each pollutant class to be thoroughly explored. To account for phylogenetic relatedness among fish species, a phylogenetic tree was constructed from the Tree of Life database (Tree of Life Web Project, 2023) including all species, using the R packages phytools (Revell, 2012) and phylobase (Hackathon et al., 2020). This tree was incorporated into a dataset with effect size and variable data using the mulTree package (Guillerme and Healy, 2020), which combines a data table with a phylogenetic tree object to form a data list. The response variable in models was effect size, while the explanatory variables were level of the relevant stressor, exposure period, number of replicates, group size, exposure type, and metric. The interaction effect between pollutant level and metric was also included where multiple levels were present within each metric. For light pollution, an interaction between the form of light exposure and treatment was included in order to separate effects of luminance from different wavelengths. Specimen, referring to different treatments both within and among papers utilising the same species, species, and sex of fish(es) were included as random effect variables. Lambda (λ) value, an indicator of the effect of phylogenetic relatedness among species on effect size, 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.

3. Results

3.1. *Literature overview*

From literature searches, 10049 papers were found, of which 488 studies of fishes were identified. Following screening, 165 papers were included in this review (Supplementary Table 1; Fig. 1). Of these, 162 were found from literature searches, while a further three were identified from reference sections of papers (Fig. 1). The vast majority of studies (156) were peer-reviewed articles, while 9 studies were found in the grey literature, consisting of nine theses ranging from Bachelor's to PhD. While studies were carried out on five of seven continents (Fig. 2a), a significant geographical bias was present, with 66% of studies being carried out in North American and European countries.

The effects of chemical and non-chemical pollutants on fish social behaviour were studied in 69 species (Fig. 2b). Of these, 20 were in the family Cyprinidae, with the most-commonly used species being the zebrafish *Danio rerio* ($n = 43$). Phylogenetic diversity of species used across studies was relatively low, and the degree of replication of studies on a given species was highly variable. Although *D. rerio* was used in multiple studies for almost all pollutants, the majority of species were used only once or twice for any given substance. Effect size of exposure to pollutants showed no dependence on phylogenetic history or relatedness ($\lambda = 6.71*10^{-5}$, $p = 1$).

Results of all studies for which effect size could be calculated ($n = 141$) are summarised in Fig. 3. Effect sizes were found to have the greatest variation in studies with intermediate sample sizes, indicating possible publication bias against smaller studies, or studies that did not observe significant results.

3.2. *Chemical pollutants*

The most commonly studied form of chemical pollutant was organic chemical pollutants ($n = 92$), studies of which covered 82 substances, compared with 15 substances in studies of inorganic chemical pollutants ($n = 24$). The least well-studied was the effects of mixtures of chemical pollutants ($n = 16$) (Supplementary Table 1; Fig. 3). Of studies of mixtures, 31% ($n = 5$) studied mixtures of organic and inorganic pollutants.

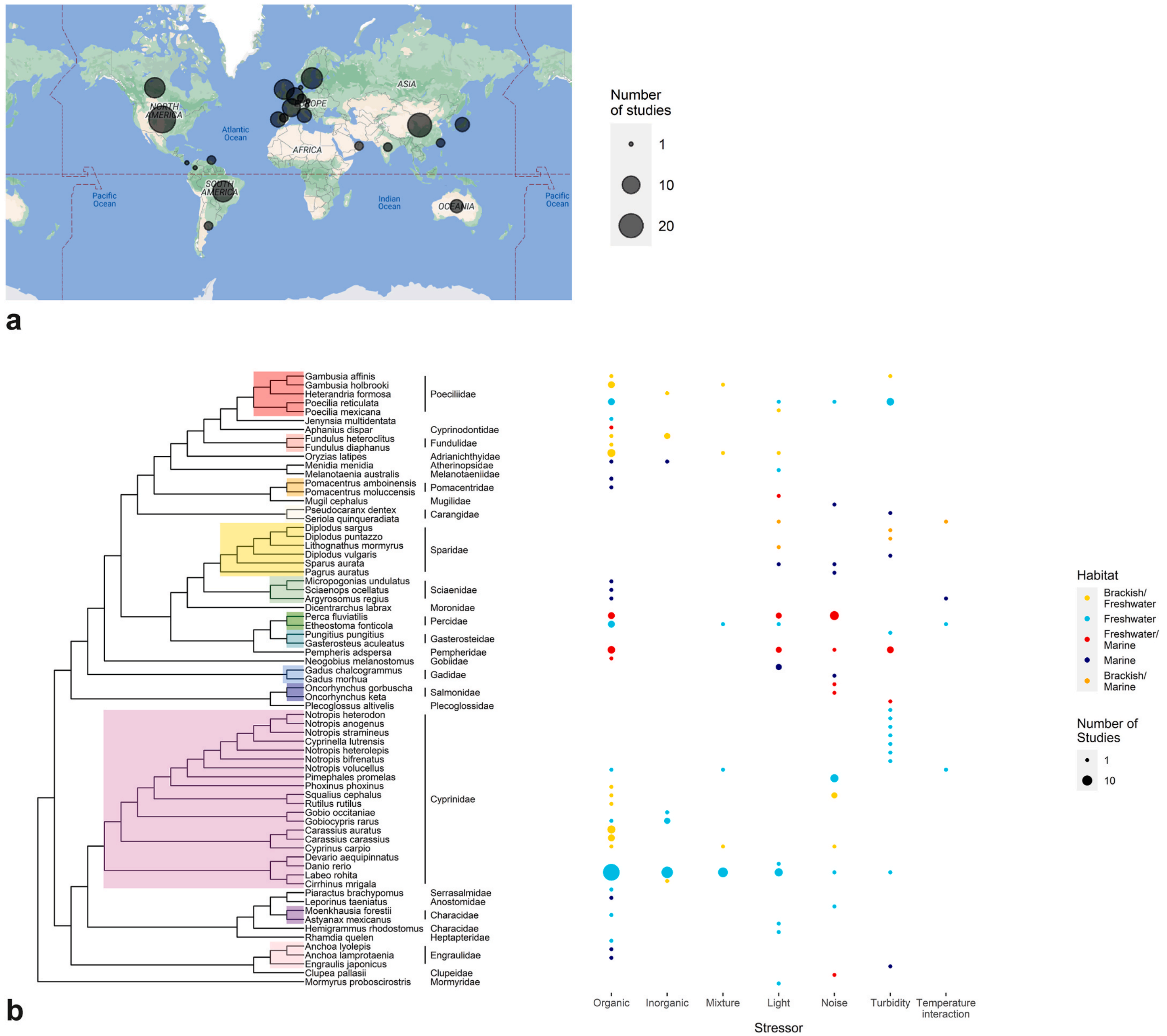

Fig. 2. a) Map showing locations of studies on the effects of pollution on sociability and/or group cohesion in fish species. Larger circles indicate more studies. b) Phylogenetic tree showing species used in studies of the effects of pollutants on fish behaviour. Family to which each species belongs is shown to the right of the tree. Colours within the tree correspond to families. The dot plot corresponds to the number of studies each species was used in, and which stressors each species was studied in relation to. Colours represent species habitat, while point size represents number of studies. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

A further 44% ($n = 7$) studied mixtures of two or more organic pollutants, while the remaining 25% ($n = 4$) used mixtures of unspecified makeup, mainly wastewater or industrial effluent. Across all studies of chemical pollutants, 39% ($n = 51$) studied group cohesion, while 53% ($n = 70$) investigated sociability, and 8% ($n = 11$) investigated both cohesion and sociability (Table 2).

Metanalysis found no effect of exposure to organic or inorganic pollutants on group cohesion, however both were associated with a significant reduction in sociability (organic PM = −0.483, $p < 0.01$) (Supplementary Table 2; Supplementary Table 3; Fig. 4a; Fig. 4b). In the case of inorganic pollutants, however, this was dependent on pollutant concentration, with greater reductions in sociability at higher concentrations (PM = −1.453, $p < 0.001$) (Fig. 4b). No effect of group size, exposure period, or number of replicates was found for organic or inorganic pollutants, however a greater reduction in social behaviour following exposure to inorganic pollutants was found when fish were subject to developmental compared with acclimated exposure (PM = −1.663, $p < 0.01$) (Fig. 5a).

For mixtures of chemical pollutants, metanalysis revealed reduced group cohesion following exposure (PM = −43.71, $p < 0.01$), and a linear effect of pollutant concentration (PM = −117.6, $p < 0.01$), with greater concentrations of pollutant mixtures producing greater reductions in cohesion (Fig. 4c). An overall increase in sociability following exposure was also found (PM = 44.27, $p < 0.01$), with greater increases in sociability at higher concentrations (PM = 118.6, $p < 0.01$) (Supplementary Table 4; Fig. 4d). Lower cohesion and sociability were also found in fishes subject to acute (PM = −0.668, $p < 0.01$) or uncontrolled exposures (PM = −2.557, $p < 0.01$), compared with acclimated exposures (Fig. 5b). The reduction in cohesion following exposure was found to be magnified in larger groups (PM = −0.242, $p < 0.01$)

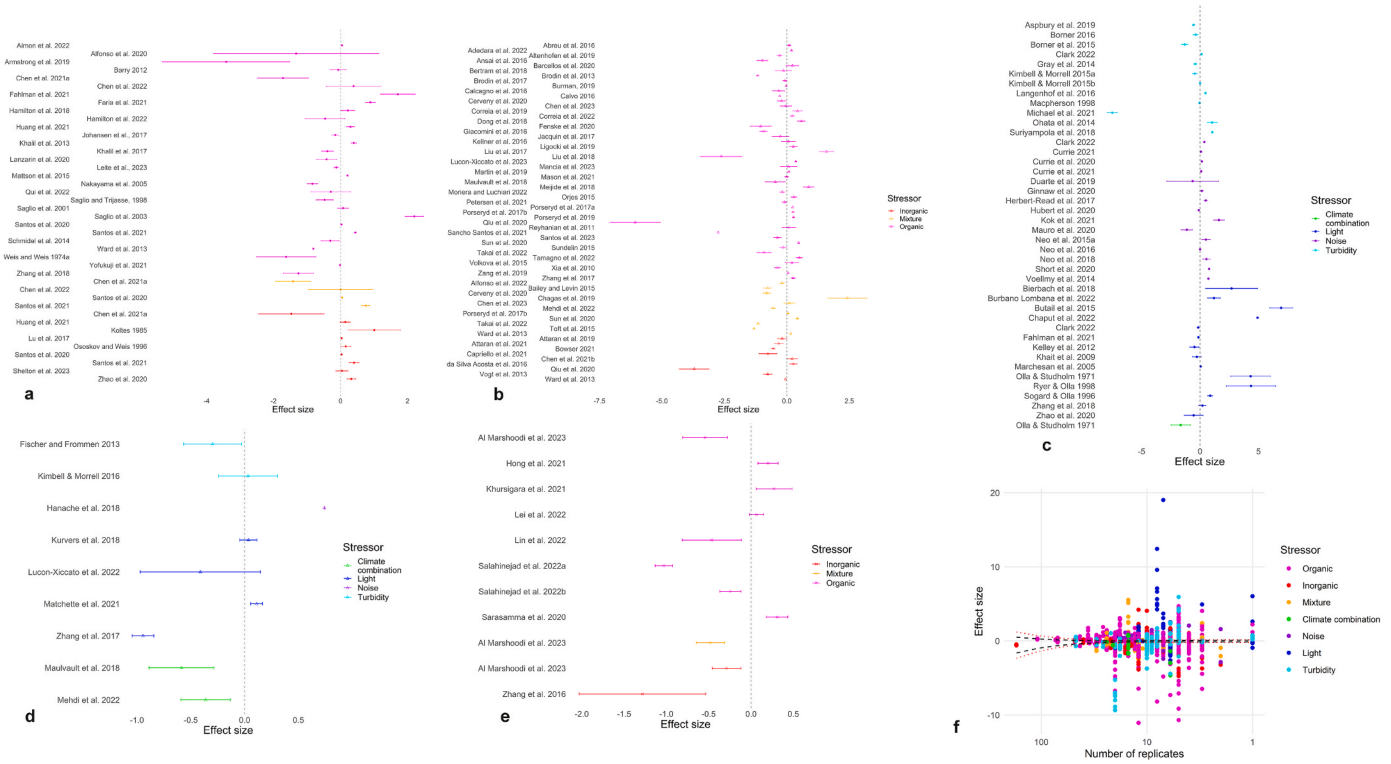

Fig. 3. Forest plots showing mean and standard error of effect sizes calculated for each study included in metanalysis. a) studies of effects of chemical pollutants on group cohesion; b) studies of effects of chemical pollutants on sociability; c) studies of effects of non-chemical pollutants on group cohesion; d) studies of effects of non-chemical pollutants on sociability; e) studies of effects of chemical pollutants on both cohesion and sociability. Circles indicate studies of group cohesion, triangles indicate studies of sociability, and crosses indicate studies of both cohesion and sociability. f) funnel plot showing effect sizes for all data points included in metanalysis. Black dashed lines indicate 95% confidence interval; red dashed lines indicate 99% confidence interval. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

(Supplementary Fig. 1).

3.3. Non-chemical pollutants

Among non-chemical pollutants, noise ($n = 22$) and light ($n = 21$) received similar amounts of research attention, with turbidity being less well-studied ($n = 15$). A significant bias towards studies of cohesion was found, with 88% ($n = 51$) of studies investigating cohesion, while only 12% ($n = 7$) of studies targeted sociability (Supplementary Table 1; Table 2; Fig. 3).

No effect of noise level (volume in dB) was found on cohesion or sociability; however, cohesion and sociability were reduced with longer exposure (PM $= -4.043$, $p < 0.01$) (Supplementary Table 5; Fig. 5c). In addition, cohesion was significantly greater following uncontrolled exposure compared with acute exposures (PM $= 406.0$, $p < 0.01$). Metanalysis for this variable was limited by a relatively high proportion of cohesion studies for which effect size data could not be calculated (7/21). Of the studies for which effect size could not be calculated, all but one (Rojas et al., 2023) found increased cohesion following noise exposure.

Neither light nor turbidity had significant effects on cohesion, nor was there any effect of exposure period, number of replicates, or group size (Supplementary Table 6, Supplementary Table 7). Individual sociability, however, was reduced in fish exposed to increased light levels (PM $= -3.038$, $p < 0.01$) (Supplementary Table 6; Fig. 4e).

4. Discussion

While studies of the effects of anthropogenic pollutants on aquatic organisms are numerous, recent work has emphasised the need to quantify ecologically relevant endpoints such as effects on group cohesion, and the associated impact on collective outcomes for gregarious species (Bertram et al., 2022a; Michelangeli et al., 2022). We aimed to review knowledge on an ecologically relevant aspect of fish ecology, namely social behaviour, and its interactions with anthropogenic pollution. Despite the range of mechanisms governing the effects of pollutants on fish species, the majority of pollutant classes were found to have some, often non-linear, effect on fish social behaviour. Differences between the effects of chemical pollutants on sociability and group cohesion were identified for both organic and inorganic substances. This indicates that individual social behavioural responses to chemical pollutants may not directly translate to changes in group dynamics, or *vice versa*. In addition, several pollutant classes varied in their effects according to exposure duration, with acute exposure sometimes being more likely than chronic exposure to reduce cohesion or sociability. However, the effects of chronic toxicity (i.e., exposure exceeding 10% of the organism's life span (Suter, 2016)) on physiology and survival are poorly understood. Also understudied are the effects of exposure to chemical pollutant mixtures (Orr et al., 2024). We observed some geographical bias in the studies found, including a complete lack of studies based in Africa. This may indicate a lack of interest or funding toward behavioural studies in some locations, although limiting our searches to English language studies may also have contributed to this bias. Still, any geographical bias may correspond to a bias in species studied or pollutants investigated, and understudied areas such as Africa and South America would benefit from research attention.

While our goal was to synthesize the effects of anthropogenic pollutants on social behaviour in fishes, the broad approach we have taken has its drawbacks. It is exceedingly difficult, when conducting a broad analysis of a large number of studies investigating different substances, to attribute results to a specific mode of action or physiological/behavioural effect. It is likely, therefore, that some apparent

Table 2
Summary of results of studies included in this review, based on effect size calculations, according to stressor(s) studied, and metric used.

Pollutant class	Metric	Results	Number of studies
Organic chemical	Group cohesion	Increased cohesion	10
		Reduced cohesion	16
		No effect	8
	Sociability	Increased sociability	18
		Reduced sociability	19
		No effect	13
	Cohesion and sociability	Increased social behaviour	3
		Reduced social behaviour	4
		No effect	1
Inorganic chemical	Group cohesion	Increased cohesion	7
		Reduced cohesion	3
		No effect	3
	Sociability	Increased sociability	1
		Reduced sociability	6
		No effect	2
	Cohesion and sociability	Increased social behaviour	0
		Reduced social behaviour	2
		No effect	0
Mixed chemical	Group cohesion	Increased cohesion	2
		Reduced cohesion	1
		No effect	1
	Sociability	Increased sociability	4
		Reduced sociability	6
		No effect	1
	Cohesion and sociability	Increased social behaviour	0
		Reduced social behaviour	1
		No effect	0
Noise	Group cohesion	Increased cohesion	15
		Reduced cohesion	3
		No effect	3
	Sociability	Increased sociability	1
		Reduced sociability	0
		No effect	0
Light	Group cohesion	Increased cohesion	9
		Reduced cohesion	4
		No effect	4
	Sociability	Increased sociability	1
		Reduced sociability	1
		No effect	2
Turbidity	Group cohesion	Increased cohesion	4
		Reduced cohesion	7
		No effect	2
	Sociability	Increased sociability	0
		Reduced sociability	1
		No effect	1

contradictions present in our results, such as effects on individual sociability but not on group cohesion, may be due to differences in the modes of action of substances used in different studies. Additionally, some compounds that have been grouped in our analysis may have conflicting effects on social behaviour resulting in nonsignificant overall trends. Nevertheless, the broad perspective that we take is valuable in identifying trends and areas of research to focus on in the future. Here we discuss potential explanations for our results in the context of the literature, and indicate directions for future research that may help to elucidate the behavioural and broader ecological impacts of anthropogenic pollutants in the aquatic environment.

4.1. Chemical pollutants

Our analysis found strong evidence of reduced individual sociability following exposure to organic and inorganic chemical pollutants in fishes, though this was dependent on concentration in the case of inorganic pollutants. Various chemical pollutants can influence social behaviour and other physiological activities in organisms through complex mechanistic processes and pathways. The behavioural responses to these chemical pollutants are contingent on factors such as exposure duration, chemical heterogeneity (including chemical pollutant class and exposure type—whether exposed to a compound in isolation or in mixtures), and pollutant concentration, which may result in antagonistic, synergistic, or additive interactions within an organism. Since behaviour is the final product of intricate developmental and physiological processes, isolating a specific behavioral response to a specific contaminant can be challenging under varying exposure conditions (Wong and Candolin, 2015).

Metals, for instance, can act as neurotoxicants, respiratory toxicants, or osmoregulatory toxicants (Wood et al., 2012) all of which may influence sociability (Pereira et al., 2016). Exposure to inorganic mercury led to bioaccumulation within the brain in white sea bream *Diplodus sargus*, resulting in impaired motor function and heightened anxiety (Pereira et al., 2016). Other metals such as copper (Cu) can accumulate in the olfactory epithelium, and were found to cause damage to olfactory receptor neurons responsible for detecting odours in fathead minnows *Pimephales promelas* and yellow perch *Perca flavescens* (Dew et al., 2014).

Organic compounds have varied modes of action that may directly or indirectly alter social behaviour. For example, 17 β trenbolone can disrupt female mate choice in wild guppies *Poecilia reticulata*, potentially influencing social interactions (Tomkins et al., 2018). A reduction in activity levels may result from exposure to the antidepressant fluoxetine, due to its inhibitory effect on the dopaminergic system (Duarte et al., 2019), potentially leading to changes in shoal dynamics (Killen et al., 2017). Pesticides, particularly organophosphates, have been shown to decrease swimming speed in California killifish *Fundulus parvipinnis* by reducing the activity of the neurotransmitter acetylcholinesterase (Renick et al., 2016). Changes to swimming speed may lead to disruption of group cohesion or fragmentation of shoals (Killen et al., 2017). Overall, the mechanistic understanding of behaviours caused by chemical pollutants, especially sociability, remains complex and expansive (Pyle and Ford, 2017).

While we found evidence for reduced sociability (Fig. 4a; Fig. 4b), we found no effect of organic or inorganic pollutants on group cohesion. This may indicate masking of behavioural effects while fish are in groups. For social species, being in a group may reduce stress and facilitate normal behaviour (Culbert et al., 2019; Nadler et al., 2016), meaning that changes in individual sociability may not translate to changes in group dynamics. While behavioural conformity may also contribute to this effect, differences in individual roles within groups may affect individual responses to stressors (Michelangeli et al., 2022). It is therefore possible that individual responses may vary in a group setting, leading to a lack of unidirectional effects. However, differences in the modes of action of different chemical pollutant compounds may have antagonistic effects on behaviour and thus make detecting effects in the model more difficult. Mode of action was not included as a factor in our metanalysis due to a relatively low number of studies on sociability and/or cohesion carried out for the majority of substances. A greater number of replicate studies, or at least studies of the same substance on different species, are therefore needed to be able to analyse the role of modes of action.

While studies of individual compounds found no effect on cohesion, a reduction in group cohesion was observed following exposure to chemical pollutant mixtures (Fig. 4c), though these mixtures also appeared to produce an increase in sociability (Fig. 4d). This may indicate masking of, or variance in, the individual response in groups (Bertram et al., 2022a; Michelangeli et al., 2022). Relatively few ($n = 5$) studies of mixtures on cohesion were found, the majority of which ($n = 4$) investigated similar chemical combinations, namely microplastics in combination with metals ($n = 3$) or with an organophosphorus pesticide (glyphosate; $n = 1$). It is possible, therefore, that the reduction in cohesion was a result of the specific combination of substances tested

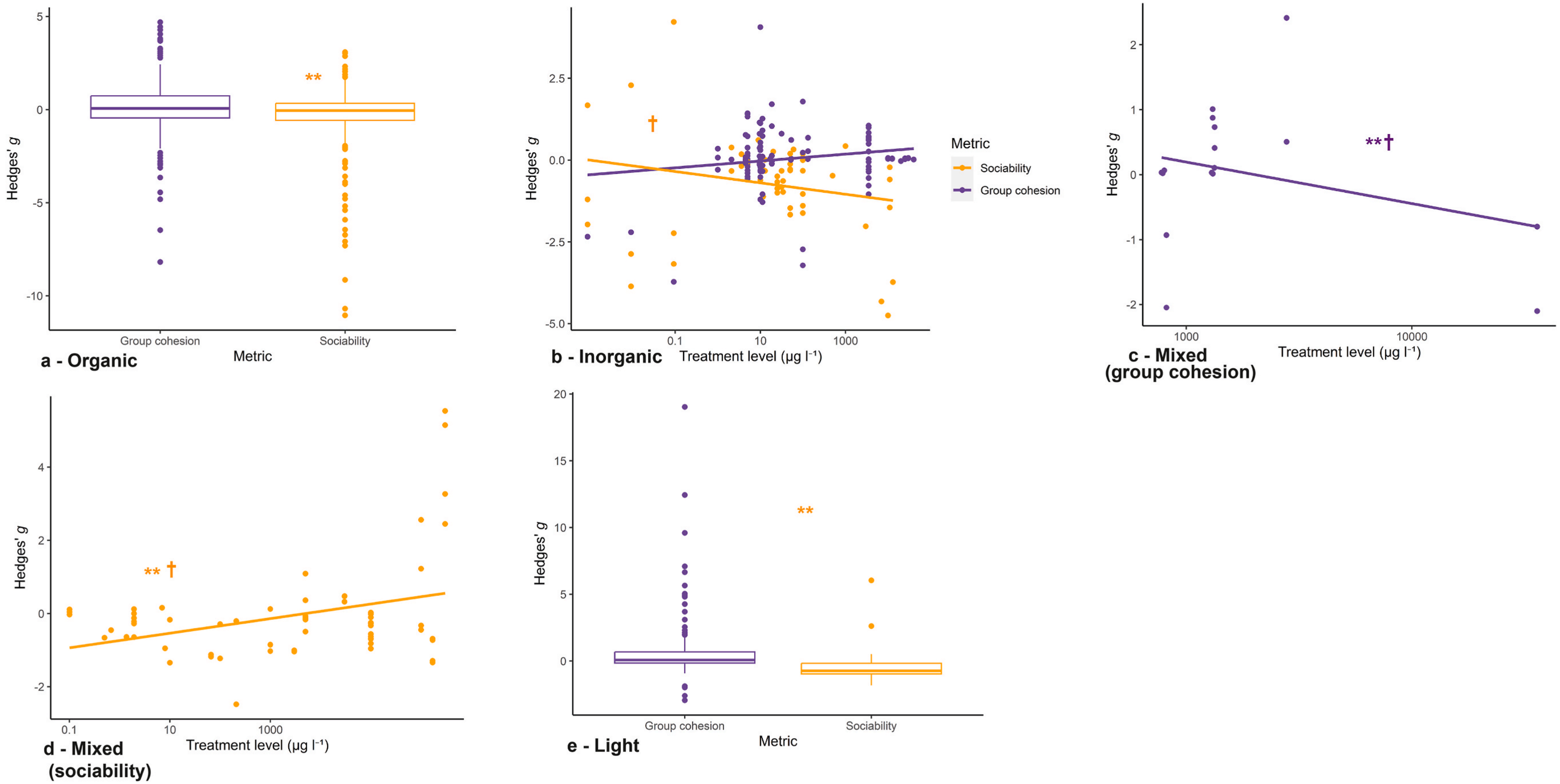

Fig. 4. Effect on sociability and group cohesion in fish species according to level of a. organic chemical pollutants, b. inorganic chemical pollutants, c. mixed chemical pollutants (group cohesion), d. mixed chemical pollutants (sociability) and e. light. Group cohesion and sociability are plotted separately in the case of mixed chemical pollutants due to the need to use a logarithmic scale for the sociability plot (y axis). Orange stars indicate a significant effect of exposure on sociability. Purple stars indicate a significant effect of exposure on group cohesion. † indicates a significant effect of treatment level on sociability or cohesion. * indicates $p < 0.05$, ** indicates $p < 0.01$, and *** indicates $p < 0.001$. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article).

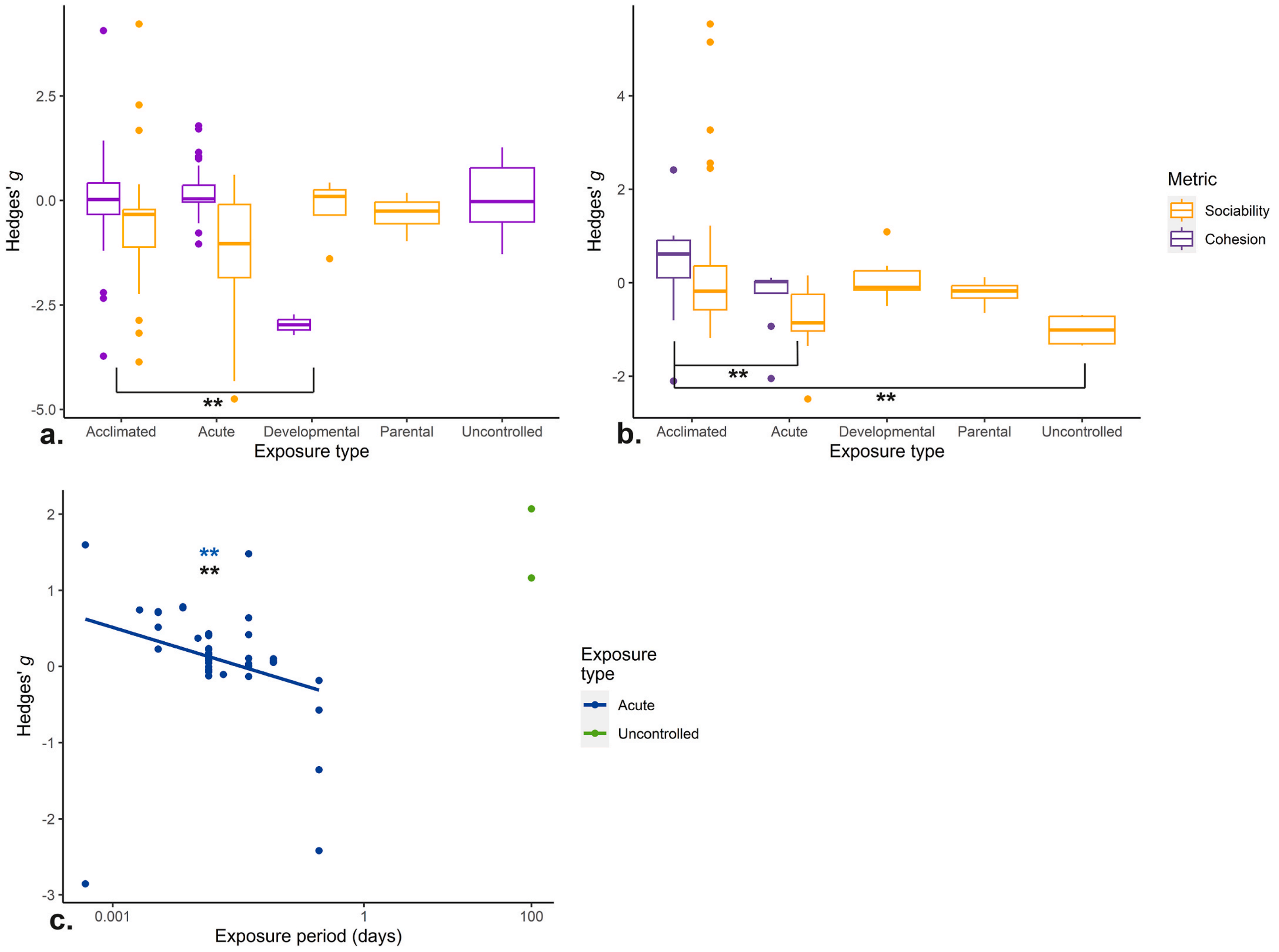

Fig. 5. Effect of a) inorganic chemical pollutant exposure, b) mixed chemical pollutant exposure and c) noise on fish group cohesion and sociability according to exposure type and period. Acclimated = >7d exposure; acute = <7d exposure; developmental = exposure during egg or larval stage; parental = parents of focal fish exposed; uncontrolled = exposure outside the lab without manually altered exposure levels e.g. wild or farmed fish. Black stars indicate a significant effect of exposure type; blue stars indicate a significant effect of exposure period. * indicates $p < 0.05$. ** indicates $p < 0.01$, and *** indicates $p < 0.001$.

rather than consistent changes in social response. This may also explain the greater reduction in cohesion following exposure when fish were tested in larger groups (Supplementary Fig. 1). Many organics or metals may have additive, synergistic or antagonistic additive effects when organisms are exposed to these in combination. For example, mixtures of chemical pollutants with similar mechanisms of action, such as lead and cadmium, may cause pollutants to compete with each other and reduce toxicity, masking any behavioural effects of the specific chemical combination.

We found no effect of organic pollutant concentration on sociability or cohesion. Given the diversity of substances that we considered as organic pollutants, this may be due to the significant variation in the threshold levels of individual chemical pollutants and duration of exposure required to illicit a response. While we transformed treatment values to z scores to minimise this effect, this may not fully compensate for very different scaling in the concentrations of some chemical pollutants. For example, in the case of some agricultural and industrial effluents, concentrations of up to 1000 mg l^{-1} (Toft et al., 2003; Yofukuji et al., 2021) were used, while some studies of medical compounds such as antidepressants used concentrations of 0.001 μg l^{-1} or less (Barcellos et al., 2020). In addition, modes of action, duration, specific water parameters, and therefore concentration required to produce a behavioural response likely differ among compounds (Escher et al., 2011), though insufficient studies and levels of replication for the majority of substances studied did not allow for metanalysis of substances individually. For organic compounds that can be metabolised, toxicity level and thus behavioural response will also depend on the toxicity and mode of action of metabolites (Escher et al., 2011). For example, primary metabolites of the plastic compound Bisphenol A induced higher incidence of lethality than the parent compound alone during embryonic development in Japanese medaka *Oryzias latipes* (Ishibashi et al., 2005).

In contrast, the relationship between sociability and exposure to inorganic pollutants was scaled with pollutant concentration (Fig. 4b), indicating that fish may be more affected by greater concentrations of inorganic pollutants. As the majority of inorganic compounds examined in the literature consist of metals and metal salts, it is likely that these have a similar mode of action in affecting fish. Metal ions compete with calcium ions (Ca^{2+}) for binding sites in tissues (Alsop and Wood, 2011; Birceanu et al., 2008; Rogers and Wood, 2004), as the majority of transition metals naturally form double-charged cations when in solution, and thus behave similarly to calcium ions (Birceanu et al., 2008; Rogers and Wood, 2004). Diffusive ion loss of sodium and potassium ions caused by endocrine stress may also play a role in the toxic effect of several metals on fish species (Alsop and Wood, 2011). Given the similar mode of action, a given concentration of metal ions may be more likely to have a similar effect on fish, meaning effects are more likely to scale with concentration, and this scaling effect was more likely to be detected by our model.

No effect of exposure period on sociability or group cohesion was found for either organic or inorganic chemical pollutants, indicating that fish may struggle to acclimate to exposure over time. Theoretically, if fish could adjust disrupted ion regulation, or gradually reduce cortisol levels over the course of acclimation to chemical pollution, this could result in a return to baseline behaviour. Effective regulation of calcium ion concentration and action is essential for the function of various systems including the action of ATPase (Rogers and Wood, 2004), and adjustments to ion balance may not fully compensate for the action of high concentrations of metal ions disrupting these pathways. Acclimation was observed in some studies (Capriello et al., 2021; Vogt et al., 2013), however it is likely that the exposure period required to elicit a response also varies among substances and modes of action. Inorganic pollutants had a greater effect following developmental exposure as compared to acute exposure (Fig. 5a), suggesting greater vulnerability at the embryonic or larval stages. However, as only two studies of developmental exposure have been carried out (Chen et al., 2021a,b), further research is needed in this area. Acute exposure to chemical pollutant mixtures appeared to produce a greater reduction in cohesion and sociability compared with acclimated exposure. This may indicate that fish are capable of acclimating to multiple pollutants, though in the case of sociability the overall positive relationship could indicate a greater effect following prolonged exposure. Multiple pollutants may, in some cases, produce opposing effects, leading to a reduction in detectable changes to behaviour and thus making apparent acclimation more likely due to the presence of the other compound. Alternatively, pollutants can bioaccumulate, leading to greater effects over time. Which of these may occur is likely dependent on the specific combination of pollutants. Pollutant mixtures remain understudied, and further investigation of specific combinations would be required to draw conclusions on the ability of fish species to acclimate, including interspecific and ontogenetic variation in acclimation ability.

While chemical pollutant mixtures are certainly relevant to investigate given the exposure to multiple pollutants in many waterways (Dutzik et al., 2009), the pollutant types, dosage, and other factors such as water parameters may all have impacts on how species respond (Morgan et al., 2001; Orr et al., 2024). The number of studies investigating mixtures of multiple chemical pollutants are limited ($n = 16$), and further research would be required to establish patterns. In particular, more studies of wild populations are required, as while metanalysis revealed a greater reduction in social behaviour in wild populations exposed to chemical pollutant mixtures, only one study investigated this in wild-exposed (uncontrolled) populations, meaning more evidence is required to draw conclusions (Fig. 5b). We also agree with the recent findings of Orr et al. (2024): studies of pollutant mixtures, and indeed studies of effects of pollutants in general, should be informed by a theoretical understanding of the modes of action of the substances involved, and should take into account the strong possibility of non-linear effects when modelling results.

4.2. Non-chemical pollutants

No effects of turbidity were found by our metanalysis on social behaviour, while effects of light and noise differed somewhat from what was expected. As shoaling and schooling behaviour have a strong visual component, light exposure may be predicted to increase cohesion and sociability. In addition, exposure to excess or artificial light may lead to stress responses, which may cause social species to move closer together (Marchesan et al., 2005). However, light exposure was found by metanalysis to reduce sociability while having no effect on cohesion (Fig. 4e). It is possible that fish respond to excess light by increasing activity in an attempt to escape stressful conditions, leading to increased movement, which may take individuals away from a shoal. The relatively high sociability observed in dark conditions may depend on fish being able to sense groupmates and engage in social behaviour under dark conditions despite a reduction in visual cues, possibly through other mechanisms such as lateral line sensing (Chaput et al., 2023). The pollutant cobalt chloride, a calcium channel antagonist that ablates the lateral line, has been found to significantly reduce shoaling in *D. rerio* both light and dark conditions, though this effect was greater in dark conditions (Chaput et al., 2023). This indicates a significant role of the lateral line in detecting the surroundings in fishes.

Metanalysis revealed no effect of exposure or of noise or light level on group cohesion, and no effect of noise on individual sociability. Noises may illicit a startle response in fishes, leading to greater cohesion as fish move together due to increased anxiety (Neo et al., 2016; Pickering and Pottinger, 1989). The effects of light and noise on cohesion may be non-linear, however this does not entirely explain the lack of statistical significance found by metanalysis. There is evidence that fish are able to habituate to sound over even relatively short exposure periods, with several studies reporting an increase in group cohesion at the start of trials followed by a return to pre-exposure levels or a decrease in group cohesion relative to pre-exposure levels as trials progressed (Currie, 2021; Currie et al., 2020, 2021; Mauro et al., 2020; Neo, 2016; Neo et al., 2015a, b), an effect that was also found by our metanalysis (Fig. 5b). Acclimation may also play a role in the response to light exposure. In rummy-nose tetra *Hemigrammus rhodostomus*, reduced cohesion was observed under dark conditions (Lafoux et al., 2023). As light level increased, fish initially formed highly cohesive and polarized groups, after which cohesion decreased again to a steady level, higher than under dark conditions (Lafoux et al., 2023).

In the case of both noise and light exposure, aspects of the stressor besides intensity alone may affect cohesion and sociability. In the case of noise, factors such as frequency, noise source, or pulse regularity affected whether or not fish responded (Neo et al., 2015b). This may relate to how fish respond to sound types associated with other stimuli in natural environments, such as predator calls (Ladich, 2019). Species identity may also be important, as the volume, rate, and frequency of noises that fish use to communicate or sense danger are likely to vary with environment and ecological niche (Ladich and Fine, 2006). Ecological variation may also apply to light exposure. While no effect of wavelength or brightness of light was found, variation in response to the wavelength and brightness of light to which fish were exposed was found among fish species. One study looking at the effect of illumination on cohesion across multiple species revealed significant interspecific differences and also an effect of increasing versus decreasing light level and wavelength (Marchesan et al., 2005). For example, *D. labrax* shoals became more cohesive in lower light conditions when light was gradually reduced, however no effect of a gradual increase was found (Marchesan et al., 2005). The opposite pattern was found in *M. cephalus* and in *S. aurata*, which tended to increase cohesion as light level was increased but did not respond to a gradual reduction (Marchesan et al., 2005). As ecological factors such as preferred depth, habitat, and nocturnal or diurnal activity pattern are likely to impact how fishes respond to different light levels, further comparisons among species would contribute significantly to our understanding of behavioural responses.

While research to date indicates some effects of non-chemical pollutants on social behaviour in fishes, various aspects of the effects of non-chemical pollutants remain under-researched. The effects of non-chemical pollutants on sociability are significantly understudied, with only seven studies included in our analysis, and although a significant effect of light on sociability was found, effects reported across studies were inconsistent for all stressors examined (Table 2). Further studies of sociability are strongly needed to determine whether changes to individual behaviour may drive changes in cohesion observed in some studies, or whether the social environment may affect the response of individuals (Michelangeli et al., 2022). In the case of noise, further studies of uncontrolled exposure i.e., exposure of wild or farmed populations are also needed. While metanalysis found a greater increase in cohesion following uncontrolled compared with acute exposure (Fig. 5c), the low number of studies ($n = 1$; Kok et al., 2021) of uncontrolled exposure limits the conclusions that can be drawn from this. The inability to calculate effect size for several papers also reduced our ability to draw strong conclusions, highlighting the need for studies to report measured levels of response to stressors, as well as model results. Finally, further studies are required to determine whether the effects of light found in this review can be extrapolated to a lasting disruptive effect of light pollution. Exposure to artificial light at night (ALAN) has been found to disrupt circadian rhythms (Bruening et al., 2015), which may affect activity or metabolism and thus disrupt social behaviour long after exposure to ALAN. However, only one study explicitly investigated the effects of ALAN (Kurvers et al., 2018). This study found no effect on social behaviour, but found increased risk-taking behaviour in *P. reticulata* previously exposed to ALAN (Kurvers et al., 2018). Changes to other behaviours are possible, therefore, and further study of ALAN as opposed to photoperiod or testing conditions alone is strongly needed in order to determine how other species may respond to increasing urbanisation resulting in light pollution.

5. Conclusions

Anthropogenic pollutants have wide-ranging and varied effects on cohesion and sociability in fishes, with evidence for effects on sociability and/or cohesion resulting from exposure to organic, inorganic, and mixtures of chemical pollutants, as well as increased light levels. In some cases, evidence of acclimation was found. Mixtures of chemical pollutants and noise exposure both showed evidence of habituation following extended exposure (Neo et al., 2018; Stubblefield et al., 1999). Concentration- or level-dependent effects were also evident in stressors such as inorganic and mixtures of chemical pollution (Barcellos et al., 2020; Kimbell and Morrell, 2015). Variation in the response to cohesion versus sociability was also found in the case of some chemical pollutants, with exposure to organic and inorganic pollutants resulting in reduced sociability but no effect on cohesion. Interactions with other behavioural responses may account for this, however further investigation of the relationship between individual and group responses to stressors would be beneficial. Further study of different chemical pollutant classes is also needed to better explain the role of different modes of action in behavioural responses.

While studies have focused on a wide variety of chemical pollutants, there are notable gaps in the literature regarding the interactions of multiple stressors. In the limited work done, however, there is evidence of exacerbation or interaction among the effects of various stressors when fish are exposed concurrently (Fahlman et al., 2021; Maulvault et al., 2018; Neo et al., 2018; Santos et al., 2020). Further study of multiple stressor interactions, as well as more wild studies, are critical (Dutzik et al., 2009). Also lacking in the literature are studies of the effects of pulsed chemical contaminant exposure, such as may be experienced from periodic wastewater outflows (Marr et al., 1995), on social behaviour. Anthropogenic stressors have been shown to have important effects on group cohesion in gregarious fish species. Behaviour is a key aspect of responses to environmental changes, and knowledge of how increasingly contaminated aquatic systems will be affected in terms of animal behaviour, and how this may translate to changes in ecology, are essential as these changes become increasingly common and severe.

CRediT authorship contribution statement

Izzy C. Tiddy: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Daphne Cortese:** Writing – review & editing, Project administration, Data curation. **Amelia Munson:** Writing – review & editing, Project administration, Data curation. **Tamzin A. Blewett:** Writing – review & editing, Writing – original draft, Methodology, Data curation. **Shaun S. Killen:** Writing – review & editing, Supervision, Software, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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